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ORIGINAL ARTICLE

**Laurie R. Santos · Heather M. Pearson ·
Geertrui M. Spaepen · Fritz Tsao · Marc D. Hauser**

Probing the limits of tool competence: Experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*)

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Abstract Non-human animals vary in their ability to make and use tools. The goal of the present study was to further explore what, if anything, differs between tool-users and non-tool-users, and whether these differences lie in the conceptual or motor domain. We tested two species that typically do not use tools—cotton top tamarins (*Saguinus oedipus*) and vervet monkeys (*Cercopithecus aethiops*)—on problems that mirrored those designed for prolific tool users such as chimpanzees. We trained subjects on a task in which they could choose one of two canes to obtain an out-of-reach food reward. After training, subjects received several variations on the original task, each designed to examine a specific conceptual aspect of the pulling problem previously studied in other tool-using species. Both species recognized that effective pulling tools must be made of rigid materials. Subsequent conditions revealed significant species differences, with vervets outperforming tamarins across many conditions. Vervets, but not tamarins, had some recognition of the relationship between a tool's orientation and the position of the food reward, the relationship between a tool's trajectory and the substance that it moves on, and that tools must be connected in order to work properly. These results provide further evidence that tool-use may derive from domain-general, rather than domain-specific cognitive capacities that evolved for tool use per se.

Keywords Cognitive specializations · Domain-general abilities · Non-human primates · Tool-use

Our species' ability to use and make tools has long been heralded as a mark of cognitive distinction. Consequently, psychologists have devoted considerable theoretical and empirical effort to the question of how humans represent tools as opposed to other kinds of objects (e.g., Keil 1989; Bloom 1996). Much of this work suggests that tools may hold a special place in the human representational system. Evidence from a number of domains including standard psychological tests (Bloom 1996), developmental work (Keil 1989), neuroimaging (Johnson-Frey 2004; Maravita and Iriki 2004), and patients with brain damage (Hillis and Caramazza 1991) suggest that humans seem to represent objects in the domain of tools differently than other types of objects. Keil and his colleagues (Keil 1989; Keil et al. 1998), for example, have demonstrated that children pay attention to different features when categorizing tools (e.g., shape, number of outside parts) than when categorizing animals (e.g., color, number of inside parts). Similarly, neuropsychologists have observed that brain damage can selectively impair an individual's understanding of tools even while sparing other domains (e.g., animals, see Hillis and Caramazza 1991; Caramazza and Shelton 1998).

These lines of work have led a number of researchers to a domain-specific view of our understanding of tools (see Hirschfeld and Gelman 1994),[1] purporting that our understanding of tools consists of a set of dedicated psychological mechanisms that operate only for the domain of tools. Such mechanisms serve to highlight the perceptual inputs that are relevant for learning about tools (e.g., perceptual

L. R. Santos (✉)
Department of Psychology, Yale University,
Box 208205, New Haven, CT, USA
e-mail: laurie.santos@yale.edu
Tel.: +203-432-4524
Fax: +203-432-7172

H. M. Pearson
School of Veterinary Medicine, Tufts University,
North Grafton, MA, USA

G. M. Spaepen
Program in Human Development, University of Chicago,
Chicago, IL, USA

F. Tsao
Department of Psychology, Hillsdale College,
Hillsdale, MI, USA

M. D. Hauser
Department of Psychology, Harvard University,
Cambridge, MA, USA

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[1] Note that such a domain-specific account of human tool understanding stands in contrast to a *domain-general* view, one in which our understanding of tools emerges as a result of our more general knowledge of physics, objects motion, and causality (see Mandler 2002 for such an account).

information about a tool's form, intended design, etc.) and, therefore, constrain how we learn about this class of objects over development. Domain-specific mechanisms are often considered evolved specializations, selected over human phylogenetic history to solve specific computational problems that were faced by our evolutionary ancestors (Cosmides and Tooby 1994); our domain-specific knowledge of tools, therefore, would likely have been shaped for the specific task of representing tools and tool-related conceptual problems.

Humans, of course, are not the only species that successfully solves tool-related problems. Like humans, a number of non-human animals can be considered *tool-users*—they frequently use tools in a variety of contexts. A tool, under our view, refers to any external object used by an animal as a means to achieve some functional end. Under this view, the majority of animals are *non-tool-users*—they rarely, if ever, exhibit spontaneous use of external objects in either naturally-living or captive settings. Interestingly, there is enormous variation in the degree to which different animals use tools. What gives rise to this variation in tool-use? How and why do species that regularly use tools differ from those that do not?

The domain-specific perspective posits that tool-using animals differ from non-tool-users at least in part because of differences in cognitive architecture. Specifically, tool-users may possess a suite of domain-specific cognitive specializations that non-tool-users lack. Like humans, tool-using animals may conceptualize tools in fundamentally different ways than their non-tool-using counterparts, with special mechanisms for recognizing the functionally-relevant features of a tool. As such, tool-using species should naturally perform better on tool-related cognitive tasks than species that do not naturally use tools. Unfortunately, although comparative psychologists have begun to unravel some of the cognitive prerequisites underlying tool-use in individual species, there have been relatively few cross-species comparisons among species that do or do not naturally use tools. Those studies that have been conducted tend to use different methods and focus on different conceptual problems. In the absence of such direct, and systematically controlled comparisons, it is not possible to determine which (if any) domain-specific cognitive capacities set tool-users apart from their non-tool-using relatives.

The present paper is an attempt to bridge this gap. Our aim was to test non-tool using species on the very conceptual problems that have previously been presented to tool-using species. To do so, we began with the most well-studied group of animals when it comes to tool-use—the primates— and chose two of the most well-studied tool-users in this order—chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Cebus apella*)—as a comparison point.[2] Both species are prolific tool users, although capuchin tool-use tends to be restricted to captive settings (Fragaszy et al. 2004, but see de Moura and Lee 2004). Both species use a variety of tools in a number of different situations, including obtaining out of reach food using sticks, sponging liquid with leaves, and cracking nuts with hammers (for reviews, see Tomasello and Call 1997; Tomasello and Visalberghi 1998; Whiten et al. 1999; Fragaszy et al. 2004).

Recent experimental work on capuchins and chimpanzees suggests that despite their natural propensities to use tools in the wild and in captivity, their comprehension of tools appears limited to perceptually-salient features as opposed to the often hidden causal-functional properties. Povinelli and his colleagues (reviewed in Povinelli 2000), for example, tested chimpanzees on a series of tool experiments each aimed at investigating a different functional problem. In one study, they trained chimpanzees to use one of two T-shaped pulling tools to obtain an out of reach food, building on prior approaches in human infants (Brown 1990) and cotton-top tamarins (Hauser 1997). During training, both tools were made out of rigid materials (PVC tubing and plywood), but once subjects mastered the pulling task, the top of one of the tools was changed. The new top was made of a flimsy material (rubber) and thus, when pulled, failed to bring the food within reach. Only one chimpanzee consistently chose the rigid-topped tool over the flimsy-topped tool. In another study, chimpanzees were given a choice of two rake-shaped pulling tools. When these tools were oriented with their tines upward and their bases placed flat on the tray (henceforth, tines up), they served as functional pulling tools; a flat base efficiently pulled the food within reach. However, when the rake was oriented with its tines facing downward, pieces of food readily slipped under the base of the tool and thus could not be retrieved. Povinelli and colleagues found that chimpanzees did not distinguish between these two orientations. Chimpanzees also failed to attend to the substrate on which pulling tools operated, ignoring the location of a vertical hole that could trap the food along its path.[3] Visalberghi and her colleagues have reported similar failures in capuchins. Although capuchins spontaneously use a stick to retrieve food placed inside a narrow transparent tube, their errors suggest little understanding of the physics involved in pushing the food out of the tube (Visalberghi and Trinca 1989). Moreover, like chimpanzees, capuchins fail to understand the relationship between a pushing tool and the substrate on which it travels (Visalberghi and Limongelli 1994). Taken together, these results suggest that despite their skillful use of tools in the wild, these two species do not understand the physics or functionality of tools.

The present studies were designed to explore whether the capacities and limitations seen in tool-using primates are also observed in primates that rarely spontaneously

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[2] Although we focus on primate tool-use, we fully acknowledge the exceptional tool-using capacities of other taxonomic groups, especially the corvids (Hunt 1996; Chappell and Kacelnik 2002, 2004; Weir et al. 2002; Hunt and Gray 2004a,b). We restrict our focus to primates for both evolutionarily-motivated theoretical reasons, as well as methodological questions of motoric capacities.

[3] Recent findings with a different group of chimpanzees (Furlong et al. 2004) suggests that the Povinelli (2000) results may not generalize to all chimpanzees. Boysen and colleagues' chimpanzee subjects succeeded in many of the conditions in which Povinelli's chimpanzees fail.

use tools. Although most of the work on primate tool-use, naturally, focuses on species that typically use tools, there is a growing body of work examining what primates that do not use tools understand about tool-related problems (e.g., lemurs, *Eulemur fulvus* and *Lemur catta*: Santos et al. 2005; cotton-top tamarins, *Saguinus oedipus*: Hauser 1997; Hauser et al. 2002a, b; Spaulding and Hauser 2005; Santos et al. 2005; marmosets, *Callithrix jaccus*: Spaulding and Hauser 2005). Hauser and colleagues (Hauser 1997; Hauser et al. 1999; 2002a, b), for example, have conducted a series of tool use experiments on cotton-top tamarins—a species that has never been observed spontaneously using tools in either captivity or in the wild. Because tamarins have relatively poor dexterity, each task was designed to minimize the confound of motor control. In the first experiment (Hauser 1997), an experimenter presented tamarins with a choice of two canes, each of which was positioned near a small food reward. Only one of the canes had the food inside its hook and thus, was effective in retrieving the food with a straight pull. Once subjects began reliably choosing the correct cane, the experimenter presented subjects with a set of new canes, each of which differed from the original across one dimension. Subjects were presented with a choice between a newly shaped (e.g., an L-shape) and a newly textured (e.g., small bumps across the front) cane, as well as a choice between a newly colored (e.g., pink) and a newly sized (e.g., wide) cane. Subjects reliably preferred newly colored and textured canes over newly shaped and sized canes, suggesting that both adult and infant tamarins regard changes of a tool's shape and size to be more important to its function than changes of its color or texture. Once subjects had completed the single feature change trials, they were presented with canes that differed from the original blue cane on many dimensions (e.g., shape, color, texture, orientation). These novel canes were pitted against the original canes positioned in incorrect orientations. Results showed that subjects spontaneously chose the novel but correctly oriented tool over the old yet ineffectively oriented tool. These results suggest that tamarins understand the properties that are relevant to a functional pulling tool and will choose canes with those properties that are relevant to the pulling task over those that are familiar but ineffective. Similar results have now been obtained with other non-tool-using primate species as well (Spaulding and Hauser 2005; Santos et al. 2005).

Although the available data on non-tool-users suggests that at least some species recognize some of the important aspects of tools, these data are unfortunately silent with respect to how these non-tool-users' understanding of tools compares to that of primate tool-users—in particular, chimpanzees. To date, researchers working with these different species have explored slightly different conceptual problems and have used different methodologies. For these reasons, we cannot yet directly compare the tool understanding of a non-tool-using species like tamarins to that of naturally tool-using species.

Here, we test tamarins on a series of conceptual problems previously presented to chimpanzees (and also capuchins) (see Table 1) using a task that was adequate for a non-tool-user's level of dexterity. As in our prior work, our interest here is in tool competence, and specifically, the capacity to discriminate among tools based on functionally-relevant properties. We, therefore, use the expression *tool use* in a somewhat more expansive sense than is traditional, focusing on subject's comprehension of the problems as opposed to their ability to create or effectively manipulate tools. We also wanted to extend our previous work on tamarins to another non-tool-using species, the vervet monkey (*Cercopithecus aethiops*). Although much is known about vervet cognition and communication in general (see Cheney and Seyfarth 1990), very little work has examined tool-use in this or other Old World species. Additionally, as is the case with tamarins, the evidence for spontaneous tool use in either captive or wild vervets is quite slim, with only one reported example (Hauser 1988).

Experiment 1: Training condition

All experiments were carried out between September 2000 and May 2001. We began by training subjects on the means-end problem used by Hauser (1997). Subjects were required to pull canes to access a food reward. As in the original training condition, subjects had to choose between two canes that differed in their position relative to the reward. Subjects completed training after two sessions in which they reliably chose the cane with the reward positioned inside the hook.

Table 1 A synopsis of the conceptual questions examined in each experiment, including the experiment number, the conceptual question explored, the species previously tested, the researcher previously testing this concept, and whether or not the species in question understood the problem

Expt	Concept	Species	Researcher	Understanding?
2	Relationship between tool rigidity and function	Chimpanzee	Povinelli (2000)	No
3	Relationship between trajectory and substrate on which tool moves	Capuchin	Visalberghi and Limongelli (1994)	No
		Chimpanzee	Povinelli (2000)	No
			Limongelli et al. (1995)	Yes?
4	Relationship between tool orientation and position of food reward	Chimpanzee	Nagell et al. (1993)	No?
			Povinelli (2000)	No
5	Tool connection	Chimpanzee	Povinelli (2000)	Yes

Table 2 Characteristics of the cotton-top tamarins participating in these experiments, including experience on tool-use experiments

Family	Subject	Sex	Age	Experience
Group I	UB	F	Adult	Y
Group II	ID	M	Adult	N
Group II	EM	F	Adult	Y
Group II	PB	M	Juvenile	N
Group II	KW	F	Juvenile	N
Group III	SP	M	Adult	Y
Group III	EN	F	Adult	N
Group IV	AC[a]	M	Adult	N
Group V	SH	F	Adult	Y
Group V	RW	F	Adult	Y

[a] Individual AC was excluded from the experiment after Experiment 5 due to a birth in his family

Methods

Subjects and materials

The cotton-top tamarin is an arboreal New World primate. Tamarins eat a variety of high-quality foods, including insects, fruit, and tree exudate (Garber 1993). Neither wild nor captive tamarins have been observed spontaneously making or using tools.

We tested 14 tamarins. Four of these subjects began the training but were excluded due to pregnancy (JG), sickness (ES), or disinterest (DD, RJ). The individual characteristics of the 10 tamarins that completed the experiments are summarized in Table 2 (for a more complete experimental history of these individuals, see Hauser et al. 2002b). All 10 were born in captivity. Subjects' weights are kept at a level which is 5% below normal ad libitum feeding weights. These reduced weights are slightly higher than those observed in the wild (Garber 1993). All individuals live in social groups consisting of a breeding pair and often, their offspring; each group lives in a stainless steel cage (1.21 m × 1.21 m × 1.83 m) equipped with natural tree branches, ropes, and wooden nest boxes.

Subjects participate in various non-invasive behavioral experiments during the day; as such, none of the animals are experimentally naive. Prior to the present studies, however, only half of the subjects had ever been tested on experiments involving tool-manipulation; some participated in a series of experiments involving cane pulling (EM, SP, & UB: see Hauser 1997) while others participated in experiments involving continuous and discontinuous cloths (SP & UB: Hauser et al. 1999; SH & RW: Hauser et al. 2002b).

Each subject received one testing session per day. During testing, experimenters moved subjects from their home-room to the testing room in transport boxes (50 cm × 50 cm × 50 cm) which were equipped with a front side that the experimenter could raise or lower to allow the subject to enter or exit the box. During testing, individuals were placed into a Plexiglas box (approximately 45 cm × 40 cm × 60 cm, see Fig. 1A–B). Subjects sat inside the transparent triangular enclosure and were able to reach out of the front panel through one of two holes (4 cm × 6 cm). We presented subjects with a choice of two tools (14 cm blue Sculpey clay canes) placed on a tray (18 cm × 45 cm) divided into two equal halves by a partition (3 cm high). Tools were placed on either side of the partition setting up a forced choice situation. The tray was presented to subjects on a two-tiered wooden stand (30 cm high).

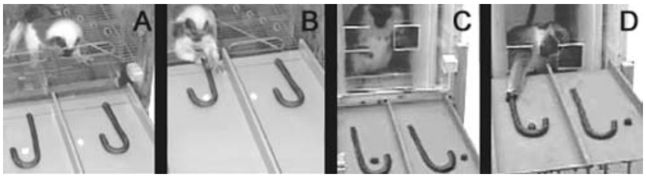

Fig. 1 The experimental set-up for tamarins (**A–B**) and vervets (**C–D**). First subjects see the two configurations when the tools are presented at the lower level (**A** and **C**). Once the tray is moved to the upper level, the subject then reaches out of one of the two openings and chooses a tool (**B** and **D**)

We also tested five vervet monkeys. Vervet monkeys are an average sized (approximately 5.5 kg) terrestrial Old World monkey species. Like tamarins, vervets do not typically use tools; there are no reports of tool use in captivity or in any of the well-studied wild populations with one exception. Hauser (1988) reported an unusual case of a female vervet monkey using a dry Acacia pod as a sponge to extract exudate from a tree; soon after her implementation of this tool, other individuals in the group did the same.

At testing, the vervet colony consisted of six adults (4–5 years) and five infants between the ages of 5–16 months. All individuals were born in captivity. Individuals were group-housed in a single large cage, filled with wooden branches and seats, swinging ropes, and live vegetation. We conducted these experiments on five of the adults, one male and four females (see Table 3). All subjects participated in non-invasive behavioral experiments during the day; these experiments involved passive listening to playbacks of species-typical vocalizations and human speech (Gil da Costa and Hauser, unpublished data; Tincoff et al. unpublished data). All five subjects were experimentally naive with respect to object manipulation and tools.

As with the tamarins, vervets moved voluntarily into a testing box from a transport cage (3.96 m × 4.27 m × 4.88 m). The test box (see Fig. 1C–D) was made of wood and Plexiglas. The transparent front wall of the testing box was equipped with small rectangular holes through which subjects could gain access to food. To prevent subjects from reaching through before presentation, we equipped the test

Table 3 Characteristics of the vervet monkeys participating in these experiments

Subject ID	Age	Sex
LA	Adult	M
EF	Adult	F
SV	Adult	F
LH	Adult	F
BH	Adult	F

box with a moving Plexiglas screen connected to the front of the testing box. We presented tools (21 cm long blue Sculpey clay canes) on a tray (38 cm × 50 cm) divided into two equal halves by a partition (3.5 cm high). Tools were placed on either side of the partition setting up a forced choice situation. As with the tamarins, the tray was presented to subjects on a two-tiered wooden stand (60 cm high). Except for scale, the test apparatus and tools were identical for both species.

Procedure

The experimenter prepared each trial out of view of the subjects, placing each of the tool-reward configurations on the tray. The experimenter then placed the tray on the lower tier of the two-tired stand for 3 s, allowing the subject to carefully observe the two configurations at this level before it was allowed to make its choice. Once the subject had clearly seen both configurations, the experimenter removed the tray from the lower tier and slid it onto the upper tier. The subject was then allowed to reach through the opening in the test box and choose one of the two tools. Because the subject had to reach through one opening, it was able to make only one choice on each trial. We defined a choice as the first tool touched. Correct choices were those in which the reward was positioned inside the hook of the cane. After subjects made a correct choice, they were allowed to pull the tool, obtain the food, and eat it. After an incorrect choice, subjects were again allowed to pull the tool, but did not obtain the food since incorrect tools were, by definition, unable to deliver the food.

Results and discussion

We began by training subjects on Hauser 's (1997) training condition (Experiment 1). Subjects received 12 trials in a random order per session each with different configurations (see Fig. 2). In trials 1–6, the configuration on the left side of the tray was correct, while on trials 7–12, the configuration on the right side of the tray was correct. Subjects continued on this training condition until they attained an accuracy of 10/12 trials for two consecutive sessions. We then tested subjects in five additional experiments, each designed to test different aspects of their comprehension of tool function. In these experiments, we were unable to test for first trial effects due to counterbalancing the order in which each subject was presented with different tool contrasts. More specifically, each individual started a session encountering a different sequence of tool pairings and thus, their experience prior to any particular pairing was different from all other subjects. Unless otherwise stated, statistical significance was set at $\alpha = 0.05$, tests are two-tailed.

Design

All subjects learned the training task. Overall tamarins required more sessions to learn the task (Mean ± SE = 9.1 ± 2.0 sessions) than did vervets (Mean ± SE = 6.0 ± 0.84 sessions), but this difference was not statistically significant ($F_{(1,\,13)} = 1.17$, $p = 0.30$). To examine the effect of experience, we divided the tamarins into two groups: those with previous experience using tools, and those without such experience. Tamarins with experience using tools learned the task four times faster (Mean ± SE = 3.6 ± 0.87 sessions) than those without experience (Mean ± SE = 14.6 ± 1.1 sessions, $F_{(1,8)} = 59.9$, $p < 0.0001$). Tool-experienced tamarins, however, learned the task at the same rate as the tool-inexperienced vervets (see Fig. 3).

These results allow us to draw three conclusions. First, both species readily learned to use a pulling tool to obtain food. Second, experience appeared to play some role among cotton-top tamarins, at least with respect to reaching criterion on this first condition. Third, although the vervets had never been tested in any experiments involving object manipulation, they performed as well as tool-experienced tamarins. This also suggests that although experience can facilitate learning the task in some individuals, success in this task does not require skills in using tools.

Having trained both species on a simple pulling tool, we next turn to the main conceptual aims of our study. Each of the following four experiments investigates a single conceptual problem (see Table 1). In each experiment, we presented subjects with only two test sessions, designed to uncover the limitations on tool comprehension in tamarins and vervets in the absence of significant, targeted training.

Experiment 2: Test of tool rigidity

Experiment 2 examined whether or not subjects take into account the material of a potential tool. Previous findings

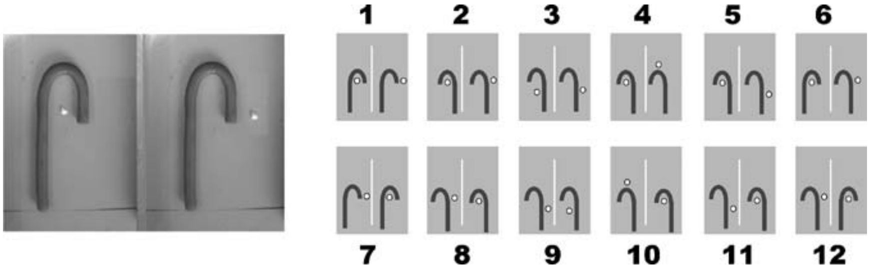

Fig. 2 The conditions of Experiment 1. The tray is indicated by the light gray rectangle, the partition by the thin white line in the middle

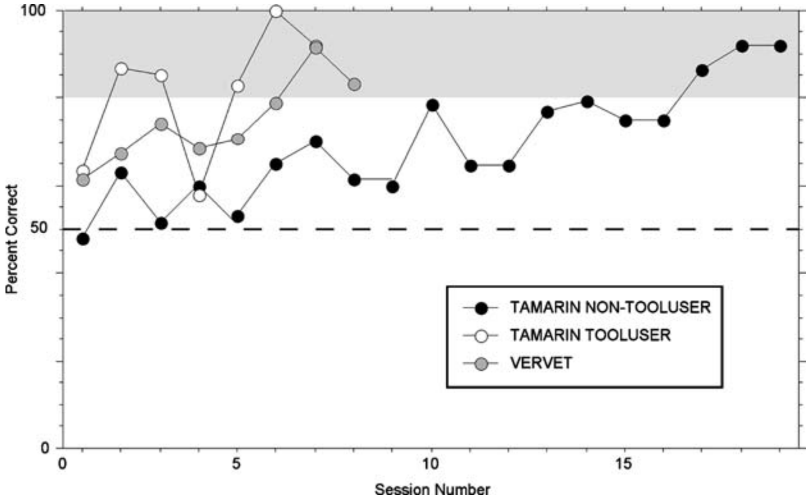

Fig. 3 Results of Experiment 1. Performance is plotted across sessions (shown as percent correct). Subjects were divided into three groups: non-tool-using tamarins, tool-using tamarins, and vervets

with tamarins suggest that infant and adult tamarins attend to some properties (shape and size), recognizing their importance in tool use; other features (color and texture) are attended to, but recognized for their functional irrelevance (Hauser 1997; Hauser et al. 1999, 2002a). Here we extend this line of reasoning to explore another featural dimension: material. A tool's material is often directly relevant to its function (probing, cracking, scratching). In the case of the pulling task presented here, the material making up the hook of a cane tool must be rigid enough to catch the food when pulled. Thus, canes made of flimsy materials will be ineffective regardless of their shape and size. Here, we examined whether tamarins and vervets recognize that a pulling tool must be rigid enough to move the food reward, a factor that chimpanzees apparently do not take into account when choosing between two pulling tools (Povinelli 2000). Although the chimpanzees' prior failure might warrant abandoning the experiment on tamarins and vervets from the start, we decided to pursue this property further for two reasons. First, Povinelli′s choice of material may have made the task particularly hard, but not for conceptual reasons. Specifically, it is possible that the chimpanzees could not discriminate, visually, the difference between flimsy rubber and plywood. In the following experiments, we used materials that, at least to the human eye, appeared strikingly different. Second, it is possible that a prior history with tools had some effect on the chimpanzees' performance; in the present case, we used naïve animals with no prior history.

We presented subjects with novel tools that differed from the original blue canes across two dimensions: color (pink instead of blue) and material (flimsy yarn instead of hardened clay). We predicted that if tamarins and vervets recognize the significance of material to a tool's function, they should disregard changes in color (see Hauser 1997; Hauser et al. 2002a) but attend to changes in material. As such, we predicted that they would reject canes made of novel flimsy materials yet readily chose rigid canes with novel colors.

Methods

Procedure

We presented subjects with tools of two colors (blue and pink) and materials (canes and ropes). As in Experiment 1, canes were made of Sculpey clay molded and then hardened into the size and shape described in the Training condition. Ropes were made of thick yarn that was knotted at each end to ensure against fraying. The yarn was chosen to be the same color and diameter as the original training canes such that the only obvious dimension differing between the two materials was rigidity.

Conditions

Each subject received two sessions of the trials outlined in Fig. 4A presented in a random order. As in the training condition, each trial was repeated twice in a single session counterbalancing across sides. As such, each subject received a total of 24 trials (4 of each pairing). As Figure 4A illustrates, these trials used all combinations of the blue/pink and rope/cane tools. For some of the combinations, both options would lead to successful retrieval of the marshmallow (e.g., 3). For others, only one of the two options would be effective (e.g., 1), while for one trial, neither of the two options would be effective (i.e., 5). To reduce the possibility of side biases, we ran subjects on one session of the training condition (see Fig. 2) in between all test sessions. Subjects that failed to reach criterion on these training sessions continued training until reaching criterion and were then returned to testing.

Results and discussion

We performed a repeated measures ANOVA with species as a between subject measure and color and material as within subjects measure (see Fig. 4B–C). There was no

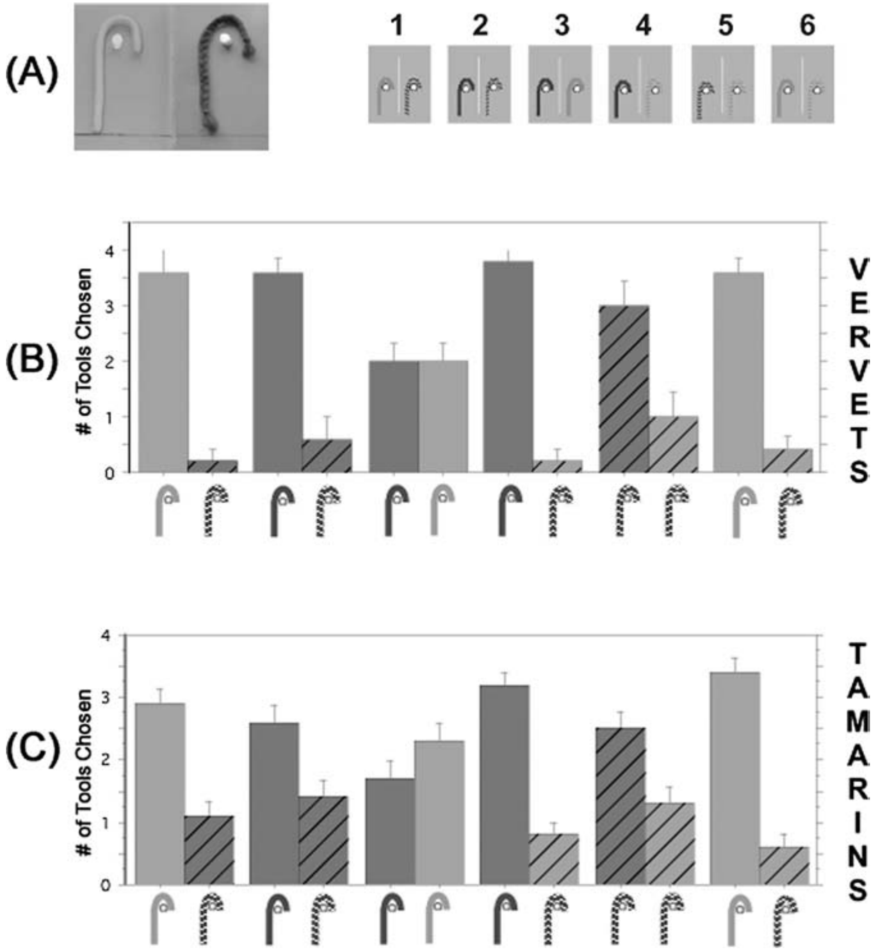

Fig. 4 **A** The conditions of Experiment 2. Pink tools are indicated by gray color, blue tools are indicated by black color. Tools made of flimsy rope material are indicated by dashed lines, tools made of rigid clay are indicated by continuous lines. **B** Vervet performance on Experiment 2 across conditions. Bar color indicates the color of the tool, while lines indicate rope tools. **C** Tamarin performance on Experiment 2 across conditions

overall effect of color ($F_{(1,13)} = 3.04$, $p = 0.10$). Although subjects had a slight preference for the blue tools over the pink tools, this preference was not statistically significant. There was also a main effect of material ($F_{(1,13)} = 133.71$, $p = 0.0001$). Subjects reliably preferred canes over ropes. There was also an interaction between tool material and species ($F_{(1,13)} = 6.60$, $p = 0.02$). Compared with the tamarins, vervets showed a stronger preference for the cane. In addition, there was an interaction between color and material ($F_{(1,\ 13)} = 15.72$, $p = 0.002$). Although subjects chose blue and pink canes equally, subjects reliably chose blue ropes over pink ropes. All other main effects and interactions were not significant.

We performed six repeated measures ANOVA on each of the tool type pairs. As such, we Bonferroni adjusted the alpha level to 0.008. In the first pairing, there was a main effect of tool type ($F_{(1,13)} = 43.72$, $p = 0.0001$). Subjects reliably preferred the pink cane over the blue rope. There was no effect of species ($F_{(1,13)} = 4.139$, $p = 0.06$). In the second pairing, there was a main effect of tool type ($F_{(1,13)} = 22.75$, $p = 0.0004$). Subjects reliably pulled the blue cane over the blue rope. There was no effect of species ($F_{(1,13)} = 4.179$, $p = 0.06$). In the third pairing, there was no main effect of tool type ($F_{(1,13)} = 0.39$, $p = 0.55$). Subjects pulled blue and red canes equally. There was also no effect of species ($F_{(1,13)} = 0.39$, $p = 0.55$). There was a main effect of tool type in the fourth pairing ($F_{(1,13)} = 88.64$, $p = 0.0001$). Subjects reliably pulled the blue cane over the pink rope. There was no effect of species ($F_{(1,13)} = 3.55$, $p = 0.08$). In the fifth pairing, there was a main effect of tool type ($F_{(1,13)} = 11.21$, $p = 0.005$). Subjects reliably pulled the blue rope over the pink rope. There was no interaction between tool type and species ($F_{(1,13)} = 0.70$, $p = 0.42$). In the sixth pairing, there was a main effect of tool type ($F_{(1,13)} = 69.64$, $p = 0.0001$). Subjects reliably preferred the pink cane over the pink rope. There was no interaction between tool type preference and species ($F_{(1,13)} = 0.31$, $p = 0.59$).

The results of Experiment 2 allow us to draw two conclusions. First, subjects trained to pull a blue cane are as likely to pull a pink cane as they are a blue one. In other words, subjects do not seem to take into account color when choosing an effective tool. Paralleling previous experiments (Hauser 1997; Hauser et al. 1999), these results suggest that tamarins recognize the distinction between functionally relevant and irrelevant features of tools; specifically, they understand that color plays no role in a tool's effectiveness. Our results also suggest that vervet monkeys, another non-tool-using species, also recognize that color is not causally relevant to pulling tools.

Second, although subjects showed no preference for cane color, they showed a striking preference for cane material. Both vervets and tamarins chose rigid canes over non-rigid canes without training. These results suggest that both species spontaneously recognize that an object's material affects its function. They further recognize that pulling tools must be made of a rigid material in order to function properly. These results stand in contrast to similar experiments with chimpanzees, who appear not to take into account a pulling tool's rigidity even after training (Povinelli 2000). In addition to the issues raised above, a further difference between these two studies, to which we return in greater detail in the General Discussion, is that the first experiment with tamarins and vervets started out with a tool consisting of rigid materials; this may have simply led to an obvious generalization in the subsequent condition. We next turn to an investigation of the relationship between a tool and the properties of the surface on which it travels.

Experiment 3: Understanding the importance of trajectory and substrate

In this experiment, we examined whether or not subjects take into account the relationship between a tool's trajectory and the substrate on which it travels. This experiment was designed as a modified version of the task used by Povinelli (2000) with chimpanzees. In Experiment 3, we presented subjects with the original blue canes placed on a modified tray that allowed the experimenter to insert and remove different surfaces. One of the surfaces was equipped with a rectangular trap. We reasoned that if subjects understand that pulling tools only function to bring food forward on smooth, continuous surfaces, then they should avoid situations in which the tool effectively pulls the reward into an inaccessible trap on the tray.

Methods

Procedure

We presented subjects with conditions in which their original blue canes moved along a modified tray. The modified tray consisted of two different foamcore surfaces (see Fig. 5A). The first surface, which we called the trap, (Fig. 5A right side) had a rectangular white hole (10 cm × 3 cm, 1.5 cm deep) positioned about 9 cm from the far end of the tray. The other surface, which we called the no-trap, had a flat white rectangle (made with white masking tape)

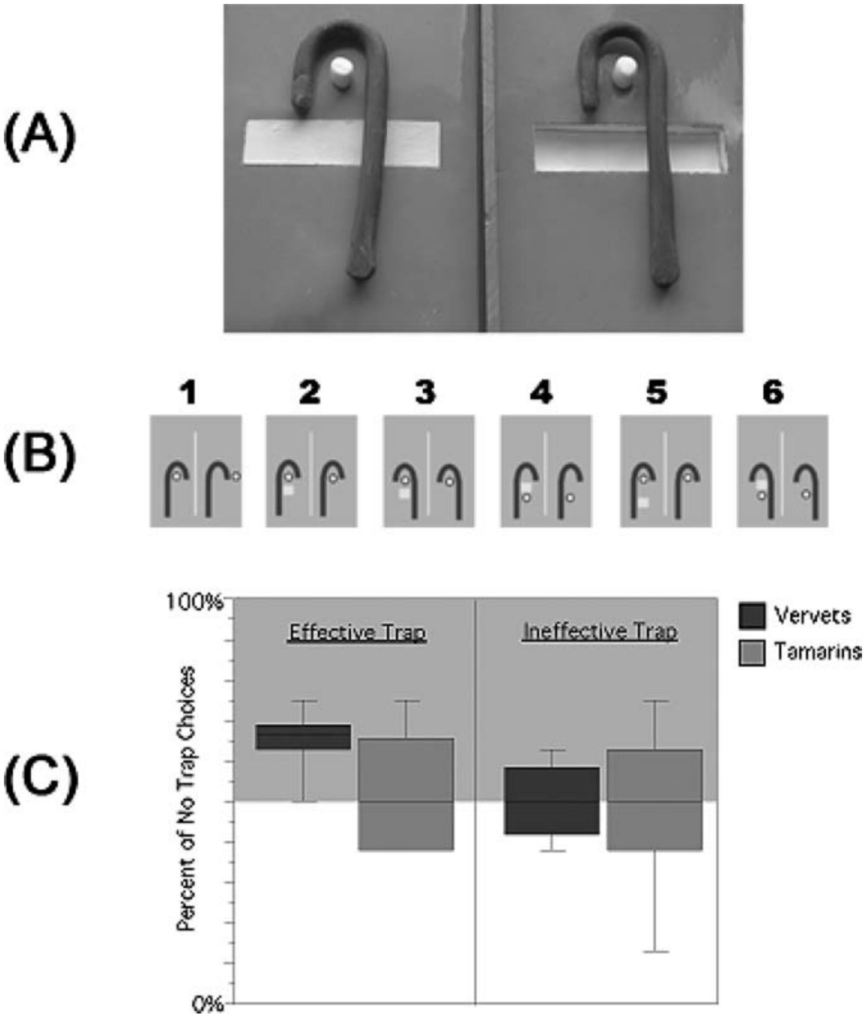

Fig. 5 **A** A photograph of the trap tray. **B** The conditions of Experiment 3. The position of the trap is indicated by a white rectangle on the tray. **C** Performance on Experiment 3. The graph depicts the percent of no-trap responses as function of trap position (effective and ineffective) and species

positioned 9 cm from the end of the surface. This white rectangle was perceptually similar to the trap, but not an actual hole. The dimensions of this white rectangle matched those of the trap.

Conditions

We tested subjects on the conditions outlined in Fig. 5B. Specifically, subjects were tested on 12 different test configurations, consisting of six different trial types and their mirror images. The first of these six trial types was from the original training condition, a condition we included to ensure that subjects were motivated and attentive. The other five trial types all incorporated the trap and no-trap surfaces. In three of these trial types (2, 3, and 5) the trap was positioned in such a way that pulling the cane caused the food reward to land inside the trap, out of the subjects' reach. In these trials, we predicted that subjects should selectively pull the cane on the no-trap surface over the cane on the trap surface. The final two trials (4 and 6) incorporated the trap and no-trap surfaces, but in these trials the trap was positioned in such a way that it would not impede the movement of the reward (i.e., it was placed in the opposite orientation and thus higher than the position of the food reward). In these trials, we predicted that subjects should randomly choose between the canes on the trap and no-trap surfaces. Again, subjects received two test sessions interspersed with testing on the original training condition.

Results and discussion

Figure 5C presents the results of Experiment 3. We performed one sample *t*-test on the trials in which the positioning of trap was functionally relevant (2, 3, and 5). Vervet monkeys performed reliably above chance, choosing the tool positioned over the no-trap surface (Mean = 65% of pulls, $t_{(4)} = 3.67$, $p = 0.02$). Tamarins, however, showed no systematic discrimination; tamarins chose the tool positioned over the trap surface just as often as they chose the tool positioned over the no-trap surface (Mean = 49% of pulls, $t_{(9)} = 0.26$, $p = 0.80$). For trials in which the trap's position was functionally irrelevant (4, and 6), both groups showed no difference from chance (Vervet: Mean = 52% of pulls, $t_{(4)} = 0.34$, $p = 0.75$; tamarins, Mean = 46% of pulls, $t_{(9)} = 0.52$, $p = 0.62$). We next carried out individual analyses across conditions. To do this, we Bonferroni adjusted the alpha level to 0.01. There was no overall difference in any of the conditions (all p-values > 0.01) or any of the interactions between condition and species (all p-values > 0.01).

The results of Experiment 3 suggest that tamarins, like capuchins and chimpanzees, do not spontaneously attend to the substrate over which a tool travels. Specifically, they do not seem to take into account whether or not a hole interrupts the trajectory of the pulled marshmallow. Vervet monkeys, however, do seem to take this factor into account. As a group, vervets reliably avoided the tool on the trap surface in only those trials in which the trap impeded the trajectory of the reward. Although vervets were significantly above chance on this task, they nonetheless failed on a relatively high proportion (35%) of trials, a rate similar to that of Povinelli's chimpanzees.

Experiment 4: The importance of a tool's 3D orientation

Next, we investigated whether subjects take into account the three-dimensional relationship between a pulling tool and the food. We presented subjects with a modified version of Povinelli′s (2000) rake task (see Nagell et al. 1993). In this task, subjects were presented with a choice of two rake tools, one with the tines facing up, the other with the tines facing down. If subjects understand that the orientation of the rake matters, then they should selectively pull the rake with tines facing up because this rake will yield more food.

Methods

Procedure

Subjects were presented with yellow rake tools (see Fig. 6A) made of Sculpey clay (tamarin rakes: 14 cm × 11 cm; vervet rakes: 21 cm × 16 cm). Each rake had four tines (tamarin rakes: 3 cm high, vervet rakes: 5 cm high) molded into the size and shape described in the Training condition. Rakes positioned in the tines up configuration were effective in pulling the food reward, as the base was flat against the tray. Rakes positioned in the tines down configuration, however, were less effective at pulling the food since the space between the base and the surface of the tray allowed food to slip through. Because we wanted to be sure the food reward would not be caught in the tines down condition, we switched the tamarin food reward from marshmallows to fruity pebbles cereal, a flatter food reward that would pass in between the tines. For vervets, we switched to four small grape pieces (each 1/4 of a grape), again, smaller portions that would not get caught in the tines down condition.

Conditions

We presented subjects with the conditions outlined in Fig. 6A. Again, subjects received six different trials and their mirror images. In the first of the six, subjects were presented with a trial from the original training condition, a condition we used to be sure subjects were performing at a normal level of motivation. The second trial type was used to be sure that subjects would use their old canes similarly with the five fruity pebbles as a reward. The other four trial types all incorporated the new rake tools. Trials 3–5 all pitted the tines-up rake configuration versus the tines-down configuration. The final trial examined whether subjects would chose a tines-up functional rake tool over their previously functional blue cane in an ineffective orientation.

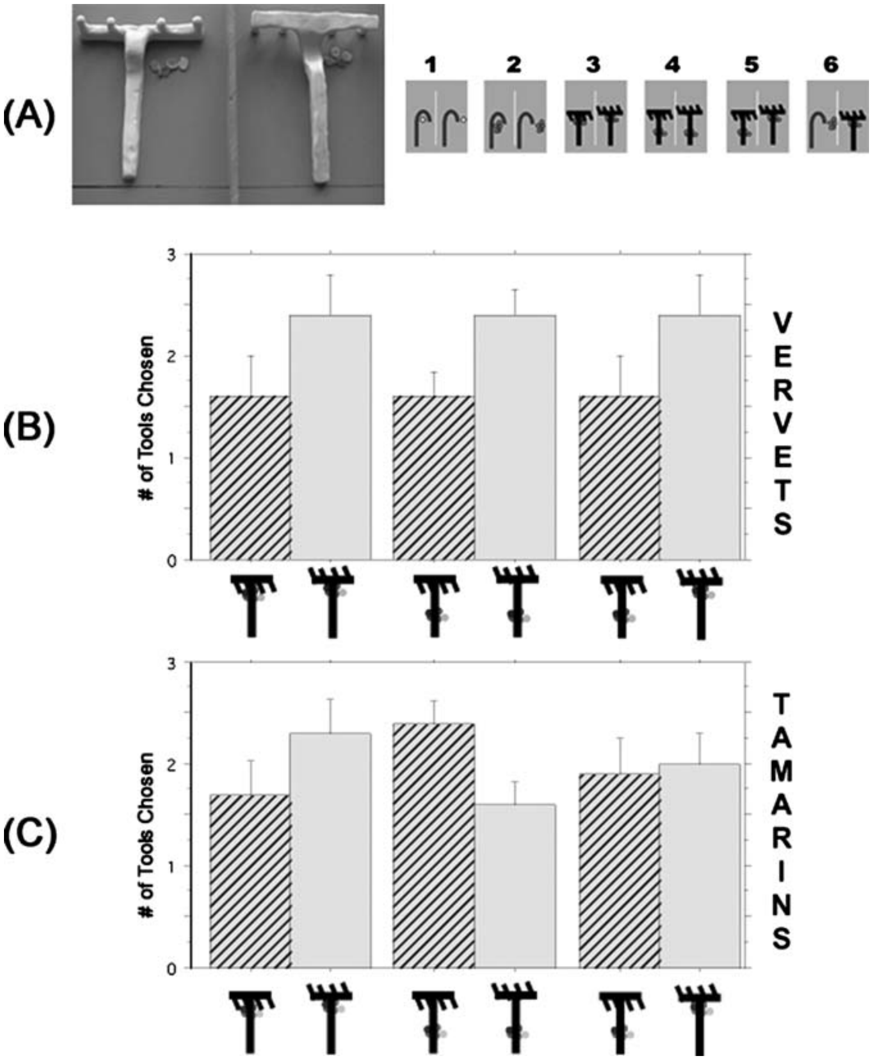

Fig. 6 **A** The conditions of Experiment 4. Small colored circles indicate fruity pebble treats. The rake tools are pictured in black. Tines up conditions are those in which the tines are oriented up and to the left. Tines down conditions are those in which the tines are oriented down and to the right. **B** Vervet performance on Experiment 4 across conditions. Diagonal bars refer to incorrect choices. **C** Tamarin performance on Experiment 4 across conditions

Results and discussion

Subjects performed well-above chance on the two cane conditions used to test motivation; tamarins performed above criterion (Mean = 84% $t_{(9)} = 7.36$, $p < 0.0001$) and vervets got all trials correct (Mean = 100%). We performed a repeated measures ANOVA with rake orientation (tines-down or tines-up) as a within subjects variable and species (tamarin or vervet) as a between subjects variable (see Fig. 6B–C). We found no effect of rake orientation ($F_{(1,13)} = 2.79, p = 0.12$). We performed *t*-tests to examine individual species effects. Vervet monkeys reliably chose the functional tines-up option more often than the ineffective tines-down option (Mean = 60% of trials, $t_{(4)} = 3.21$, $p = 0.03$). Four of the five vervets showed this preference, but the result was not significant with non-parametric analyses (Fisher's Exact Probability Test: $p = 0.19$). Tamarins, in contrast, showed no preference (Mean = 52% of trials, $t_{(9)} = 0.361$, $p = 0.73$). There was no interaction between species and rake orientation ($F_{(1,13)} = 1.43, p = 0.25$). Subjects did, however, perform well on the final test condition, pitting an ineffective blue cane which subjects had been trained on against an effective rake (Mean = 73% correct trials, $t_{(15)} = 3.98$, $p = 0.001$). Both species showed this pattern reliably (Vervets: Mean = 70% of trials, $t_{(4)} = 4.00$, $p = 0.02$; Tamarins: Mean = 74% of trials, $t_{(9)} = 2.88$, $p = 0.02$).

Again, tamarins do not spontaneously take into account a tool's three-dimensional orientation when choosing between two possible tools. Tamarins make no clear distinction between rakes that are positioned in a more functional, tines-up orientation and those that are positioned in a less functional, tines-down orientation. Vervet monkeys, on the other hand, seem to be more sensitive to the rake's three-dimensional orientation. Vervet monkeys tend to chose tines-up over tines down rakes, suggesting that they may recognize the functional relevance of orientation. However, it is important to note that although vervet monkeys performed above chance, they chose the more effective tool on only 60% of the trials, about at the level of chimpanzees tested previously.

Experiment 5: Broken canes

In this experiment, we investigated whether or not subjects take into account the intactness of a pulling tool when choosing between two potential tools. In particular, we presented subjects with broken versions of their original blue tool. If vervets and tamarins, like chimpanzees, understand that pulling tools must be intact, then they should selectively choose intact tools over broken ones. In addition, subjects should further distinguish between tools broken at functionally relevant points as opposed to functionally irrelevant points (e.g., for the blue cane, a small break at the base of the stem is functionally less significant than a break between the stem and the hook).

Methods

Procedure

Subjects were presented with intact and broken versions of the original blue canes. We used three types of broken canes (see Fig. 7A). One type of broken cane was broken at the base, 2 cm from the bottom of the cane (with a 1 cm gap); this is an irrelevant break because subjects can reach the longer piece above the smaller, but closer one, and nonetheless retrieve the food. The second type was broken in the middle of the hook, 2 cm from the end of the hook (1 cm gap); the far piece was out of reach and the near piece was ineffective in pulling the food closer, at least with a straight pull. The third type of broken tool was broken in the middle of the stem, 8 cm from the bottom of the cane (1 cm gap); pulling the stem failed to bring the food near, while the far piece was out of reach.

Conditions

We presented subjects with the conditions outlined in Fig. 7A. Again, subjects received six different trials and their mirror images. In the first trial, we presented subjects with a trial from the original training condition, a condition we used to be sure subjects were performing at a normal level of motivation. In trials 2–4, subjects were given a choice between one type of broken cane and an intact cane. In trials 5 and 6, subjects were given a choice between two broken canes.

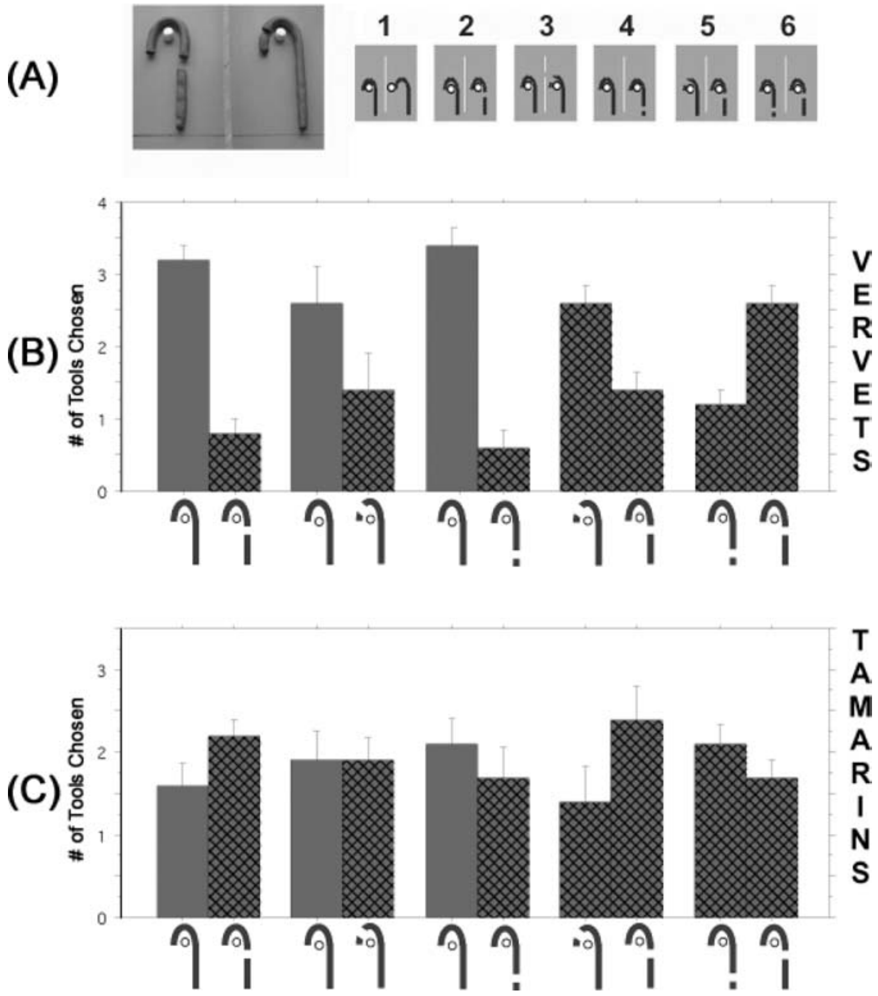

Fig. 7 **A** The conditions of Experiment 5. Broken canes are indicated by gray breaks in the cane. **B** Vervet performance on Experiment 5 across conditions. Crossed bars indicate broken tools. **C** Tamarin performance on Experiment 5 across conditions

Results and discussion

All subjects performed well on the first motivational cane tool condition (Vervets: Mean= 85% of trials, $t_{(4)} = 3.50$, $p = 0.02$; Tamarins: Mean = 75% of trials, $t_{(9)} = 3.35$, $p = 0.008$). We then examined subjects' overall performance on trials 2–4 in which intact canes were paired with broken canes (see Fig. 7B–C). There was a significant species effect ($F_{(1,13)} = 15.96$, $p = 0.0015$). Vervets chose the intact cane reliably more often (Mean ± SE = 78 ± 4% of trials) than tamarins (Mean ± SE = 47 ± 5% of trials). Vervets' choice of the intact cane differed from chance ($t_{(4)} = 8.63$, $p = 0.001$), while tamarins chose at random ($t_{(9)} = 1.15$, $p = 0.28$).

Given these overall effects, we next explored subjects' trial by trial performance. Our Bonferroni adjusted alpha level was $\alpha = 0.01$. In condition 2, there was no preference for the intact over the broken cane ($F_{(1,13)} = 7.16$, $p = 0.02$). There was an interaction between cane preference and species ($F_{(1,13)} = 19.90$, $p = 0.0006$). Vervet monkeys preferred the intact cane while tamarins showed no preference. There was no preference for the broken cane in condition 3 ($F_{(1,13)} = 1.18$, $p = 0.30$), and no species difference ($F_{(1,13)} = 1.18$, $p = 0.30$). In condition 4, there was a preference for the intact cane over the broken cane ($F_{(1,13)} = 10.27$, $p = 0.007$) but no significant species difference ($F_{(1,13)} = 5.78$, $p = 0.03$). There was no significant preference across condition 5 ($F_{(1,13)} = 0.28$, $p = 0.87$). There was also no interaction between species and tool-type ($F_{(1,13)} = 3.34$, $p = 0.09$). In condition 6, there was no overall cane preference ($F_{(1,13)} = 2.46$, $p = 0.14$). There was a significant interaction between species ($F_{(1,13)} = 7.98$, $p = 0.01$). Vervet monkeys showed a preference for the cane that was broken in the middle while tamarins showed no preference.

This pattern of results suggests that vervet monkeys, but not tamarins, tend to choose an intact tool over a broken tool without training. Like chimpanzees, vervets seem to recognize that the bottom of a pulling tool must be continuous with its base in order for it to function properly. Note however, that when two broken were pitted against each other, vervets did not always chose the most functional of the two broken tools; on condition 6, for example, vervets reliably chose the tool that was broken in the middle, which might be considered less functional than the one with a higher break. Taken together, vervets seem to recognize the difference between broken and unbroken tools, but may not reason sophisticatedly about which breakages are most detrimental to the function of these broken tools.

Tamarins, on the other hand, do not show a preference for unbroken tools. Without training, they make no distinction between broken and intact tools. These results stand in contrast to the results presented in Hauser et al. (1999), in which tamarins learned to attend to the connectedness of a pulling tool made of cloth. In this study, however, tamarins received many sessions of training on the broken cloth problem; in some cases, subjects required over 80 sessions to learn the distinction between an intact and broken cloth. Taken together, then, these results suggest that although tamarins can learn about the importance of a tool's intactness, they do not take this feature into account spontaneously.

Experiment 6: Final cumulative condition

In the final experiment, we presented subjects with a cumulative condition. In this condition, subjects were given trials from all of the previous experiments. This condition was used to ascertain whether subjects had developed learning set strategies within each experiment or whether they had acquired a more general level of comprehension of tool-related problems. We also tested subjects on novel combinations of the tools used in different experiments (e.g., rakes from Experiment 4 vs. ropes from Experiment 2), again to test for the generality of their comprehension.

Methods

Procedure

All subjects participated in Experiment 6 except one tamarin (AC). This subject could no longer be run due to a birth in his cage. Subjects were presented with a variety of tool problems involving traps, rakes, broken canes, and inefficient materials (see Fig. 8). The testing procedure was the same as in all previous experiments.

Conditions

We presented subjects with the conditions outlined in Fig. 8. The first three conditions presented subjects with tool combinations they had previously experienced in Experiments 2–5, and showed poor levels of performance. In the first condition, we presented subjects with a trial

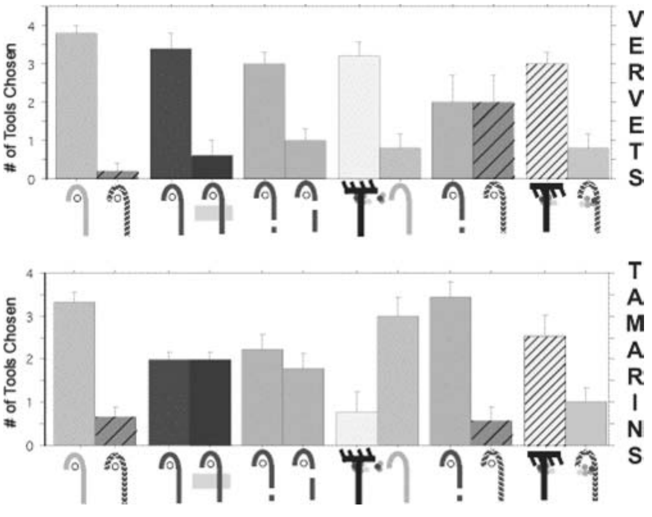

Fig. 8 Performance on Experiment 6 by condition and species. Bar color and pattern illustrates the different experimental conditions

from Experiment 2, the critical condition in which subjects had to choose between a tool with a new material and a tool with a new color. In condition 2, we presented subjects with a trap condition from Experiment 3. In condition 3, we presented subjects with a condition from the broken tools experiment in which subjects had to choose between two different broken canes, one of which was effective and one ineffective. In conditions 4–6, subjects were tested on combinations of tools from all the different experiments. These conditions allowed us to ask if subjects preferred some of the modified tools over others, and given the patterns, dissect the cause of such preferences.

Results and discussion

We first examined subjects' overall performance on all trials (see Fig. 8). There was a significant effect of species ($F_{(1,12)} = 5.90$, $p = 0.03$). Vervets chose the more efficient tool more often than did tamarins. Nonetheless, both species performed above chance (vervets: Mean = 77%, $t_{(4)} = 5.30$, $p = 0.006$; tamarins: Mean = 62%, $t_{(8)} = 2.86$, $p = 0.02$).

To explore trial-by-trial performance, we carried out six repeated measures ANOVAs on each of the tool type pairs and Bonferroni adjusted the alpha level to 0.008. In condition 1, there was a significant preference for the hard pink cane over the blue yarn ($F_{(1,12)} = 78.89$, $p < 0.0001$), but no interaction between cane preference and species ($F_{(1,12)} = 1.75$, $p = 0.21$). Both species correctly chose the tool with the new color over the tool with the new material. In condition 2, there was a significant preference for the no trap tool over the trap tool across both species ($F_{(1,12)} = 12.6$, $p = 0.003$) but this preference was due entirely to the vervets. Tamarins showed no discrimination between the trap and no trap options, while vervets reliably chose the tool associated with the continuous surface ($F_{(1,12)} = 12.6$, $p = 0.003$). In condition 3, there was no preference for the cane broken at the base over cane broken on the top ($F_{(1,12)} = 4.99$, $p = 0.05$) with no difference between the two species ($F_{(1,12)} = 2.02$, $p = 0.18$). There was no significant preference across condition four, ($F_{(1,12)} = 0.018$, $p = 0.89$). There was, however, a significant interaction between species and tool type ($F_{(1,12)} = 11.99$, $p = 0.005$). Vervet monkeys showed a preference for the rake tool, while tamarins showed a preference for the incorrectly oriented pink cane. In condition 5, there was no overall cane preference ($F_{(1,12)} = 4.42$, $p = 0.06$). Although tamarins performed better than vervets in this condition, there was no difference across species ($F_{(1,12)} = 4.42$, $p = 0.06$). In the last condition, there was an overall preference for the rake over the pink rope ($F_{(1,12)} = 11.10$, $p = 0.006$). Both species demonstrated this preference and thus there was no interaction between species ($F_{(1,\ 12)} = 0.33$, $p = 0.58$).

The results of this final experiment are important for a number of reasons. First both species showed nearly the same pattern of successes and failures as they had demonstrated in the previous experiments. Although it is possible that subjects learned these particular strategies during the course of their initial exposure to the new tools, the results of this final experiment suggest that subjects' performance was not due simply to learning particular exemplars within each experiment, or to developing a learning set strategy. Second, both species consistently performed well on the material change condition, choosing a cane of a new color over a cane of a new material. Third, as in previous experiments, vervet monkeys tended to outperform tamarins across many of the problems. Vervets performed consistently better at the trap condition than tamarins, suggesting again that they seem to take into account the substrate on which a tool operates. Lastly, vervets, but not tamarins, successfully used rake tools over other less functional cane-shaped tools. Interestingly, however, vervets did not show the same performance on the broken condition of this experiment (condition 3) as they had in Experiment 5 (condition 6); in this condition, they showed no reliable preference across the two tools as they had in Experiment 5. This result, the only inconsistency with previous conditions, suggests that vervets' comprehension of broken tools is fragile at best and not as stable across the conditions as their comprehension of other aspects of the problem.

General conclusions

We introduced these studies with the question of whether a non-tool-user's comprehension of how tools work differs from that of natural tool-users. To this end, we presented two non-tool-users—tamarins and vervets—with conceptual problems that had previously been explored with other exceptional tool users, especially chimpanzees. In our study, however, no training was involved except in the initial phase of the experiment; following the initial phase, we explored tool choice in the absence of reinforcing particular object choices. We found that both non-tool-using species consistently performed similarly to tool-users. Like chimpanzees, both tamarins and vervets performed poorly on the rake tool task. Tamarins chose at random between effectively and ineffectively oriented rakes. Vervet monkeys performed better than chance (around 60% of trials), but still chose the ineffective tool on a large percentage of trials. This level of performance is similar to that of chimpanzees on their first experiment with inverted rake tools (57.1% success overall, see Chapter 6, Povinelli 2000). Similarly, both species performed poorly on a condition in which a trap impedes the trajectory of a tool. Vervets chose the no-trap surface reliably more often than chance but they nonetheless failed to retrieve the food reward on a large percentage of trials (35%). Again, the vervets' performance is similar to that of tool-using species, with chimpanzees in Povinelli's (2000) experiment failing on 36.2% of trials (see also Visalberghi and Limongelli 1994 for similar failures in capuchins on a slightly different task).

There are two conditions, however, where our non-tool users differ slightly from their tool-using counterparts. The first of these is in the broken cane condition. Although vervet monkeys, like chimpanzees (see Povinelli 2000), successfully chose tools that were intact over those that were broken, tamarins failed to discriminate between broken and intact tools. This suggests that tamarins fail to detect a feature of a functional tool, its intactness, that tool-users like chimpanzees do. Nonetheless, it is important to note that even in the absence of added experience, vervet monkeys still performed at high rates (78%), comparable to those of chimpanzees on their first experiment with broken tools (78.6%, Povinelli 2000).

The other condition where tool-users perform differently from non-tool-users is in Experiment 1. Both vervet monkeys and tamarins reliably chose tools of new colors over tools of new materials, suggesting that they recognize the functional significance of material (particularly, hardness) in the effectiveness of a pulling tool. The results of Povinelli (2000) suggest that chimpanzees do not take this feature into account; they fail to discriminate between hard and flimsy pulling tools (succeeding on only 57.5% of trials, see Chapter 7). One way to account for this difference is to consider the role of particular material properties. Povinelli′s experiments used rubber as a flimsy material; the rubber used was very similar in size and texture to that of the hard material, plywood. In contrast, the flimsy material we used in our studies, yarn, was visually very different from clay, and perhaps easier to detect as a different and thus potentially ineffective material. It is possible that chimpanzees would succeed on a similar task if tested on the types of materials we used in our study. Conversely, it is possible that tamarins and vervets would fail with the flimsy rubber material.

These results may seem at odds with past studies of tool choice in tamarins. In most of these earlier studies (Hauser 1997; Hauser et al. 2002a, b; Spaulding and Hauser 2005), tamarins have demonstrated what seemed to be a rather sophisticated understanding of the relevant properties of tools (but see Santos et al. 2005, for more recent failures on more complex tool tasks). The results of the present experiments suggest that their comprehension is more limited than previously stated. More specifically, tamarins seem to recognize the functional relevance of many features—shape, size, and orientation— but seem not to use this information when solving some problems, such as determining a tool's correct three-dimensional orientation as in Experiment 4.

Taken together, the studies reported here suggest that at least one non-tool using species—the vervet monkey—performs a suite of tool choice tasks at the level of a natural tool-user—the chimpanzee. Vervets seem to share both the abilities and the limitations of their tool-using counterparts. These results suggest that a sensitivity to the functional aspects of an object is not restricted to tool-users. More specifically, our findings suggest that the capacities displayed by tool-users may not be specialized for tool-use, as a domain-specific view of these capacities might predict. Instead, it seems that non-human primates reason about the functional properties of tools using more domain-general mechanisms. Such domain general mechanisms are likely to include a sensitivity to simple object mechanics (see Spelke 1991), including an understanding of solidity (Hauser 2001; Santos and Hauser 2002), material transformations, and possibly causality.

The challenge presently facing comparative psychologists and biologists is to determine whether or not tool-users and non-tool-users differ in other aspects of their comprehension of tools. Much of the comparative work so far has investigated how different species assess the functional aspects of tools, the physics underlying how tools move and operate. As a number of cognitive scientists have pointed out, however, humans think about tools as more than objects with particular physical and functional properties. Bloom (1996, 1998), for example, has argued that humans think about a tool's intentional history when categorizing different functional objects. He contends that an important part of what makes a hammer a hammer is that it was created by a designer who intended to use it to hammer things. To date, however, no studies have examined whether or not non-human animals possess a notion of intentional history or attend to intentional histories when reasoning about tools. Work of this nature may begin to tease apart where different species diverge in their understanding of tools (Hauser & Santos, in press).

Our results present a number of methodological challenges to those investigating tool-use in non-human species. Throughout the experiments presented here, vervet monkeys outperformed tamarins. Despite many of the tamarin subjects' extensive experience with tools, they nonetheless performed worse than the vervets who not only had no experience with tools, but virtually no experience in any experiment involving object manipulation. We are unclear why this is the case, but we see at least one possible reason for the observed difference. Adult tamarins, unlike adult Old World monkeys, are known to have problems with perseveration and inhibition that sometimes impede performance on means-end tasks (see Diamond 1991; Santos et al. 1999). Additionally, vervets are, impressionistically at least, more dexterous than tamarins. It is possible, then, that the cane pulling task was more suited to vervet monkeys than tamarins. This raises an important methodological caveat: in order to compare conceptual abilities across species, researchers must develop procedures that are sensitive to constraints imposed by different species' sensory-motor limitations. In order to successfully explore conceptual abilities across species, comparative psychologists must develop ways to check if their tasks are equally applicable, not only across species but also across domains of knowledge. One way to achieve this is to test multiple species on the same conceptual problem using multiple methodologies. These methodologies should not only include active search tasks like the one presented here, but should also incorporate tasks without motor and inhibitory constraints like habituation measures and expectancy violation paradigms (see Hauser and Carey 1998).

There is a second possible reason for the difference in performance between the two species, raising a slightly different methodological caveat. Vervet monkeys may have outperformed tamarins because of the different experimental histories of the two groups. This explanation seems, initially at least, counterintuitive. Prior to the current experiments, most of our tamarins had participated in a wide variety of conceptual tasks involving object manipulation (Hauser 1997; Hood et al. 1998; Hauser et al. 1999; Santos et al. 1999; Hauser et al. 2001; Kralik and Hauser 2002). The vervets, in contrast, had no such experience. It is possible that the tamarins' experience in object manipulation tasks negatively influenced their performance in the present tasks, causing them to focus on irrelevant dimensions of the task demands; vervets with no experimental history were not constrained. This counterintuitive pattern speaks to the fact that it is often difficult to ascertain how a subject's experimental history will either positively or negatively influence its performance on future conceptual tasks. This is an extremely important caveat in a field where most experimental subjects have had some type of experimental history (see also Hauser et al. 2002b).

Ultimately, however, the experiments presented here suggest that a natural competence for tool-use does not necessarily indicate a more sophisticated (or more specialized) ability to recognize the functional properties of tools. Taken together, our experiments suggest that at least some non-tool-users succeed and fail on the same types of problems as natural tool-users like chimpanzees. We hope these studies will provide the foundation for a long tradition of comparative work, studies that will compare across different species, different methodologies, and different conceptual domains.

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