Journal of Experimental Psychology:
Animal Behavior Processes
2010, Vol. 36, No. 4, 409–422

0097-7403/10/$12.00 DOI: 10.1037/a0019296

Great Apes Select Tools on the Basis of Their Rigidity

Héctor Marín Manrique, Alexandra Nam-Mi Gross, and Josep Call
Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

Wild chimpanzees select tools according to their rigidity. However, little is known about whether choices are solely based on familiarity with the materials or knowledge about tool properties. Furthermore, it is unclear whether tool manipulation is required prior to selection or whether observation alone can suffice. We investigated whether chimpanzees (*Pan troglodytes*) ($n = 9$), bonobos (*Pan paniscus*) ($n = 4$), orangutans (*Pongo pygmaeus*) ($n = 6$), and gorillas (*Gorilla gorilla*) ($n = 2$) selected new tools on the basis of their rigidity. Subjects faced an out-of-reach reward and a choice of three tools differing in color, diameter, material, and rigidity. We used 10 different 3-tool sets (1 rigid, 2 flexible). Subjects were unfamiliar with the tools and needed to select and use the rigid tool to retrieve the reward. Experiment 1 showed that subjects chose the rigid tool from the first trial with a 90% success rate. Experiments 2a and 2b addressed the role of manipulation and observation in tool selection. Subjects performed equally well in conditions in which they could manipulate the tools themselves or saw the experimenter manipulate the tools but decreased their performance if they could only visually inspect the tools. Experiment 3 showed that subjects could select flexible tools (as opposed to rigid ones) to meet new task demands. We conclude that great apes spontaneously selected unfamiliar rigid or flexible tools even after gathering minimal observational information.

Keywords: tool use, object properties, problem solving, primates

Tool-using tasks have traditionally been used to investigate the knowledge that primates, and more recently corvids, possess about objects and their spatial, causal, and featural interrelations (Antinucci, 1989; Seed, Call, Emery, & Clayton, 2009; Seed, Tebbich, Emery, & Clayton, 2006; Tomasello & Call, 1997). It is still currently debated whether tool use is based on practical knowledge (i.e., subjects learn to use tools by trial and error with little understanding about the features that make a tool effective) or whether it is also supported by some form of conceptual knowledge about the relation between tool features and task demands (Limongelli, Boysen, & Visalberghi, 1995; Mulcahy & Call, 2006; Povinelli, 2000; Seed et al., 2006; Tebbich & Bshary, 2004; Visalberghi & Limongelli, 1994). Some authors have suggested that even if apes possess some form of conceptual knowledge about tool use, it is limited to perceptually salient features (Povinelli, 2000). Likewise, Köhler's (1925) classical work stressed the importance that perceptual factors (mostly visual information) play in chimpanzee problem solving.

Although the importance of perceptual factors in tool use is undeniable, it is also true that most tool-using tasks have primarily relied on visual information, perhaps at the expense of other types of information such as tactile or propioceptive information (but see Seed et al., 2009; Tebbich, Seed, Emery, & Clayton, 2007). Thus, numerous studies have investigated several tool properties including length (Chappell & Kacelnik, 2002; Hihara, Obayashi, Tanaka, & Iriki, 2003; Mulcahy, Call, & Dunbar, 2005), diameter (Chappell & Kacelnik, 2004), shape (Hauser, Pearson, & Seelig, 2002; Povinelli, 2000; Santos, Miller, & Hauser, 2003; Weir, Chappell, & Kacelnik, 2002), color (Santos, Pearson, Spaepen, Tsao, & Hauser, 2006), continuity, and support (Hauser, Kralik, & Botto-Mahan, 1999; Herrmann, Wobber, & Call, 2008; Spinozzi & Potí, 1989). Much less is known about nonvisual properties such as tool rigidity (Kacelnik, Chappell, Weir, & Kenward, 2006; Povinelli, 2000; Santos et al., 2006). Wild chimpanzees appear to be able to judge rigidity as they are able to select tools on the basis of this property depending on the resources that they want to exploit. Chimpanzees select pliable materials such as herbs for insertion in termite mounds with irregularly shaped galleries (Goodall, 1986). In some cases, chimpanzees use a tool set comprising a rigid stick to drill an access hole to the termite underground tunnels and a flexible fishing probe that serves to catch the termite soldiers (Fay & Carroll, 1994; Sanz, Morgan, & Gulick, 2004; Sugiyama, Koman, & Sow, 1988). In other cases, a tool set is used to puncture beehives and get access to honey, a process that involves up to four different tools in a specific order and that ends with the use of a slender flexible probe to collect the honey (Brewer & McGrew, 1990).

Although selecting rigid or pliable tools depending on the task's demands suggests that wild chimpanzees are selecting tools on the basis of their rigidity, other alternative explanations are still viable. For instance, it is unclear whether individuals rely on the familiarity of the materials rather than on a concept of rigidity that is independent of the visual properties of the stimuli. We do not know whether chimpanzees presented with unfamiliar objects would immediately select those that are rigid enough. Moreover,

This article was published Online First August 16, 2010.

Héctor Marín Manrique, Alexandra Nam-Mi Gross, and Josep Call, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany.

We thank Elisabetta Visalberghi for suggesting that we use the table condition. Héctor Marín Manrique was supported by a postdoctoral contract funded by the Spanish Programa de Ayuda a la Movilidad del Ministerio de Ciencia e Innovacion (Micinn).

Correspondence concerning this article should be addressed to Héctor Marín Manrique, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany. E-mail: hector_manrique@eva.mpg.de

we are missing information about how wild chimpanzees acquire the knowledge that they possess. Is it based on trial and error and perceptual identification, or do individuals possess some conception of what makes a tool suitable? In a similar vein, it is unclear what kinds of information individuals require to judge whether a particular tool is suitable. More specifically, is it enough to simply observe that a tool is flexible (or rigid), or do subjects need to manipulate objects to acquire and use this information effectively? In order to answer these questions, a more experimental approach that complements observational data is required.

Povinelli (2000) investigated whether chimpanzees possess a conceptual understanding of the relation between the rigidity of a tool and its ability to move an object. Seven adolescent chimpanzees were confronted with two rakes presented side by side on a table in front of the subject. However, the head of one rake was made of rigid wood, and the head of the other rake was made of flimsy rubber. The rake with the rigid head could easily drag an apple, whereas the one with the flimsy head could not. During orientation trials, subjects were presented with a single rake with the rigid head and allowed to use it to retrieve the reward a number of times. Then prior to the test in which they had to choose between the two rakes, the experimenter demonstrated the properties of each rake by repeatedly tapping on the head of the rigid rake and successively lifting up and dropping down the head of the flimsy rake. After the demonstration both rakes were placed on the table, and a piece of apple was set directly in front of each of them. Subjects could select which rake they wanted to pull toward them. Interspersed with these test trials, chimpanzees also received a number of trials in which they were presented with a single rake with a rigid head. All chimpanzees except one (who always chose the rake with the rigid head) chose randomly between both rakes, exhibiting an obvious lack of understanding of the critical feature that accounted for the tool effectiveness (i.e., rigidity). Additionally, a follow-up test suggested that the successful subject had not selected the correct tool on the basis of rigidity but on her avoidance of flimsy materials in general. The results of this study and the remaining experiments included in Povinelli's (2000) book showed that even when chimpanzees seem to use the same relevant perceptual features of the tasks as do humans, they fail to transfer this knowledge to novel conceptually similar problems, which argues against a deep conceptual understanding.

One possible factor that may have contributed to these results is the way the tools were presented for subjects to make a choice. In Povinelli's (2000) study the two rakes were positioned on the platform with the reward already arranged in front of their head, which meant that the only response left to the animals was to pull one of the two rakes. However, Girndt, Meier, and Call (2008) found that this mode of presentation was problematic in the context of another task, the trap–table task (Povinelli, 2000). More specifically, when representatives of the four great ape species were confronted with two tools (each with food in front of it) placed side by side, they failed to select the one without a trap located in front of the food. However, those same subjects successfully avoided the trap when they were provided with a single tool and they had to decide which one of the two rewards they were going to try to get.

Furlong, Boose, and Boysen (2008) proposed a different explanation for Povinelli's (2000) results. They argued that the results may have been a product of the impoverished rearing history of the chimpanzees that he studied. Furlong et al. (2008) used the exact same procedure as did Povinelli (2000) with enculturated and semienculturated chimpanzees. Although both groups of chimpanzees tested by Furlong et al. (2008) solved the original task that Povinelli's chimpanzees had failed, the interpretation of the results is problematic because of the administration of orientation trials prior to (and interspersed with) the test trials. Recall that during orientation trials, subjects were reinforced for using the rigid rake. Therefore, it is conceivable that apes came to prefer the correct rake during the course of the orientation trials regardless of their knowledge of rigidity. This interpretative problem is further aggravated by the fact that the two rakes not only differed in their head's rigidity but also in other visual features such as the head's color, which means that they could have selected the rakes on the basis of other features besides head rigidity.

In a follow-up experiment, Furlong et al. (2008) solved both potential problems by eliminating the orientation trials and minimizing the visual differences between rakes. The latter was accomplished by covering the rake's rigid head with the same material used to construct the flimsy head of the other rake. Results indicated that the chimpanzees' performance deteriorated to some extent in comparison with the previous experiment (5 chimpanzees decreased their performance and 1 improved it), although chimpanzees as a group still selected the correct rake on 69% of the trials, which was above chance levels. However, it is unclear whether they selected the correct tool in the first trial, thereby opening the possibility that subjects learned to select the correct rake during the course of testing rather than through the application of a concept of rigidity to both tests.

Finally, Kacelnik et al. (2006) tested a New Caledonian crow (Betty) with the flimsy rake paradigm. Prior to the test, Kacelnik et al. (2006) exposed the subject for several days to two rakes that differed in the rigidity of their heads. One was made of solid wood, and the other was made of flimsy thin plastic. Upon completing the familiarization phase, the two rakes were placed side by side into a box with a transparent lid, and two food-filled cups were arranged in front of the head of each rake. In order to retrieve the food, Betty had to pull the rake with the solid head—something that she did in the first trial of every session. However, in subsequent choices the bird's preference for the rigid rake decreased in favor of the flimsy one. The authors argued that the reason for this decrease was that Betty simply lost interest in the food after the first trial. However, note that this was not the case in other studies in which the same subject consistently retrieved the reward without seemingly losing interest in the reward (Chappell & Kacelnik, 2002, 2004). Perhaps the appearance of the rakes' heads (or other methodological details) could have contributed to Betty's response pattern, because the flimsy rake appeared less conspicuous than did the rigid one. Thus, although these results are intriguing, additional work is required to reach more solid conclusions on New Caledonian crows' ability to select between flimsy and rigid tools.

Santos et al. (2006) also investigated tool rigidity in vervet monkeys and cotton-top tamarins, two species that typically do not use tools. Santos and colleagues trained subjects to pull one of two rigid hooked canes in order to retrieve a food reward. Although each of the canes had a reward in front of it, only one reward was placed inside the hook. Once their subjects reliably chose the cane with the reward located inside the hook, Santos et al. conducted a second experiment in which new tools were presented. These tools

differed from those in the original training in color or material (flimsy yarn rope instead of hardened clay cane). Subjects of both species chose the functional rigid tools over the flexible nonfunctional ones, irrespective of their color. Unfortunately, first trial choices were not presented, and therefore it is not possible to assess the contribution of associative strategies in performance. Moreover, despite the changes in color, it is conceivable that subjects still simply preferred new tools that were made of the same material as were those that worked in the past. In a sense, one could argue that although subjects disregarded the tool's arbitrary features (e.g., color), the tools were not completely new because the materials were the same as that which they had experienced before. This means that subjects' success could be based on a familiarity strategy rather than an appreciation of the relationship existent between the tool features and the task demands.

The aim of this study was to investigate whether great apes could discriminate between tools on the basis of their rigidity (Experiments 1 and 3) and, if so, whether they could extract information about rigidity by observation (rather than manipulation) alone (Experiments 2a and 2b). In our set-up, subjects had to select either the rigid one of three possible tools and transport it to another location to solve one of two different apparatuses (string and table) or the flexible one out of three alternatives to solve a third apparatus (angled tube). Several key features of our set-up deserve comment. First, we used multiple tool sets formed by tools that were unfamiliar to the subjects when we first introduced them. Tools varied in terms of color, material, weight, and critically, rigidity. We paid particular attention to the first choices made by the subjects. The tools had not been used yet, and therefore their perceptual features could not be associated with the food retrieval. This way we assessed the contribution of associative strategies in performance.

Second, we dissociated the tool presentation from the tool use by presenting the tools in a location different from that where the baited apparatus was located. Thus, subjects had to first select the tool, then transport it to the location with the baited apparatus, and then use it. This situation may not only bypass some problems that Girndt et al. (2008) identified with certain types of tool presentation, but it may also increase the ecological validity of the test because wild apes usually select the tool in a location different from that where they use it. Third, we presented simple straight tools to avoid the possibility that the manipulation requirements of more complex tools such as a rake may mask the knowledge that subjects may possess about tool rigidity. Fourth, we used three different apparatuses (string, table, and angled tube) and multiple tool sets to assess the subjects' flexibility, that is, not only will they always have to choose perceptually different tools but they will also have to use a different set of motor responses in order to succeed. Fifth, we explored the role that visual exploration, not just manipulation, may play in assessing tool rigidity. Finally, the inclusion of representatives of each of the great apes allowed us to assess whether the ability to select tools on the basis of their rigidity is widespread in the great ape clade.

Experiment 1

Methods

Subjects. Five chimpanzees (*Pan troglodytes*), five orangutans (*Pongo pygmaeus*), four bonobos (*Pan paniscus*), and two gorillas (*Gorilla gorilla*) housed at the Wolfgang Kohler Primate Research Center (WKPRC) in the Leipzig Zoo (Leipzig, Germany) participated in this study (see Table 1 for details). There were 5 male apes and 11 female apes ranging in age from 12 to 34 years. Nine subjects were mother-reared and 7 nursery-reared. Subjects were housed in social groups consisting of 6–18 individuals and spent the day in indoor enclosures (175–430 m^2) or outdoor enclosures (1400–4000 m^2), depending on the weather. Both enclosures were spacious and naturally designed, equipped with climbing structures and enrichment devices to foster extractive foraging activity that included the use of tools. The subjects were tested individually in special testing cages (5.1–7.3 m^2) interconnected by lockable doors. The tests were always conducted in accordance with ethical principles for noninvasive research, which also satisfied American Psychological Association (APA) ethical standards. The apes were free to decide whether to carry on with the test or to stop participating at any time. Subjects were provided with fresh fruits, vegetables, eggs, cereals, leaves, and meat distributed in three main meals (7:30 a.m., 1:30 p.m., and 5:00 p.m.). Some more food was dispensed between 7:30 a.m. and 1:30 p.m. (mainly fresh fruit) and at 3:30 p.m., as part of the enrichment program. This daily feeding routine was not modified at all during the period of testing. Food and water were also available ad libitum during testing. Subjects had participated in a variety of cognitive studies in which the use of tools was required (see Table 1).

Apparatus. The three tasks required subjects to use a rigid tool to secure a food reward (either a 4-cm banana piece or a bunch of 4–5 grapes) located outside of the subject's direct reach. There were two apparatuses.

String. The reward was suspended from a string approximately 40 cm from the floor and 28 cm from the front of the cage mesh. The weight of the reward required subjects to use a rigid tool to bring it within reach. There were four tool sets each comprising three tools. Tool Sets 1–3 comprised three visually distinct tools (all 28.5 cm long) that differed in color, material, diameter, and critically, rigidity (see Figure 1 for details). Tool Set 4 comprised three visually identical tools made of cane bits (2–3 cm long × 0.5 in diameter) held together by either a string or a wooden kebab stick running through the center of the cane bits (see Figure 1). We treated this fourth set as a different task, given its special characteristics. The three tools were identical in terms of length, color, and diameter but differed in terms of their rigidity depending on whether a string (flexible) or a stick (rigid) ran through the center. Only one tool in each set was rigid enough to work as an effective tool. All tools were unfamiliar to the subjects. Because two orangutans, Padana and Dunja, repeatedly destroyed the cane tool set during the manipulation phase, a functionally equivalent tool set consisting of a white and blue rope of 1 cm in diameter was used with them. We created a rigid tool by inserting a metal stick through the center of the rope.

Table. The reward was situated 28 cm away from the cage mesh and placed on a plastic platform (40 cm × 80 cm) flush against the mesh. The friction of the reward against the platform required subjects to use the rigid tool to rake in the reward. We used Tool Sets 1–3 as in the string task.

Procedure. All subjects received the string task first, and once completed they moved to the table task. Each task consisted of a pretest and a test phase. During the pretest, subjects were confronted with the baited apparatus in Cage A and provided with a

Table 1
Demographics of Subjects

Subject	Gender	Age (years)	Rearing history	Experiment participation	Previous experience on tool-use tasks
Chimpanzee					
Fifi	Female	14	Mother	1, 3	b, d, e, f
Fraukje	Female	31	Nursery	1, 2a, 2b, 3	d, e
Sandra	Female	14	Mother	1, 3	d, e, f
Frodo	Male	14	Mother	1, 2a, 2b	d
Ulla	Female	30	Nursery	1, 2a, 2b	d
Patrick	Male	10	Mother	2a, 2b	d
Tai	Female	5	Mother	2a	
Jahaga	Female	15	Mother	2a, 2b	d, e
Trudi	Female	14	Mother	2a, 2b	d, e
Bonobo					
Joey	Male	25	Nursery	1, 2a, 2b, 3	b, c, d, e
Kuno	Male	11	Nursery	1, 2a, 2b, 3	c, d, e, f
Limbuko	Male	12	Nursery	1, 2a, 2b, 3	c, d, e
Yasa	Female	10	Mother	1, 2a, 2b, 3	c, d, e
Orangutan					
Dokana	Female	18	Mother	1, 2a, 2b, 3	a, b, c, d, e, f
Dunja	Female	34	Nursery	1, 2a, 2b, 3	a, c, d, e
Padana	Female	10	Mother	1, 2a, 2b, 3	d, e
Pini	Female	19	Mother	1, 2a, 2b, 3	a, b, c, d, e, f
Bimbo	Male	27	Nursery	1, 2a	a, b, d, e
Kila	Female	7	Mother	2a, 2b	e
Gorilla					
N'diki	Female	29	Mother[a]	1	a, d, e
Viringika	Female	12	Mother	1	a, b, d, e, f

Note. a = Mulcahy, Call, and Dunbar (2005); b = Mulcahy and Call (2006b); c = Mulcahy and Call (2006a); d = Girndt, Meier, and Call (2008); e = Martin-Ordas et al. (2008); f = Martin-Ordas and Call (2009).
[a] Wild caught.

wooden stick (30 cm long) to get the reward. In order to advance to the test phase, subjects had to retrieve the reward five times within 5 min in each of two consecutive sessions. All subjects successfully completed the pretest immediately (only five trials were required) and advanced to the test phase.

The test took place in two adjacent cages (A and B) connected by a sliding door (see Figure 2). Prior to the test, the experimenter introduced the three tools that would be used in that session inside the cage so that subjects could manipulate and inspect them. After the subjects abandoned the tools (usually within 5 min at most), they were retrieved by the experimenter and placed on the floor of Cage B parallel to each other (5 cm apart) and parallel to the subject's approach trajectory (see Figure 2). After the tools were positioned, the experimenter baited the apparatus in front of Cage A and opened the door connecting the two cages so that the subject was allowed to go into Cage B and get the tools. To solve the problem, subjects had to select and transport the rigid tool to Cage A and use it to get the reward. As soon as the subject returned to Cage A, the experimenter closed the door between both cages to prevent her from getting additional tools in case some tools still remained there. Subjects were allowed to attempt to get the reward with the tools that they brought. If the reward had not been obtained within 1 min, the experimenter retrieved the tools and prepared the next trial. If subjects brought the correct tool, they invariably got the reward within 1 min.

Subjects received one daily session per tool set. Each session consisted of three consecutive trials with the position of the tools counterbalanced across trials so that each tool appeared the same number of times in the middle, right, and left positions. The appearance of Sets 1 to 3 was counterbalanced across sessions and between subjects, whereas Set 4 was administered after the other three sets had been completed, and it involved three testing sessions instead of just one. Set 4 was used only with the string apparatus, and because of its special features (high similarity between tools), we considered it (and analyzed it) as a separate task (i.e., cane task). Thus, we used Tool Sets 1–3 with the string and table apparatuses, which constituted the string task and the table task. Additionally, we used Tool Set 4 with the string apparatus, and we designated this as the cane task. Overall, subjects received three trials for Sets 1–3 (nine trials in total for both the string and table tasks) and nine trials for Set 4 (cane task).

Data scoring and analysis. We videotaped all trials and scored the first tool used by the subject to retrieve the reward defined as inserting the tool through the mesh where the reward was located. To calculate interobserver reliability, Josep Call scored 20% of the trials selected randomly. Interobserver reliability was perfect (Cohen's $\kappa = 1$).

Our dependent measure was the percentage of correct responses defined as using the rigid tool in the first attempt of every trial. We analyzed the data with two-tailed exact nonparametric statistics. We used the Kruskal–Wallis test to analyze the effect of order of presentation and species on the percentage of correct responses. The Wilcoxon's test was used to assess whether subjects selected the correct tool more than would be expected by chance ($p = .33$). The percentage of correct trials between the different tool sets within each condition was compared with Friedman tests. We also

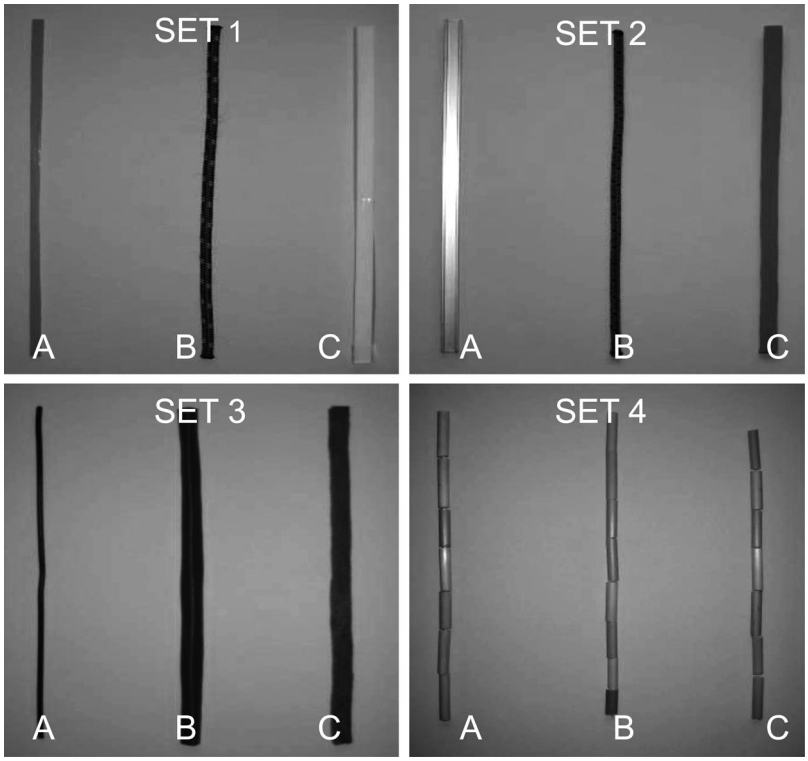

Figure 1. Tool sets used in Experiment 1. Each tool consisted of one suitable tool (panel A) and two unsuitable tools (panels B and C). Set 1: (A) gray plastic stick, 0.7 × 0.7 cm; (B) blue cord, 1 cm in diameter; and (C) white square paper stick, 1 cm side length. Set 2: (A) gray U-shaped metal rail, 1 cm edge length; (B) gray cord, 0.7 cm in diameter; and (C) blue foam stick, 1 × 0.3 cm. Set 3: (A) green wire, 0.4 cm in diameter; (B) red PVC strip, 1 × 0.3 cm; and (C) gray felt stick, 1 × 0.3 cm. Set 4: the three tools consisted of pieces of cane 2–3 cm long and 0.5 cm in diameter stuck together to form a 20-cm-length tool. While in (B) and (C), a string held the pieces together; in (A) a rigid wooden kebab stick served the same function.

assessed the performance on the first trial and the first trial of each set with the binomial test. Although Tool Set 4 was used with the string task only, for purposes of enhancing clarity of exposition and given the special features of the tools in this set, the data on this tool set are presented separately from those of the rest of the other tool sets that were used with the string apparatus. Finally, we also used a Wilcoxon's test to analyze whether subjects transported from their initial location to the task's location a greater percentage of suitable tools than of unsuitable tools. Descriptive statistics include the median and the interquartile range (IQR).

Results

The order of presentation of the three tools sets had no significant effect on the percentage of correct trials in the string task (Kruskal–Wallis test: $\chi^2_4 = 3.68$, $p = .45$, $N = 16$) or in the table task (Kruskal–Wallis test: $\chi^2_4 = 5.71$, $p = .36$, $N = 15$). Therefore we collapsed the percentage of correct trials across order of presentation of the various tool sets for all subsequent analyses. Figure 3 presents the median percentage of correct trials as a function of species and task. There were no significant differences between species in the percentage of correct trials for any of the three tasks (Kruskal–Wallis tests: string task: $\chi^2_3 = 2.13$, $p = .55$; cane task: $\chi^2_3 = 4.02$, $p = .27$; table task: $\chi^2_3 = 2.83$, $p = .53$, $N = 14$ for all cases). Similarly, there were no significant differences between tasks in the percentage of correct trials (Friedman test: $\chi^2_2 = 5.00$, $p = .08$, $N = 16$). Subjects performed above chance levels in all three tasks (Wilcoxon's tests: string task: $Z = 3.50$, $p < .001$, $N = 15$, median = 100, IQR = 11; cane task: $Z = 3.58$, $p < .001$, $N = 16$, median = 94.5, IQR = 30.2; table task: $Z = 3.69$, $p < .001$, $N = 15$, median = 100, IQR = 0).

There was no evidence of improvement in the percentage of correct trials across the three sessions of each task (Friedman tests: string task: $\chi^2_2 = .29$, $p = 1$; cane task: $\chi^2_2 = 1.33$, $p = .55$; table task: $\chi^2_2 = 1.40$, $p = .67$). Focusing on the first trial of each set revealed that subjects used the correct tool above chance levels in all tasks (Wilcoxon's tests: string task: $Z = 3.44$, $p < .001$, median = 100, IQR = 33.3; cane task: $Z = 3.56$, $p < .001$, median = 100, IQR = 0; table task: $Z = 3.56$, $p < .001$, median = 100, IQR = 0, $N = 14$ for all cases). Similarly, restricting our analyses to the first trial that subjects received in each task produced equivalent results. Fifteen out of 16 subjects used the correct tool in the string, cane, and table tasks (binomial test: $p < .001$).

Table 2 presents the median percentage of suitable and unsuitable tools transported from Cage B to Cage A by each species. Subjects transported significantly more suitable than unsuitable tools in all tasks (Wilcoxon's tests: string task: $Z = 3.26$, $p < .001$,

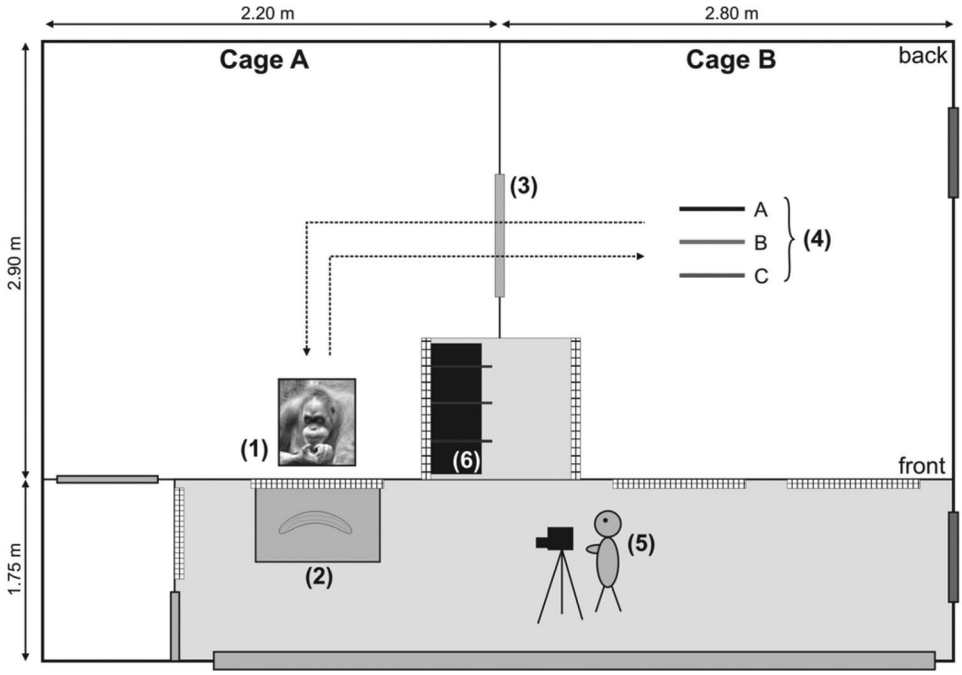

Figure 2. Schematic representation of the procedure. The test took place in two adjacent cages (panels A and B) of about the same size connected by a sliding door (3). The tool-set (4) consisting of one suitable tool (panel A) and two unsuitable tools (panels B and C) was placed in Cage B so that the tools were parallel to each other and to the subject's approach trajectory. The reward (2) was either hung (string task) or deposited on a platform (table task) outside Cage A with a mesh impeding the subject's ability to reach it. To solve the task the subject had to go to Cage B and get the tools and then return to Cage A to get the reward. In Experiments 2a and 2b the tools were deposited on a sliding platform (6) outside the same Cage A where the reward was hung.

$N = 16$; cane task: $Z = 3.41$, $p < .001$, $N = 15$; table task: $Z = 3.42$, $p < .001$, $N = 16$). There were no significant differences between species for transporting suitable tools (Kruskal–Wallis tests: string task: $\chi^2_3 = 4.07$, $p = .25$; cane task: $\chi^2_3 = 3.29$, $p = .35$; table task: $\chi^2_3 = 3.01$, $p = .39$; $N = 16$ for all cases).

Discussion

Subjects preferentially transported and used the rigid tools over the flexible tools above chance levels in both the string and table apparatuses and for each tool set. This means that rigid tools were selected over flexible ones regardless of their material, color, or diameter. Even when tools were visually identical (Tool Set 4, also referred as *cane task*), subjects still selected the rigid tools over the flexible tools well above chance levels. Subjects' marked preference for rigid tools was evident in the first trial even though subjects had never used any of those tools before. Their strong preference for rigid tools is more striking given the very limited manipulative experience that subjects received before the test (which in no case involved using the tools to get an out-of-reach reward). Furthermore, subjects' marked preference for the rigid tools was observed both in the string and table tasks even though the motor responses required differed markedly. The string task required subjects to displace the tool laterally, whereas the table task required subjects to pull the tool straight back and down.

Despite subjects' clear preference for the rigid tools, it is unclear what type of information subjects used to judge whether the tools were appropriate. One possibility is that the tactile feedback that they obtained prior to the test allowed them to judge their suitability. Thus, perceiving the effects of their actions on the tools both in terms of the visual and particularly the tactile feedback may have been critical to judge tool suitability. It is unclear whether subjects would be able to extract information about tool pliability only on the basis of observing the effects that someone else's action has on the tools or simply by observing the tools themselves motionless. After all, much of the information that subjects extract from tool properties is thought to be linked to the effects of their own actions on the tools, but this does not mean that subjects are unable to extract information about object properties (e.g., pliability) by observation alone.

Experiment 2

In Experiment 2a we investigated the role that observation alone played in rigidity assessment by presenting subjects with a new set of tools in one of two conditions. In one condition, subjects could manipulate the tools prior to their selection and use, thus mirroring Experiment 1. In the other condition, subjects could not manipulate the tools prior to its selection, but they could only observe the effect (bending or not the tool) that the experimenter's action had on the tools. In Experiment 2b we administered a visual static condition that consisted of presenting the tools on the platform without manipulating them in any way so that subjects could only gather information about their visual appearance. If subjects per-

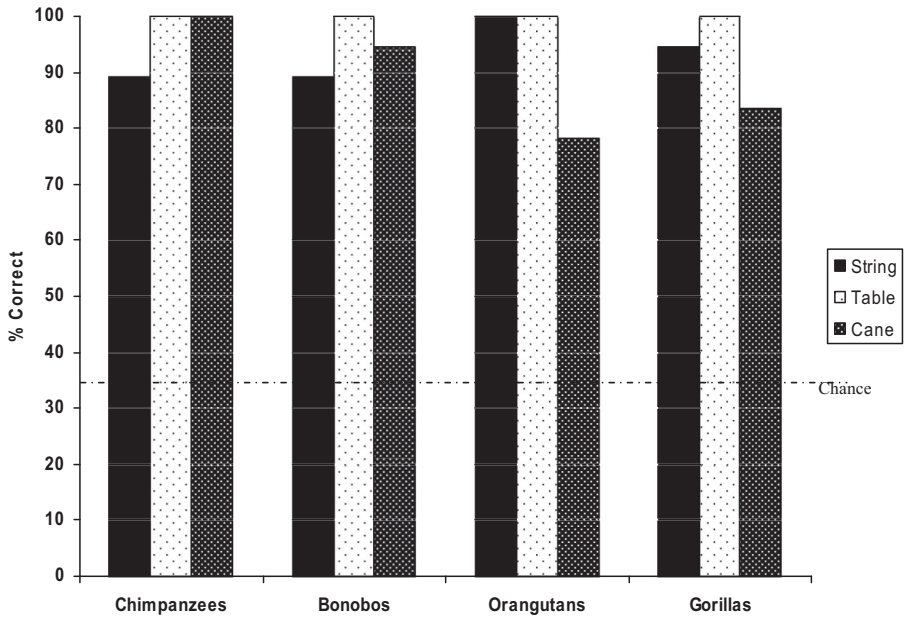

Figure 3. Median percentage of correct choices as a function of task and species.

formed at the same level as in the observation condition of Experiment 2a, we would conclude that witnessing the experimenter's action on the tools provided no additional information about the tools' rigidity. However, if a decrement in performance occurred, we would conclude that subjects benefited from the information provided by the experimenter's manipulation of the tools.

Methods

Subjects.

Experiment 2a. Six orangutans (*Pongo pygmaeus*), 7 chimpanzees (*Pan troglodytes*), and 4 bonobos (*Pan paniscus*) housed at the WKPRC participated in this experiment. There were 6 males and 11 females ranging in age from 5 to 34 years. Ten subjects were mother-reared and 7 nursery-reared. Five orangutans, all bonobos, and 3 chimpanzees had participated in Experiment 1 (see Table 1). The remaining 5 subjects were completely naïve to our experimental protocol. Although these 5 subjects had participated in studies in which they had to use a tool to retrieve a reward that was outside of reach on a table or a tube (see Table 1), they had never faced a task in which they had to select a rigid tool over a pliable tool. All the information regarding housing, animal handling, and feeding routines was the same as in Experiment 1.

Experiment 2b. We tested the same subjects as in Experiment 2a (see Table 1) except for the orangutan Bimbo and the chimpanzee Tai, who refused to participate.

Apparatus.

Experiment 2a. We used the string task from Experiment 1 but changed the tools' sets and their mode of presentation. Each three-tool set was presented on a sliding platform perpendicular to a Plexiglas panel with three hole in the left, center, and right positions. Each tool was placed perpendicular to the panel and parallel to the other tools, separated from each other by 29 cm. Tool sets comprised three visually distinct tools (all 28.5 cm long) that differed in color, material, diameter, and critically, rigidity (see Figure 4 for details). Only one tool in each set was rigid enough to work as an effective tool. All tools were unfamiliar to the subjects. We also presented three wooden straight tools during the warm-up phase. One tool was long (50 cm), and two were short (5 cm). All tools had a diameter of 0.6 cm. The baited apparatus and the tools were 90 cm apart

Table 2
Median Percentage (Interquartile Range) of Suitable (ST) and Unsuitable (UT) Tools Transported From Cage B to Cage A in Experiment 1

	String task		Cane task		Table task	
Species	ST	UT	ST	UT	ST	UT
Chimpanzees	88.9 (38.9)	27.8 (41.7)	100 (5.6)	16.7 (25.0)	100 (38.9)	5.6 (41.7)
Bonobos	94.4 (19.4)	44.4 (58.3)	94.4 (19.4)	47.2 (81.9)	100 (0)	44.4 (72.2)
Orangutans	100 (0)	33.3 (47.3)	88.9 (16.6)	50.0 (41.6)	100 (5.6)	27.8 (48.4)
Gorillas	94.4 (11.1)	11.1 (11.1)	83.3 (33.3)	33.3 (33.3)	66.7 (66.7)	0 (0)

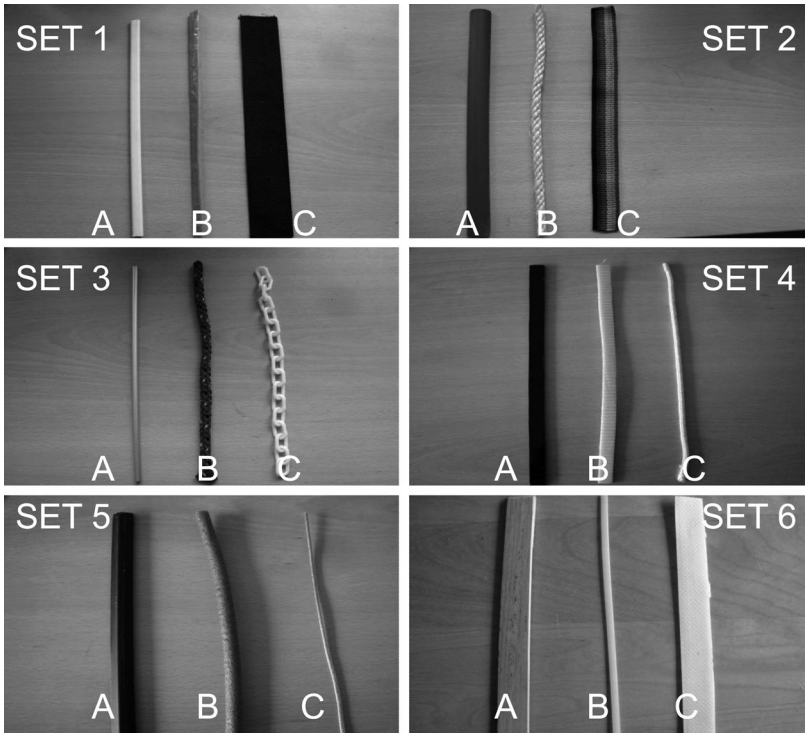

Figure 4. Tool sets used in Experiment 2a. Each tool consisted of one suitable tool (panel A) and two unsuitable tools (panels B and C). Set 1: (A) white hollowed metal bar, 1 × 0.5 cm; (B) brown triangular-shaped paper stick, 1 cm side length; and (C) black ribbon, 4 × 0.2 cm. Set 2: (A) violet semicircular wooden stick, 2.2 × 0.8 cm; (B) cream rope, 0.9 cm in diameter; and (C) multicolor ribbon, 2.5 × 0.2 cm. Set 3: (A) gray hollowed metal stick, 0.6 cm in diameter; (B) red cord,1 cm in diameter; and (C) white plastic chain, 1.4 × 0.3 cm. Set 4: (A) black plastic stick, 1.5 × 0.5 cm; (B) green polystyrene foam stick, 1.2 × 0.4 cm; and (C) white cord, 0.6 cm in diameter. Set 5: (A) brown triangular-shaped plastic stick, 1.5 × 0.7 cm; (B) foam round stick, 1 cm in diameter; and (C) gray electric wire, 0.2 cm in diameter. Set 6: (A) cream wooden stick, 1.9 × 0.4 cm; (B) white plastic stick, 0.5 × 0.1 cm; and (C) white Velcro strip, 2 × 0.1 cm.

and were visible at the time that subjects selected one of the tools.

Experiment 2b. We used the same apparatus as in Experiment 2a but replaced its tool sets for the tool sets (1 to 3) from Experiment 1. We decided to reuse those tools because it was hard to find novel tools that were not variations on previously experienced tools. Note that more than 20 months had elapsed since the last time (and only time) that subjects encountered those tools, and it is likely that they had forgotten about their properties. Even if they had not, this would provide a more stringent test of our hypothesis, because memory and visual appearance may contribute to the subjects choosing correctly.

Procedure.

Experiment 2a. We used the same basic procedure as in Experiment 1 (i.e., confronting subjects with an out-of-reach reward and offering them three tools to choose from to get the reward), except that subjects received both a manipulation condition (as in Experiment 1) and an observation condition. In the observation condition, subjects could not manipulate the tools but they could only observe the effect of the experimenter's actions on them. Implementing this condition meant that we had to present the tools on a platform outside of the same Cage A where the reward was hung, and subjects could only select one tool by placing their finger in front of one of the tools (see Figure 2). There was a warm-up phase and a test phase.

During the warm-up phase, subjects selected between the long tools and the short tools prior to retrieving the reward. More specifically, the experimenter baited the apparatus and placed one long stick and two short sticks on the sliding platform (each in front of a hole in the Plexiglas panel) and called the subject's attention. Once the subject was in front of the sliding platform, we waited up to 3 s before pushing it against the panel and the animal could then pick up one tool by touching it. To minimize the potential of cueing the animal, the experimenter was standing up and closed his eyes when pushing the platform forward. After the subject chose one of the tools, the experimenter withdrew the remaining tools to prevent her from making a second choice. Subjects received two warm-up trials in each session.

Once the warm-up was completed, subjects advanced to the test phase. Just as in Experiment 1, prior to the test, subjects received information about the pliability of each tool in the set. There were two different types of information corresponding to two conditions:

Manipulation. The experimenter introduced the three tools inside the subjects' cage so that she could freely manipulate them.

Thus this is equivalent to the condition used in Experiment 1. Once subjects stopped manipulating the tools, we retrieved them and placed them on their preassigned locations on the platform.

Observation. The experimenter placed the three tools on their preassigned locations on the platform, called the subject's attention and manipulated the tools for 5 s each. In the course of doing so the flexible tools were repeatedly bent in different directions while the rigid tool remained straight. When manipulating the tools, the experimenter looked at the subject to detect whether she was paying attention, and the 5 s counted only provided the subject watched the manipulation; otherwise we stopped the demonstration and restarted when the attention was redirected to the tool. After the manipulation of each tool was concluded, it was deposited in its corresponding location. At that time the experimenter looked only at the tool and the platform to avoid involuntarily cueing the subject.

Once the tools were in their designated locations, the experimenter closed his eyes and waited 3 s before pushing the sliding platform forward for the subjects to choose. The experimenter opened his eyes only when the platform collided with the three-holed panel. At that point the first tool that the subject tried to get, by touching it or pointing to it, was given to her. Only one choice was permitted. All subjects received both the manipulation and observation conditions in different days with the order of presentation counterbalanced across subjects, that is, half of the subjects received the manipulation condition first and the other half received it second. Subjects received one condition per day on two consecutive days. Each day comprised two warm-up trials and six test trials (2 trials per tool set). Thus, overall, subjects received 4 warm-up trials and 12 test trials (6 manipulation and 6 observation). We also counterbalanced the position of the tools within each set across trials so that the rigid tool appeared the same number of times in the left, middle, and right positions.

Experiment 2b. This experiment was intended as a control for the observation condition of Experiment 2a by ascertaining whether or not subjects benefited from our demonstration of the tool properties. Therefore, the basic procedure was the same as in the observation condition of Experiment 2a except that subjects were prevented from seeing the experimenter placing the tools on the platform. This was done to eliminate any information that subjects may gain from observing the tools being manipulated by the experimenter. Consequently, tools were always handled behind an occluder that was removed only after the tools were situated on their preassigned locations. Upon removal of the occluder, subjects could observe the tool set for 15 s, which corresponded to the time they had to observe the experimenter manipulating the tools in Experiment 2a. When the 15 s were over, the experimenter closed his eyes and counted up to three before pushing the sliding platform forward for the subjects to choose.

Data scoring and analysis. We videotaped all trials and scored whether the subject chose the rigid tool and if she did not, whether she attempted to use the tool to get the reward defined as inserting the tool through the mesh where the reward was located. To calculate interobserver reliability, Josep Call scored a random selection of 20% of the trials. Interobserver reliability was perfect (Cohen's $\kappa = 1$). We used the same analytical procedures as in Experiment 1.

Results

Experiment 2a. During the pretest, subjects selected the long tool in 100% of the trials. There was no significant effect of the order of presentation in the observation condition (Mann–Whitney test: $Z = 1.54$, $p = .15$, $N = 17$) or the manipulation condition (Mann–Whitney test: $Z = 1.05$, $p = .31$, $N = 17$). Therefore we collapsed the data across order of presentation for all subsequent analyses. Figure 5 presents the median percentage of correct trials

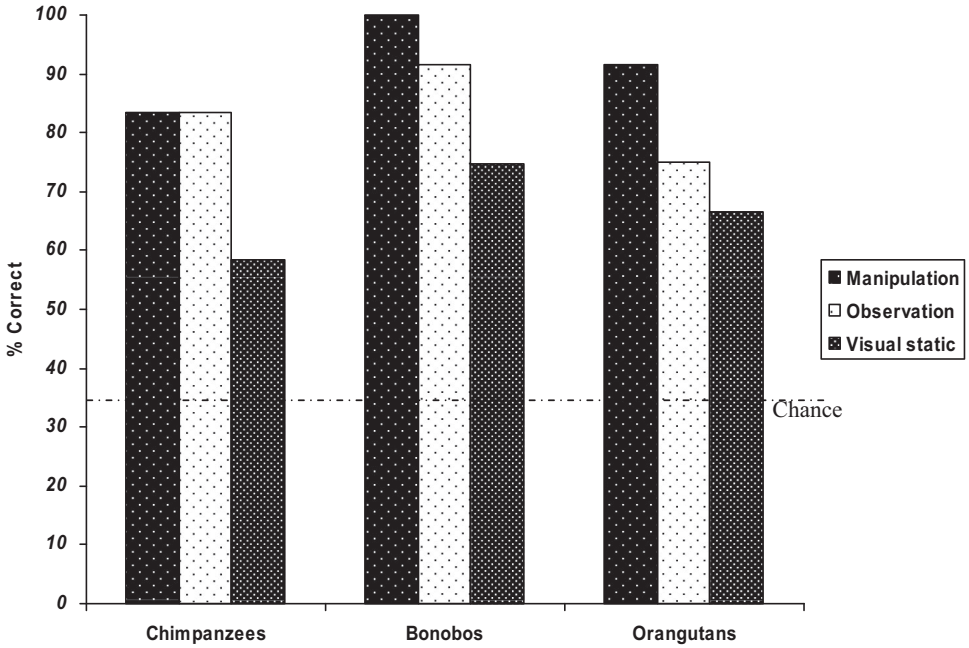

Figure 5. Median percentage of correct choices for the three species studied as a function of condition. *Manipulation* and *Observation* bars represent data from Experiment 2a and visual static from Experiment 2b.

as a function of condition and species. There were no significant differences between species in the percentage of correct trials in the observation condition (Kruskal–Wallis test: $\chi^2_2 = .58$, $p = .77$, $N = 17$) or the manipulation condition (Kruskal–Wallis test: $\chi^2_2 = 1.22$, $p = .58$, $N = 17$). Similarly, there were no significant differences between conditions in the percentage of correct trials (Wilcoxon's test: $Z = 1.42$, $p = .18$, $N = 12$). Subjects performed above chance in both conditions (Wilcoxon's tests: observation condition: $Z = 3.41$, $p < .001$, median = 83.3, IQR = 50; manipulation condition: $Z = 3.69$, $p < .001$, median = 100, IQR = 33.3; $N = 17$ for both cases). We found no evidence that subjects who participated in Experiment 1 performed better than did those who did not for the observation condition (Mann–Whitney test: $Z = 1.20$, $p = .26$, $N = 17$) or manipulation condition (Mann–Whitney test: $Z = 0.29$, $p = .86$, $N = 17$).

There was no evidence of a significant improvement across the three tool sets in the manipulation condition (Friedman test: $\chi^2_2 = 2.96$, $p = .23$, $N = 17$) or the observation condition (Friedman test: $\chi^2_2 = 5.51$, $p = .072$, $N = 17$). Pooling together the data of the first trial for all tool sets revealed that subjects used the correct tool above chance levels in both the manipulation condition (Wilcoxon's test: $Z = 3.70$, $p < .001$, $N = 17$, median = 100, IQR = 33.3) and the observation condition (Wilcoxon's test: $Z = 3.38$, $p = .001$, $N = 17$, median = 66.7, IQR = 66.7).

Experiment 2b. Figure 5 presents the median percentage of correct trials for the visual static condition as a function of species. Subjects showed a significantly lower percentage of correct trials in the visual static condition than in the observation condition of Experiment 2a (Wilcoxon's test: $Z = 2.09$, $p = .032$, $N = 11$). Nevertheless, on average, subjects still selected the rigid tool in 55% of the trials, which is above chance (Wilcoxon's test: $Z = 2.70$, $p = .003$, $N = 12$). However, subjects chose randomly if only the first trial of each set is considered (Wilcoxon's test: $Z = 0.29$, $p = .81$, $N = 15$). Chimpanzees, bonobos, and orangutans were successful in 27.8%, 50%, and 33.3% of their first trials, respectively. Moreover, subjects also showed a significantly lower percentage of correct trials in the visual static condition than in the string condition of Experiment 1 both in terms of overall performance (Wilcoxon's test: $Z = 2.71$, $p = .004$, $N = 10$) and in the first trial (Wilcoxon's test: $Z = 2.72$, $p = .004$, $N = 9$).

Discussion

Subjects participating in Experiment 2a selected the rigid tool above chance levels, thus replicating the results of Experiment 1 with a different set of tools. More important is that subjects were capable of selecting the correct tools on their first exposure to each tool set even when they were only provided with visual information about the effect that an experimenter's actions had on the tools. Although there was no overall significant difference between the manipulation and observation conditions, subjects performed slightly better in the manipulation condition when the analysis was restricted to the very first trial in each condition. In fact, there was some indication that subjects appeared to improve their performance during testing in the observation condition but not in the manipulation condition.

Nevertheless, subjects' performance in the observation condition was remarkable, considering that subjects in this condition could only gather visual information rather than visual and tactile information as in the manipulation condition, even more so since they received only 5 s of visual feedback in the observation condition. Furthermore, the subject's intervention in the production of the observed effects did not seem to play a decisive role here because even without such a link, subjects selected the tools above chance levels.

Subjects participating in Experiment 2b were less likely to select the rigid tool when they could only visually inspect the alternatives than when they witnessed the experimenter manipulate the tools (Experiment 2a) or when they manipulated the tools themselves (Experiment 1). This means that removing the information about tool manipulation significantly decreased the subjects' performance. This decrease, however, was not so dramatic as to prevent subjects from selecting tools above chance levels. This means that subjects may be able to extract some information about rigidity by just observing the tools' visual appearance or perhaps by remembering those tools from the test that took place 20 months ago. Nevertheless, we interpret the observed decrease as an indication that the bending and unbending of the tools performed by the experimenter constituted an important source of information in order to judge the tools' rigidity. Moreover, note that subjects did not perform above chance levels in the first trial, which suggests that their visual inspection or memories were not totally effective.

Experiment 3

Having tested the hypothesis about the importance of static visual information in judging tool rigidity, we turned our attention to the complement of rigidity: pliability. In the previous experiments, subjects were able to choose the appropriate rigid tools. However, it is unclear whether subjects tailored their tool choices to meet the task demands or simply preferred rigid tools regardless of the task demands. Note that up to this point, rigid tools had always been successful. In the current experiment we changed this situation and introduced an apparatus that required the use of flexible tools (rigid tools were ineffective) to get the reward. This manipulation allowed us to investigate whether subjects would be able to select flexible tools when the task required them to do so.

Methods

Subjects. We tested the same subjects that took part in Experiment 1, except for the chimpanzees Ulla and Frodo, who failed the training phase (see below), and the orangutan Bimbo, who refused to participate (see Table 1).

Apparatus. The apparatus consisted of a transparent plastic tube presenting an angle of approximately 90°. When attached to the mesh, a hole of 4 cm in diameter on the subject's side allowed the introduction of a flexible tool to reach for the yogurt or grape juice placed in the tube's bottom. The reward would then adhere to the tool, allowing the subject to lick it off. There were four tool sets each comprising three visually distinct tools (all 37 cm long) that differed in color, material, diameter, and critically, rigidity (see Figure 6 for details). In every set, only one tool was flexible enough to bend round at the tube's angle and reach the reward.

Procedure. The task comprised a pretest and a test phase. During the pretest, subjects were confronted with the baited apparatus in Cage A and provided with a flexible willow branch (37 cm long) to get the reward. In order to advance to the test phase,

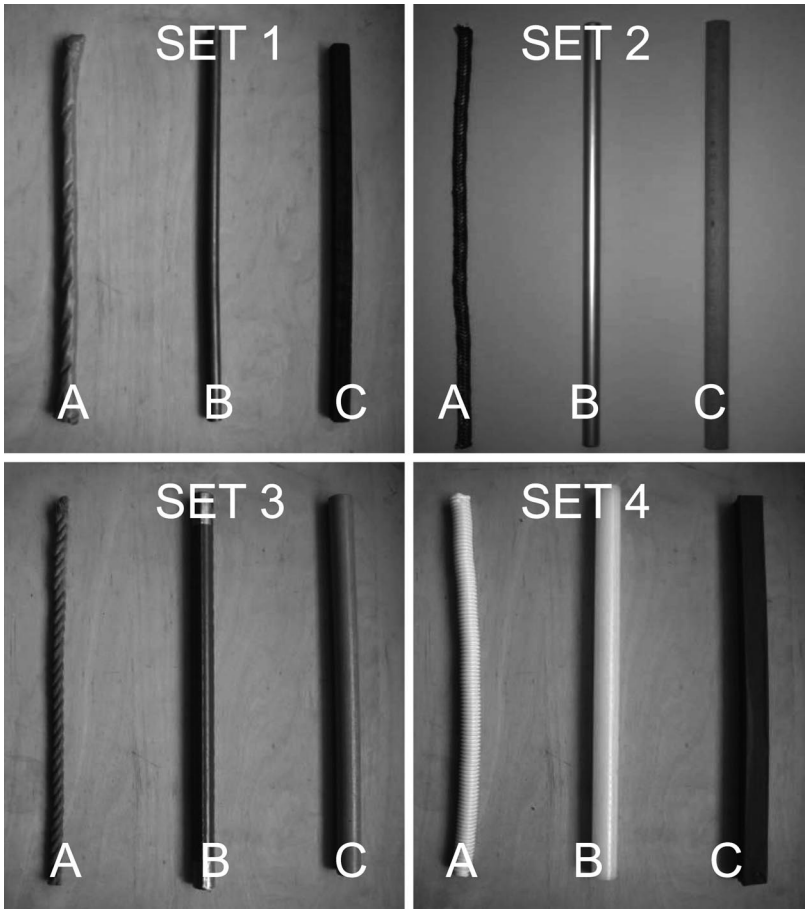

Figure 6. Tool sets used in Experiment 3. Each tool consisted of one suitable tool (panel A) and two unsuitable tools (panels B and C). Set 1: (A) rope wrapped in gray duct tape (diameter = 1 cm), (B) copper pipe (diameter = 1 cm), and (C) black wooden stick (1.5 × 1.5 cm). Set 2: (A) orange and green nylon rope (diameter = 1 cm), (B) silver metal bar (diameter = 1.3 cm), and (C) brown rounded wooden stick (diameter = 1.5 cm). Set 3: (A) orange cord (diameter = 0.7 cm), (B) plastic-covered green metal stick (diameter = 1.5 cm), and (C) yellow dowel (diameter = 2 cm). Set 4: (A) beige fluted plastic pipe (diameter = 1.5 cm), (B) white rounded plastic stick (diameter = 2 cm), and (C) wooden square stick wrapped in red tape (2 cm × 2 cm).

subjects had to dip the branch in the reward five times within 5 min in each of two sessions conducted on two consecutive days. If the subjects did not spontaneously insert the branch into the tube, the experimenter showed them how to do it. All subjects successfully completed the pretest and advanced to the test phase. The test took place in two adjacent cages (A and B) connected by a sliding door (see Figure 2). The way the tools were placed as well as the testing protocol stayed the same as in Experiment 1 except that here subjects had to select the flexible tool. Subjects received one daily session per tool set. Each session consisted of three consecutive trials with the position of the tools counterbalanced across trials so that each tool appeared the same number of times in the middle, right, and left positions. The order of Sets 1 to 4 was counterbalanced across sessions and between subjects.

Data scoring and analysis. We videotaped all trials and scored the first tool used by the subject to retrieve the reward defined as inserting the tool through the mesh where the reward was located. To calculate interobserver reliability, Josep Call scored 20% of the trials selected randomly. Interobserver reliability was perfect (Cohen's $\kappa = 1$). We used the same analytical procedures as in Experiment 1.

Results

Table 3 presents the median percentage of suitable and unsuitable tools transported from Cage B to Cage A as a function of species. Although subjects did not significantly transport more

Table 3
Median Percentage (Interquartile Range) of Suitable (ST) and Unsuitable (UT) Tools Transported From Cage B to Cage A in Experiment 3

Species	ST	UT
Chimpanzees	41.7 (41.7)	37.5 (41.7)
Bonobos	58.3 (45.8)	45.8 (33.4)
Orangutans	83.3 (12.5)	54.17 (33.3)

suitable tools than unsuitable tools to Cage A (Wilcoxon's test: $Z = 1.29$, $p = .21$, $N = 11$, Table 3), subjects used flexible tools (correct response) more often than would be expected by chance (Wilcoxon's tests: $Z = 2.31$, $p < .02$, $N = 9$; median = 50, IQR = 33.34). Species did not significantly differ in the percentage of correct trials (Kruskal–Wallis test: $\chi^2_2 = 0.33$, $p = .87$; chimpanzees: median = 41.67, IQR = 41.67; bonobos: median = 50, IQR = 22.92; orangutans: median = 54.16, IQR = 39.59; $N = 11$ for all cases).

Focusing on the first trial of each set indicated that subjects did not use the correct tool above chance levels (Wilcoxon's test: $Z = 0.09$, $p = .09$, $N = 11$). Chimpanzees, bonobos, and orangutans succeeded on average in only 41.7%, 25%, and 43.7% of their first trials, respectively. However, there was no evidence of improvement across sessions (Friedman test: $\chi^2_2 = 4.21$, $p = .25$).

Discussion

Subjects of all three species showed a preference for using the appropriate flexible tool. Unlike previous experiments on rigidity (e.g., Experiment 1), this preference was not observed in the first trial. However, the lack of a significant improvement over time in the preference for the flexible tool paired with an overall above-chance performance suggests that subjects can easily switch from selecting rigid to flexible tools. It is unclear why subjects found selecting flexible tools slightly harder than selecting rigid ones, and we can only speculate at this point. One possibility is that this difference simply reflects an order effect, because the work on rigid tools took place prior to the work on flexible tools. This would make the test on flexible tools particularly stringent because subjects had to refrain from picking rigid tools, which had been reinforced until then. The fact that overall they selected flexible tools above chance shows that they could overcome this putative preference, although not in the first trial. Additionally, most of the tools that subjects need to use to get food from enrichment devices in our facility require the use of rigid sticks, which again could bias them toward choosing rigid tools in general.

General Discussion

Great apes preferentially selected rigid tools as opposed to flexible ones from 10 different novel tool sets to solve two different tasks. Such preference was evident in the first trial regardless of the perceptual appearance of the tools and whether they themselves manipulated the tools prior to their use or whether they merely observed a human manipulating them. In comparison with these conditions, simply observing the tools resulted in a marked decrease in performance. Subjects were also able to select flexible tools (as opposed to rigid ones) when the task required it, although preference for flexible tools was not evident in the first trial. We found no evidence of significant differences between ape species regardless of their different propensities to use tools in the wild.

One main conclusion from the current study is that apes can spontaneously judge the suitability of novel tools on the basis of their rigidity, in some cases even before subjects had a chance to use the tool to get a reward. Thus, our results confirm those of Furlong et al. (2008) in showing that contrary to previous work (Povinelli, 2000), chimpanzees and other apes can quickly discriminate tools on the basis of their rigidity or pliability. However, we differ from Furlong et al. (2008) in the emphasis placed on the rearing history as the main explanation for the observed discrepancies between studies. Without denying the importance of epigenetic factors in tool use and other abilities (Call & Tomasello, 1996; Tomasello & Call, 2004), Furlong et al.'s (2008) explanation cannot fully account for our positive results, because none of the apes included in our study was enculturated, yet they performed well. Moreover, even Furlong et al.'s semienculturated chimpanzees solved two versions of the flimsy rake task. We would like to call attention to task presentation as an important contributing factor to the final outcome.

Our task involved a differentiated tool selection phase and a tool use phase. Dissociating these two steps is not only important from a point of view of ecological validity but also as a way to guard against the possibility that task presentation per se, rather than subjects' abilities (or lack of), is responsible for the observed outcome. In a previous study, Girndt et al. (2008) found that presenting two tools side by side in the trap–table task was problematic, because it underestimated the knowledge that subjects possessed about the effect that a trap has on the trajectory of a moving reward. It is true that Furlong et al.'s (2008) chimpanzees were able to solve the task above chance levels even with this type of presentation, but their performance was far from perfect (69% correct) and much lower than the results in the current study (91%–81% correct in Experiments 1 and 2, respectively). It would be interesting to know how chimpanzees who were tested with the original set-up would do in the current set-up. Our prediction is that they would do much better than with the original presentation.

Let us emphasize that we do not think that mode of presentation is the sole explanation for the poor results available in the literature, but we argue that it is an important contributing factor. It is also important to mention that monkeys can also solve the task successfully even when presented with the two-option set-up used in the original flimsy rake situation. But again their performance is far from perfect, and it appeared after monkeys were initially trained on one of the tools for a number of trials. Note that apes presented with a similar set-up to those of the monkeys and without the initial training do not perform at high levels (Herrmann et al., 2008). Even with the simplest tasks, apes as a group rarely scored above 70% correct.

Our study showed that apes were able to select rigid or flexible tools that met the task demands. Although subjects did better with rigid tools than with flexible tools, we can rule out the possibility that this result was due to a strong preference for rigid tools. Otherwise, subjects would have also shown that preference in the first trial of the flexible tools task (Experiment 3), and they did not, and overall they would not have shown a preference for flexible tools in that experiment, which they did. Moreover, the fact that wild chimpanzees selected rigid or pliable tools depending on the task at hand without a clear preference for one or another type of tool also weakens the idea that subjects might have simply preferred rigid tools regardless of the task. Note that even if the subjects in the current study were to select rigid tools for every task, this would not challenge the fact that subjects can quickly judge what is rigid and what is not. These data are inconsistent with solving the task via perceptual identification of familiarity, because all the tools were new. Additionally, our data showed that tool selection was not totally dependent on prior manipulative experience with the tools or the visual appearance of tools. These

data are consistent with the idea that subjects have some knowledge about rigidity that goes beyond sensorimotor schemas and that at the very least allowed subjects to classify new exemplars of tools appropriately. Future studies are needed to pinpoint the precise nature of this knowledge.

Another pending key question is the type and amount of experience required to develop the knowledge they may possess about tool rigidity. Although the apes in the current study had never used the tools that we supplied them with prior to the test, they had used wooden sticks and branches to get out-of-reach rewards in the past. It is very likely that those experiences played a crucial role in the development of their knowledge about tool rigidity. It is clear that even those experiences are minimal and relatively simple in comparison with the problems faced by some wild chimpanzee communities that extract insects practically on a daily basis and that are exposed to such activities from the very beginning of their lives. In some cases, a rigid tool is required to drill a hole and a pliable one to navigate the tunnels and extract the termites. Such complex situations experienced from early in life may foster the development of knowledge systems even more developed than those observed here. Recently, Visalberghi et al. (2009) have reported that wild capuchin monkeys are capable of selecting new tools to crack open nuts on the basis of their weight and hardness. This result is analogous in some ways to the data described here, and it may suggest that both chimpanzees and capuchin monkeys can develop knowledge about tool properties that goes beyond particular familiar exemplars. Future research will be needed to ascertain whether chimpanzee's and capuchin's knowledge about tool properties is essentially similar or differs in important ways.

It is noteworthy that subjects in the current study did not need to manipulate the tool to decide whether it was suitable—something that is especially remarkable considering that they received only minimal exposure to the tools prior to their use and that such exposure was not embedded in a problem-solving situation and that just seeing the tools in the absence of any manipulation considerably reduced their success. With regard to the information that they extracted from tools prior to their use, one could argue that tool appearance (not its functional properties, i.e., flexibility) was enough to help them determine whether tools were rigid enough. However, the results of Experiment 2b weaken this possibility, because subjects' performance deteriorated if they could only see the tools without manipulating them or seeing the experimenter manipulating them. Although it is possible that subjects gained some information about tool properties via visual inspection alone (after all, they performed above chance in Experiment 2b), the slightly worse performance in the observation condition in comparison with the manipulation condition (Experiment 2a) and the observation that several subjects touching the tools in succession before deciding which one to take (Experiment 1) again indicated that tool appearance provided less-than-perfect information about the tool properties.

Additionally, the data supporting the visual-inspection-alone hypothesis needs to be cautiously interpreted, because subjects had used those tools in the past, and therefore they might remember them.

The finding that apes select tools on the basis of their rigidity may not seem new or surprising to some. After all, field researchers have noted for a number of years that chimpanzees select pliable materials for some tasks and rigid ones for others (e.g., Goodall, 1986; McGrew, 1992; Sanz et al., 2004). However, the goal of the current study was to probe further the mechanisms responsible for the selection of appropriate tools. We now know that chimpanzees do not require familiarity with tools to select appropriate tools and that they can use their existing knowledge to classify new exemplars. Furthermore, we know that they can do this after minimal exposure to the tool properties in the absence of direct manipulation.

The current study has documented that chimpanzees are not alone in their ability to select tools on the basis of their rigidity. We found that bonobos and orangutans possess comparable abilities to those of chimpanzees. This finding leads us to postulate that if their habitat were to require them to use rigid tools to solve certain problems, they would be able to do so quite effectively. Regarding gorillas, the information that we have is more fragmentary, but when it comes to tool use they seem to also perform in comparable ways to the other great apes (e.g., Fontaine, Moisson, & Wickings, 1995; Girndt et al., 2008; Mulcahy et al., 2005), something that does not appear to be the case for each domain (e.g., inhibitory control; Amici, Aureli, & Call, 2008).

In conclusion, chimpanzees, bonobos, and orangutans spontaneously select tools to get an out-of-reach reward on the basis of the tools' rigidity, disregarding other properties such as material, color, and diameter. They were capable of doing so even though the items presented were unfamiliar to the subjects and they were only allowed to manipulate the items briefly before making a choice. Moreover, merely observing an experimenter manipulate the objects (as opposed to themselves manipulating them) was enough to provide them with enough information to make appropriate choices. Moreover, subjects could quickly select rigid or flexible tools to meet the task demands. Studies such as the current one complement the findings discovered in the natural habitats by bringing into close scrutiny the possible ways of acquisition and use of information regarding tool properties.

References

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology, 18*(18), 1415–1419. doi: 10.1016/j.cub.2008.08.020

Antinucci, F. (1989). *Cognitive structure and development in nonhuman primates.* Hillsdale, NJ: Erlbaum.

Brewer, S. M., & McGrew, W. C. (1990). Chimpanzee use of a tool-set to get honey. *Folia Primatologica, 54*(1–2), 100–104. doi: 10.1159/000156429

Call, J., & Tomasello, M. (1996). The effect of humans on the cognitive development of apes. In A. E. Russon, K. A. Bard, & S. T. Parker (Eds.), *Reaching into thought: The minds of the great apes* (pp. 371–403). New York, NY: Cambridge University Press.

Chappell, J., & Kacelnik, A. (2002). Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition, 5*(2), 71–78. doi: 10.1007/s10071-002–0130-2

Chappell, J., & Kacelnik, A. (2004). Selection of tool diameter by New Caledonian crows *Corvus moneduloides. Animal Cognition, 7*(2), 121–127. doi: 10.1007/s10071-003–0202-y

Fay, J. M., & Carroll, R. W. (1994). Chimpanzee tool use for honey and termite extraction in central Africa. *American Journal of Primatology, 34*(4), 309–317. doi: 10.1002/ajp.1350340403

Fontaine, B., Moisson, P., & Wickings, E. (1995). Observations of spontaneous tool making and tool use in a captive group of Western lowland gorillas (*Gorilla gorilla* gorilla). *Folia Primatologica, 65*(4), 219–223.

Furlong, E. E., Boose, K. J., & Boysen, S. T. (2008). Raking it in: The impact of enculturation on chimpanzee tool use. *Animal Cognition, 11*(1), 83–97. doi: 10.1007/s10071-007–0091-6

Girndt, A., Meier, T., & Call, J. (2008). Task constraints mask great apes' ability to solve the trap-table task. *Journal of Experimental Psychology: Animal Behavior Processes, 34,* 54–62. doi: 10.1037/0097–7403.34.1.54

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior.* Cambridge, MA: Harvard University Press.

Hauser, M. D., Kralik, J., & Botto-Mahan, C. (1999). Problem solving and functional design features: Experiments on cotton-top tamarins, *Saguinus oedipus oedipus. Animal Behaviour, 57*(3), 565–582. doi: 10.1006/anbe.1998.1032

Hauser, M. D., Pearson, H., & Seelig, D. (2002). Ontogeny of tool use in cottontop tamarins, *Saguinus oedipus*: Innate recognition of functionally relevant features. *Animal Behaviour, 64*(2), 299–311. doi: 10.1006/anbe.2002.3056

Herrmann, E., Wobber, V., & Call, J. (2008). Great apes' (*Pan troglodytes, Pan paniscus, Gorilla gorilla, Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology, 122,* 220–230. doi: 10.1037/0735–7036.122.2.220

Hihara, S., Obayashi, S., Tanaka, M., & Iriki, A. (2003). Rapid learning of sequential tool use by macaque monkeys. *Physiology & Behavior, 78*(3), 427–434. doi: 10.1016/S0031-9384(02)01006–5

Kacelnik, A., Chappell, J., Weir, A. A. S., & Kenward, B. (2006). Cognitive adaptations for tool-related behaviour in New Caledonian crows. In E. A. Wasserman & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 515–528). Oxford, England: Oxford University Press.

Köhler, W. (1925). *The mentality of apes.* London, England: Routledge & Kegan Paul.

Limongelli, L., Boysen, S. T., & Visalberghi, E. (1995). Comprehension of cause–effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 109,* 18–26.

Martin-Ordas, G., & Call, J. (2009). Assessing generalization within and between trap-tasks in the great apes. *International Journal of Comparative Psychology, 22,* 43–60.

Martin-Ordas, G., Call, J., & Colmenares, F. (2008). Tubes, tables and traps: Great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition, 11,* 423–430.

McGrew, W. C. (1992). *Chimpanzee material culture: Implications for human evolution.* Cambridge, England: Cambridge University Press.

Mulcahy, N. J., & Call, J. (2006a). Apes save tools for future use. *Science, 312,* 1038–1040.

Mulcahy, N. J., & Call, J. (2006b). How great apes perform on a modified trap-tube task *Animal Cognition, 9*(3), 193–199. doi: 10.1007/s10071-006–0019-6

Mulcahy, N. J., Call, J., & Dunbar, R. I. M. (2005). Gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) encode relevant problem features in a tool-using task. *Journal of Comparative Psychology, 119,* 23–32.

Povinelli, D. J. (2000). *Folk physics for apes: The chimpanzee's theory of how the world works.* Oxford, England: Oxford University Press.

Santos, L. R., Miller, C. T., & Hauser, M. D. (2003). Representing tools: How two non-human primate species distinguish between the functionally relevant and irrelevant features of a tool. *Animal Cognition, 6*(4), 269–281. doi: 10.1007/s10071-003–0171-1

Santos, L. R., Pearson, H. M., Spaepen, G. M., Tsao, F., & Hauser, M. D. (2006). Probing the limits of tool competence: Experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Animal Cognition, 9*(2), 94–109. doi: 10.1007/s10071-005–0001-8

Sanz, C., Morgan, D., & Gulick, S. (2004). New insights into chimpanzees, tools, and termites from the Congo basin. *American Naturalist, 164*(5), 567–581. doi: 10.1086/424803

Seed, A. M., Call, J., Emery, N. J., & Clayton, N. S. (2009). Chimpanzees solve the trap problem when the confound of tool use is removed. *Journal of Experimental Psychology: Animal Behavior Processes, 35,* 23–34.

Seed, A. M., Tebbich, S., Emery, N. J., & Clayton, N. S. (2006). Investigating physical cognition in rooks, *Corvus frugilegus. Current Biology, 16*(7), 697–701.

Spinozzi, G., & Potí, P. (1989). Causality i: The support problem. In F. Antinucci (Ed.), *Cognitive structure and development in nonhuman primates* (pp. 114–119). Hillsdale, NJ: Erlbaum.

Sugiyama, Y., Koman, J., & Sow, M. B. (1988). Ant-catching wands of wild chimpanzees at Bossou, Guinea. *Folia Primatologica, 51*(1), 56–60.

Tebbich, S., & Bshary, R. (2004). Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida. Animal Behaviour, 67*(4), 689–697. doi: 10.1016/j.anbehav.2003.08.003

Tebbich, S., Seed, A. M., Emery, N. J., & Clayton, N. S. (2007). Non-tool-using rooks, *Corvus frugilegus,* solve the trap-tube problem. *Animal Cognition, 10*(2), 225–231. doi: 10.1007/s10071-006–0061-4

Tomasello, M., & Call, J. (1997). *Primate cognition.* New York, NY: Oxford University Press.

Tomasello, M., & Call, J. (2004). The role of humans in the cognitive development of apes revisited. *Animal Cognition, 7*(4), 213–215. doi: 10.1007/s10071-004–0227-x

Visalberghi, E., Addessi, E., Truppa, V., Spagnoletti, N., Ottoni, E., Izar, P., et al. (2009). Selection of effective stone tools by wild bearded capuchin monkeys. *Current Biology, 19,* 213–217. doi: 10.1016/j.cub.2008.11.064

Visalberghi, E., & Limongelli, L. (1994). Lack of comprehension of cause–effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 108,* 15–22.

Weir, A. A., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science, 297*(5583), 981. doi: 10.1126/science.1073433

Received May 8, 2009
Revision received January 19, 2010
Accepted January 19, 2010 ■