How Prosimian Primates Represent Tools: Experiments With Two Lemur Species (*Eulemur fulvus* and *Lemur catta*)

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The authors examined how 2 lemur species (*Eulemur fulvus* and *Lemur catta*) reason about tools. Experiment 1 allowed subjects to use 1 of 2 canes to retrieve an inaccessible food reward. Lemurs learned to solve this problem as quickly as other primates. Experiment 2 then presented subjects with novel tools differing from the originals along one featural dimension. Subjects attended more to tools' sizes than to their colors and made no distinction between tools' shapes and textures. Experiments 3 and 4 presented problems in which some of the tools' orientations had to be modified relative to the food. Subjects performed well on these problems, sometimes modifying the position of the tool. These results are discussed in light of the performance of other primates on this task.

Over the past few decades, scientists have gathered a wealth of data examining the nature of tool use in nonhuman animals (for review, see Beck, 1980; Hauser, 2000; Tomasello & Call, 1997). These data have demonstrated that the ability to use tools flexibly varies greatly throughout the animal kingdom and even within individual taxonomic groups. For example, consider the variation in tool use within the primate order—undoubtedly the most well-studied group of animals when it comes to tools. Some primates are known to modify and use objects to solve a variety of different means-end problems; wild chimpanzees (*Pan troglodytes*), for example, use a variety of different objects as tools (e.g., sticks, stones, leaves) in contexts as diverse as feeding, grooming, and social interactions (McGrew, 1992; Whiten et al., 1999). Other primate species (e.g., prosimians) rarely manipulate objects (see Jolly, 1964; Torigoe, 1985) and have never been observed using objects as tools either in the wild or in captivity.

The question now facing scientists is why primates exhibit such behavioral variation in their use of tools. In short, why do some primates use tools whereas others do not? One possibility is that differences in primate tool use map onto differences in primate conceptual abilities. Under this view, tool-using primates are able to use objects flexibly to solve means-end problems because they possess a suite of cognitive capacities that non-tool-using species lack. In particular, tool-using primates may differ from non-tool-using species in that only tool users possess an understanding of the causally relevant aspects of tool use (cf. Fujita, Kuroshima, & Asai, 2003; Povinelli, 2000). If this were the case, then one would expect tool-using primates to reason about tool-related means-end problems differently than non-tool-using species. In particular, tool users should be better able than non-tool users to hone in on the causally relevant features of a means-end problem.

To explore this issue, Visalberghi and colleagues began an elegant series of studies aimed at exploring what one tool-using species understands about the causal aspects of tools. They tested tufted capuchin monkeys (*Cebus apella*), a species that uses tools regularly in captivity and occasionally in the wild (see Fragaszy, Visalberghi, & Fedigan, 2004). In one study, Visalberghi and Trinca (1989) presented captive capuchin subjects with problems in which a stick could be used to obtain a piece of food placed inside a tube. Although all subjects spontaneously used the stick to obtain the food, capuchins' errors in solving the task revealed that they tended to solve the stick problem via trial and error learning. Capuchins chose and attempted to use novel tools at random, with little regard toward the causally relevant aspects of a successful probing tool (e.g., that it must be thin enough to fit inside the tube). When the capuchin subjects later became successful at this probing task, Visalberghi and Limongelli (1994) modified the tube apparatus such that it contained a small trap that would catch the pushed food. Again, subjects initially failed to reason about the physical properties of the trap, solving the problem instead through trial and error learning. Limongelli, Boysen, and Visalberghi (1995) then presented a similar trap problem to chimpanzees. Of the 5 chimpanzees tested, 2 performed above chance on this trap problem, successfully avoiding the trap without the use of an associative learning strategy (but see Povinelli [2000] for a more recent chimpanzee study demonstrating failures similar to those seen in the capuchins).

Although these experiments and others with capuchins and chimpanzees have provided some insight into how these two species reason about the functional aspects of tool-use problems, the methods typically used in these studies are unsuitable for

testing a wide variety of primate species. Many primate species, for example, would be physically incapable of manipulating a stick into a tube to obtain food, as capuchins and chimpanzees easily do. As such, researchers interested in how other less dexterous primates reason about tools have been unable to incorporate many of the methodologies previously used to test dexterous primates like capuchins and chimpanzees. Hauser and his colleagues have attempted to circumvent this issue by developing a task that could be used to test primates with differing levels of dexterity, particularly those that do not naturally use tools (Hauser, 1997; Hauser, Pearson, & Seelig, 2002; Santos, Pearson, Spaepen, Tsao, & Hauser, in press). The new task was an adapted version of a methodology previously used to test human infants (Brown, 1990). In his original version, Hauser (1997) tested what the cotton-top tamarin (*Saguinus oedipus*), a species that never spontaneously uses tools in the wild or in captivity, knows about the properties of simple pulling tools. He presented tamarin subjects with a choice of two small, blue cane-shaped tools that could be used to obtain out-of-reach food rewards. The two tools differed with respect to their orientation to the food; one tool was effectively placed, meaning that pulling the tool straight back would result in the reward moving forward, whereas the other tool was ineffectively placed, meaning that a straight pull would not be able to move the food. Once subjects began reliably choosing the correct cane, they were presented with a series of new canes, each of which differed from the original along one dimension: the new cane had either a new color, size, shape, or texture. The logic behind this condition was that tamarins should choose between these two potential tools on the basis of which features they found most important for a successful pulling tool. Tamarins reliably preferred newly colored and textured canes over newly shaped and sized canes. These results suggest that tamarins regard changes to a tool's shape and size to be more important to its functionality than changes to the tool's color or texture. Hauser then presented subjects with problems in which effectively oriented canes with multiple novel features were pitted against the original canes positioned in incorrect orientations. Tamarins reliably picked the novel tool more often than the ineffectively oriented familiar tool. Taken together, these results suggest that tamarins understand at least some of the features that are relevant to a functional pulling tool and will preferentially choose tools with these correct properties (e.g., a correct orientation relative to the goal object) over those that are familiar but ineffective.

Unlike the trap-tube test used with capuchins and chimpanzees, the pulling task developed by Hauser and colleagues can be easily applied to a wide variety of primate subjects; because the pulling task requires that the subject merely choose between two possible tool–food combinations, it does not require a high level of dexterity for successful performance. As such, the pulling task potentially can be used with a wide variety of species. Since Hauser's (1997) original study, the cane-pulling task has been used with many different primate species, including tamarins (Hauser, 1997; Hauser, Pearson, & Seelig, 2002; Spaulding & Hauser, 2005; Santos, Pearson, et al., in press; Santos, Rosati, Sproul, Spaulding, & Hauser, 2005), common marmosets (*Callithrix jaccus*; Spaulding & Hauser, 2005), vervet monkeys (*Cercopithecus aethiops*; Santos, Pearson, et al., in press), and capuchin monkeys (*Cebus apella*; Cummins-Sebree & Fragaszy, 2001; Fujita et al., 2003).[1] Surprisingly, the various species tested on this task tend to perform

relatively similarly. First, all species tested on Hauser's original training condition learn to pull the correctly oriented tool within a small number of training sessions (usually between 5 and 15). In addition, all of the species tested to date have successfully attended to at least some of the causally relevant features of the pulling tool. However, which particular features a given species attends to tends to be based on how that subject would be affected by a change in a particular feature—specifically, whether a change in that feature would affect the subject's ability to successfully obtain the food with the tool. Tamarins, whose body size limits their general pulling ability, pay attention to many of the tools' different features (their size, shape, material, and orientation) when choosing which tool to pull; tamarins, for example, pay strong attention to the size of a pulling tool and reject tools that are too long or too wide to be easily moved. However, tamarins care little about the color of the tool, which in no way affects their ability to grab and manipulate the cane. In contrast to tamarins, larger bodied capuchin subjects pay relatively little attention to the size or shape of the tool (which matters little to their ability to move the cane) and instead pay most attention to whether the tool is correctly oriented with respect to the cane; this is the only varied feature that would truly affect a capuchin's ability to obtain the food. Taken together, these results suggest that a number of monkey species successfully attend to at least some of the causally relevant aspects of a pulling tool. Moreover, these findings suggest that a primate's understanding of tools may not be correlated with successful tool-using behavior.

Although the pulling cane choice test has provided an excellent method for exploring what primates understand about tools, this specific task has to date been used only with New and Old World monkey species. In this series of experiments, we extend the pulling cane methodology to a group of primates that have rarely before been tested in cognitive tasks—the prosimians. In particular, we explore how two lemur species—ring-tailed lemurs (*Lemur catta*) and brown lemurs (*Eulemur fulvus*)—reason about simple pulling tools. Lemurs, like the other prosimian primates, have never been observed using tools in either the wild or captivity. Moreover, this taxonomic group has largely been neglected in studies of physical cognition more generally (see Tomasello & Call, 1997). As such, very little is known about their ability to represent tools and other objects. This oversight is unfortunate, as comparisons across phylogenetically diverse primate species are necessary to determine how and why different cognitive capacities evolve.

We began our investigation by replicating Hauser's (1997) original tamarin tool task with brown and ring-tailed lemurs. As in this original study, we presented subjects with an initial tool-training condition (Experiment 1), in which subjects were presented with a choice between two simple cane-shaped tools that differed in their orientation relative to a small food reward. Once subjects succeeded on this initial training condition, we then observed how they generalized to tools with novel features (Experiment 2) and novel connections (Experiments 3 and 4).

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[1] Variants of the cane-tool task involving food rewards placed on cloth-pulling tools or attached to rope-pulling tools have also been used with chimpanzees (Povinelli, 2000) and tamarins (Hauser, Kralik, & Botto-Mahan, 1999; Hauser, Santos, Spaepen, & Pearson, 2002).

Experiment 1

Method

Subjects. We tested 6 adult lemurs (see Table 1): 3 ring-tailed lemurs (*Lemur catta*) and 3 brown lemurs (*Eulemur fulvus*). Ring-tailed lemurs are native to south and southwestern Madagascar, whereas brown lemurs inhabit eastern and western Madagascar; both species are omnivorous and live in social groups of between 7 and 15 individuals. Neither species has yet been observed using tools in the wild. Our 6 subjects were born in captivity and are currently housed at the Lemur Conservation Foundation's reserve in Myakka City, Florida. The Myakka City Lemur Reserve consists of a 13-acre (40,469-m^2) slash pine forest enclosure surrounded by an electrified chain-link fence. Although subjects are normally free to range throughout the entire enclosure, the reserve also has a number of smaller outdoor and indoor enclosures that can be used to isolate animals during times of environmental stress or poor health. During the time of testing, the 2 brown lemurs inhabited one of these indoor–outdoor enclosures (5.8 m $\times$ 5.6 m). The other 4 lemurs were free-ranging. Free-ranging subjects were provided with a diet of monkey chow, which they were fed in between the morning and evening testing sessions, and were also allowed to eat the existing indigenous vegetation in the forest, which had been supplemented by plantings of mango, passion fruit, guava, grapes, banana, persimmon, and bamboo species already found to be widespread in Florida. The two enclosed lemurs were fed a diet of various fruits and chow once daily in between morning and evening testing sessions. Our 6 subjects were well habituated to humans, as caretakers and experimenters work daily on the reserve around the animals. All subjects were tested on a looking-time experiment on numerical competency concurrent with these experiments (Santos, Barnes, & Mahajan, 2005). The 3 ring-tailed lemurs and 1 brown lemur had previously been tested in a handedness experiment involving reaching into a tube to obtain food (Chapman, 2004). All subjects were naive with respect to means-end tasks involving manipulation of tools.

General apparatus and set-up. We closely followed the design and set-up of Hauser's (1997) methodology for testing tamarin monkeys (see Figure 1). At the beginning of each session, a subject was isolated and lured into the 1 m $\times$ 4 m $\times$ 4 m testing enclosure. The testing apparatus was set up in the cage opposite the testing enclosure such that a mesh-wire panel separated the subject and the testing apparatus; as such, both the apparatus and the subject were isolated from the other individuals in the colony. The cage mesh was sized such that the subject could reach its hands through to access the front of the test apparatus but could not physically approach the apparatus in any other way.

The testing apparatus consisted of a 31-cm-long $\times$ 30-cm-wide $\times$ 3-cm-high tray, divided into two sections (left and right) by a 0.75-cm partition, and a 51-cm $\times$ 33-cm $\times$ 18-cm stage on which the tray could sit. Both the stage and the presentation tray were constructed of white foam core. The test objects were constructed with Sculpey, a nontoxic oven-bake

Table 1
Subject Information

Subject	Species	Sex	Age (years)
Alexandra[a]	*Lemur catta*	F	9
Gideon	*Eulemur fulvus*	M	17
Guinness	*Lemur catta*	M	11
Redlake	*Eulemur fulvus*	F	21
Redwood	*Eulemur fulvus*	F	10
Valgius	*Lemur catta*	M	9

Note. F = female; M = male.
[a] Alexandra was eliminated from the study after Experiment 2 because of disinterest in participation.

Figure 1. A photograph of the set-up of our experiments. Subjects sat within a wire-mesh cage enclosure and were allowed to reach out and manipulate one of the tools on each trial.

clay. In each experiment, the subjects were required to manipulate a test object to gain access to a food item reward: either a half of a red grape or a cantaloupe cube of equal size, depending on the subject's preference.

General procedure. Once the subject was isolated, the test session began. Two experimenters ran each session. The first served as the presenter, manipulating the tools and the tray. The second experimenter filmed each session from behind the first experimenter. During each trial, subjects were presented with a choice of two tools, one positioned on either side of the tray. At the beginning of each trial, the presenter placed the tools on the tray in their designated locations (see specific experiments below). The experimenter then placed the tray on the stage such that it was out of reach of the subject. The subject was then shown each food item in succession and was allowed to smell it before it was placed on the tray near the tool. Once the subject had attended to each side of the tray, the experimenter averted her eyes and waited 2–4 s before pushing the tray forward and allowing the subject to select one tool with which to try to obtain the food item. Because the food item itself was out of the subject's reach, the subject was able to access the food item only by manipulating the tool. The subject was allowed to select only one tool in each trial; once the subject had touched one of the two tools, that tool was taken as the "selected" object, and the subject was not permitted to select the other tool. Hence, when the subject selected the "incorrect" tool (one that the subject could not manipulate to drag the food item closer), the trial was terminated. If the subject selected the correct tool, it was allowed to manipulate the object until receiving the food item.

Design. Experiment 1 served to introduce subjects to a single tool (i.e., a hard lime-green cane) that could be used to pull a food reward into reach. As in Hauser (1997), we presented subjects with sessions of 12 randomly ordered trials, each with a different tool configuration (see Figure 2). Each trial presented subjects with two identical tools on either side of the tray; the tools differed only in their orientation relative to the food reward (see Figure 2). In each trial, one food reward was located inside the tool such that if the subject pulled the tool straight back, the hook of the tool would pull the food item within reach; this tool was considered the correct choice. The other food reward was located outside of the tool's hook (e.g., above, to the left, to the right), such that pulling the tool straight back did not result in moving the food item closer to the subject. The subjects could, however, access the food item with this incorrect tool by manipulating the tool in novel ways (e.g., twisting it to the side and using the back of the tool to
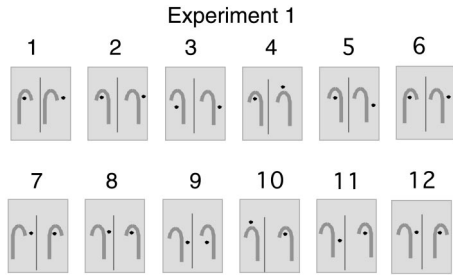
Experiment 1

Figure 2. A depiction of the tool combinations used in Experiment 1.

push the food item). As such, a "correct" pull was defined as a pull in which the subject either picked the correct tool or in which the subject was able to manipulate the incorrect tool (grape located outside of hook) in such a way as to pull the food item within grasping range. Subjects continued on Experiment 1 sessions until they reached a criterion of 80% correct pulls (i.e., 10 out 12 trials) for two consecutive sessions.

Results

Subjects reached criterion on two consecutive sessions on average in 10.5 sessions ($SD = 4.97$ sessions; see Figure 3). There was no difference between performance in brown lemurs ($M =$

11.67 sessions) and ring-tailed lemurs ($M = 9.33$ sessions). We then compared our subjects' performance with that of monkey tested in previously published studies (Fujita et al., 2003; Hauser, 1997; Hauser, Pearson, & Seelig, 2002; Santos, Pearson, et al., in press). Our lemur subjects performed about as quickly as tamarins ($M = 9.4$ sessions, $SD = 4.19$), capuchins (range = 15–19 sessions), and vervet monkeys ($M = 6$ sessions, $SD = 0.84$).

Discussion

Despite the fact that they rarely manipulate objects functionally in the wild, our lemur subjects performed well on the means-end task presented to them in Experiment 1. All subjects completed the training in only a few sessions. Moreover, our lemur subjects performed at the same rate as other monkey species: capuchins, tamarins, and vervet monkeys. The fact that our lemur subjects learned this means-end task as quickly as capuchin monkeys is striking; unlike lemurs, capuchins are known to use tools spontaneously both in the wild (Izawa & Mizuno, 1977) and in captivity (Anderson, 1990; Ottoni & Mannu, 2001; for review, see Fragaszy et al., 2004). Consequently, our results suggest that lemurs, which have never been observed using tools, can learn a simple took task as quickly as a more dexterous tool-using species like the capuchin.
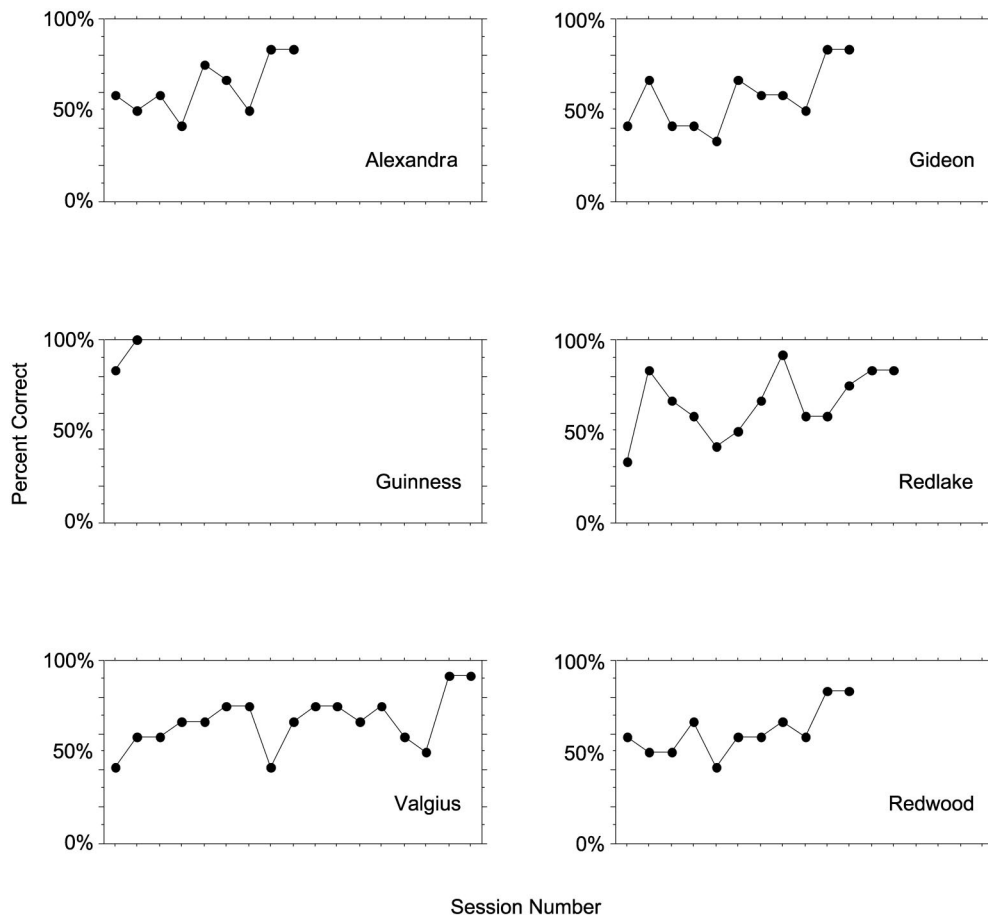

Figure 3. Learning curves for each subject tested in Experiment 1.

Having established that lemurs can successfully use simple pulling tools, we turned to the question of how they represented the objects they used in these tasks. Did subjects simply learn to choose particular orientations of lime-green canes? Or did subjects learn something more general about which objects could be used as pulling tools? In Experiment 2, we sought to answer these questions by exploring how lemurs would generalize to novel tools.

Experiment 2

Method

Subjects. We tested the same 6 individuals as in Experiment 1.

Design. Experiment 2 again mimicked the design of Hauser (1997) to explore the specific features that lemurs attend to when choosing between one of two available tools. To do so, we created new tools that differed from the original lime-green cane tool along one featural dimension: color, size, shape, or texture (see Figure 4). As in Hauser (1997), lemurs were presented with a choice of two novel featurally changed tools, both of which were set up such that the food reward was located within the hook of the tool—that is, in a readily accessible orientation. Because both novel tools were positioned with this functional orientation, subjects could easily retrieve the food by pulling either of the two novel tools. However, because the objects differed across some features, we were able to examine whether lemurs would prefer some featural changes over others.

Subjects were tested with both a color versus size comparison and a shape versus texture comparison in a randomized order. Each of these comparisons was presented as a single test session of 12 trials each (see Figure 4). As in Hauser (1997), we presented each comparison twice to obtain multiple samples of each pairing. In between these test sessions, subjects were presented with a training session identical to that used in Experiment 1; subjects were required to achieve criterion (over 80% correct) on these training sessions before returning to the Experiment 2 tests. These training sessions ensured that subjects would attend to the differences between the two tools throughout Experiment 2 testing.
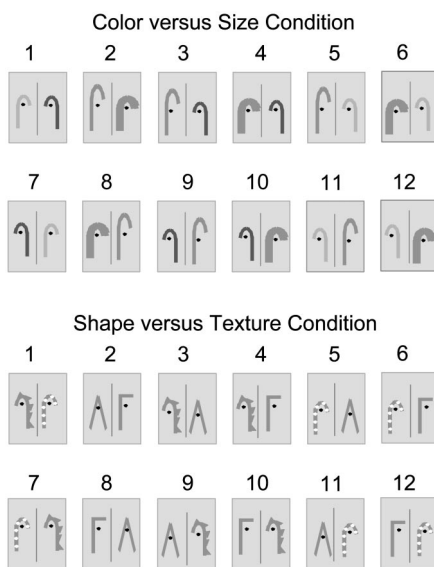

Figure 4. A depiction of the tool combinations used in the color–size and shape–texture conditions of Experiment 2.

In the color versus size condition (see Figure 4), subjects were presented with tools that were the same shape and size as the original tool but different colors (either pink or purple) and with tools that were the original lime-green color but either 1.5 times as long or 1.5 times as wide as the original tool. In the shape versus texture condition, we presented subjects with tools that were novel shaped (V-shaped or L-shaped) or had novel textures (dotted with small evenly spaced holes or jagged with triangular peaks). The order of individual trials within a session was randomized as in Experiment 1.

Results

We first explored how subjects performed on the color versus size condition by examining subjects' preferences during within- and between-features comparisons (see Figure 5). Within color, subjects chose equally between pink ($M = 50\%$) and purple (50%) tools. Within size, subjects showed a mild preference for the wide tool ($M = 79\%$) over the long tool (21%), $t(5) = 2.44$, $p = .058$. In between-features comparisons, subjects showed a marked preference for the wide tool over both the pink tool (87% vs. 13%), $t(5) = 6.71$, $p = .001$; and the purple tool (92% vs. 8%), $t(5) = 7.91$, $p = .0005$. Subjects showed no difference between the long tool and either the pink tool (67% vs. 33%), $t(5) = 1.35$, *ns*; or the purple tool (54% vs. 46%), $t(5) = 0.35$, *ns*. We then explored whether subjects preferred color changes to size changes. Collapsed across all trials, the results show that subjects reliably chose tools that changed in size over tools that changed in color ($M = 75\%$ of trials), $t(5) = 5.86$, $p = .002$. Of the 6 subjects, 4 exhibited this size change preference on their first trial. Much of this preference for newly sized tools stemmed from subjects' overwhelming preference for the wide tool.

We then explored subjects' preferences across within- and between-features comparisons in the shape versus texture condition. When tested with texture changes, subjects chose equally between jagged ($M = 58\%$) and dotted tools (42%), $t(5) = 1.00$, *ns*. Within shape changes, subjects chose equally between the V-shaped tool (62%) and the L-shaped tool (38%), $t(5) = 1.58$, *ns*. Subjects also failed to discriminate on any of the between-features contrasts (see Figure 5; all *p*s were nonsignificant). Collapsed across all trials, the results indicate that subjects showed no difference in choice between tools that changed in shape (48% of choices) and tools that changed in texture (52% of choices), $t(5) = 0.30$, *ns*.

Discussion

When presented with novel tools that differed from the original green tool across single featural dimensions, lemurs preferred some featural changes over others. When presented with changes to the color and size of the tool, lemurs reliably preferred newly sized tools over newly colored tools. This pattern of data was mostly due to subjects' preference for the wide-sized cane. The wide tool was 1.5 times thicker than the original tool and was much easier for a lemur hand to grasp. In contrast, a color change had little to no effect on the subject's ability to manipulate the tool; as such, subjects seemed to show no attention to color changes. Similarly, subjects showed no attention to shape and texture changes. Unlike the size changes, shape and texture changes did not seem to impact subjects' ability to maneuver the tool. As such,
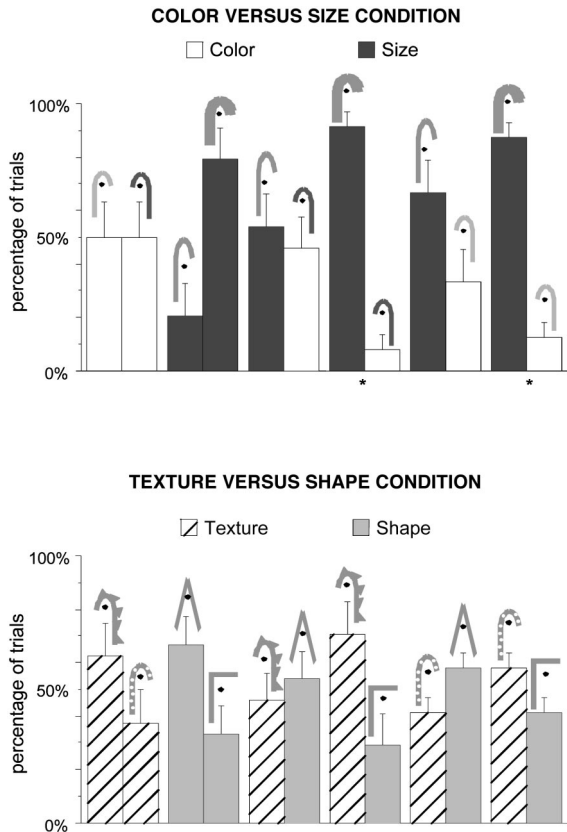
COLOR VERSUS SIZE CONDITION

TEXTURE VERSUS SHAPE CONDITION

Figure 5. Mean percentage of trials (± *SE*) in which subjects chose each tool in Experiment 2. Asterisks indicate significant comparisons.

lemurs did not take into account these changes and chose equally across novel shaped and textured tools.

Taken together, the results of Experiment 2 provide some insight into how lemurs represent the pulling tools they used in Experiment 1. In particular, these results suggest that lemurs succeeded on this task not simply by memorizing particular spatial patterns and choosing on the basis of a particular tool's familiarity. Instead, lemurs generalized to new functional tools, even when these new tools differed in shape, color, size, or texture. Moreover, lemurs seemed to learn something more general about pulling tools—namely, that any correctly oriented, easily graspable object can serve as a functional puller. Additionally, our results suggest that subjects spontaneously attended to the specific features of the tool that matter most for their ability to pull the tool (i.e., the width and graspability of the object) and disregarded other equally salient but irrelevant changes (e.g., color changes).

Our subjects' pattern of performance closely matches that of other primates, although there are some slight differences. Lemurs, like tamarin monkeys, seem to attend more to some featural changes than to others. We find it interesting that the particular featural changes that mattered (size in the case of lemurs or shape in the case of adult tamarins) seem specific to the particular species involved. Hauser, Pearson, and Seelig (2002), for example, found that infant tamarins (who were small enough to have trouble manipulating larger sized tools) were less tolerant than adult tamarins of size changes. A similar phenomenon seems to hold for

our lemur subjects; for adult lemurs, size again seemed to be the relevant featural dimension because it alone affected subjects' ability to grab the tool. Our lemurs' performance also matched that of a primate species that naturally uses tools: the capuchin monkey. Lemurs, like capuchins, successfully generalized to tools with novel colors, shapes, texture, and sizes (see Cummins-Sebree & Fragaszy, 2001; Fujita et al., 2003). Unlike lemurs, however, capuchins did not show special interest in the wider sized cane. Again, this is likely due to the fact that capuchins, unlike lemurs, are dexterous enough to easily manipulate both thin and wide sized tools.

Having established that lemurs distinguish between functionally relevant and irrelevant featural changes in Experiment 2, we decided to further explore subjects' knowledge of functional tools in Experiment 3. Here, we again presented subjects with a series of novel tools, but this time, we positioned the novel tools in both effective and ineffective orientations. Our goals for Experiment 3 were twofold: We first hoped to explore whether subjects would spontaneously choose effectively oriented novel tools over ineffectively oriented but more familiar tools. Second, we aimed to assess whether lemurs would spontaneously attempt to change the orientation of the ineffectively placed tools, converting them to an orientation that could successfully move the food reward into position.

Experiment 3

Method

Subjects. We tested 5 of the 6 lemurs that completed the previous two experiments. The 6th subject (Alexandra) was not tested because of disinterest in participation.

Design. Again replicating the conditions of Hauser (1997), Experiment 3 introduced subjects to nine new tools that varied from the original along a variety of dimensions: shape, color, size, texture, and orientation (see Figure 6). The following tools were used: a multicolored bumpy textured V-shape, a purple ring shape, a yellow and blue spiraled cane, a multicornered geometric shape, a blue and orange upside-down U-shape, a green cane that stood perpendicular to the tray with a flat base (this cane had to be placed down flat to pull the tool), an upside-down green cane, and a "tunnel-shaped" cane in which the hook end was turned up like a tunnel (this cane also had to be repositioned down flat to obtain the food). Some tools varied from those used in a previous experiment by only one dimension (e.g., the purple ring shape). Other tools varied by some combination of the dimensions (e.g., the blue and orange upside-down U-shape). Additionally, the trials of Experiment 3 differed from those of Experiment 2 in that some of
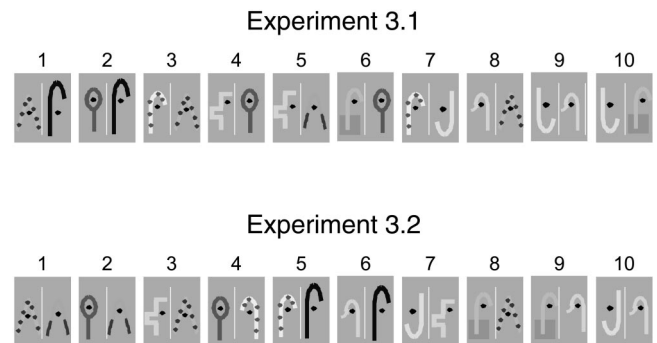
Experiment 3.1

Experiment 3.2

Figure 6. A depiction of the tool combinations used in Experiment 3.

the new tools would not move the food closer if simply pulled straight; instead, these convertible tools had to be manipulated in novel ways (e.g., an upside-down cane-shaped tool would need to be slid to the side and then pulled straight back) in order to obtain the food (see Figure 6).

As in Hauser (1997), Experiment 3 was divided into two subexperiments, each with 20 trials per session. The order of trials within each session was randomized, and each trial paired two of the novel tools discussed above. Hence, some trials included both a possible tool, which could be pulled straight back to bring the food within grasping range, and a convertible tool, which had to be manipulated in a novel way to yield the same result. Other trials included either two possible or two convertible tools. Within each session, each pairwise combination of novel tools was balanced by its reversal (tool on the right moved to the left and vice versa). All subjects received two sessions of each subexperiment, for a total of 80 trials pitting novel tools (both possible and convertible) against each other.

Results

Figure 7 illustrates subjects' performance on all pairwise comparisons. We first explored whether subjects preferred possible over convertible tools. As predicted, subjects reliably chose possible over convertible tools, $t(4) = 3.38$, $p = .027$. We then decided to explore how subjects performed on trials in which they chose the convertible tool. In other words, were subjects able to rearrange the tool and obtain the food even on trials involving ineffective orientations? All together, subjects successfully retrieved food on 10 of the 121 trials ($M = 8.3\%$) in which they pulled a convertible tool. All 10 of these instances involved the upside-down convertible tool. In these cases, subjects were able to maneuver the top edge of the upside-down tool such that it pulled

POSSIBLE VERSUS CONVERTIBLE CONDITION

Figure 7. Mean percentage of trials ($\pm$ *SE*) in which subjects chose each tool in Experiments 3. Asterisks indicate significant comparisons.

the food toward them. All subjects except Guinness were able to convert tools at least once.

Discussion

The first aim of Experiment 3 was to investigate how our lemur subjects performed with a series of new novel tools, some of which were oriented in ineffective ways. To do so, we presented lemurs with novel tools in effective (possible) and ineffective (convertible) orientations. When given a choice between possible and convertible orientations, subjects reliably chose the possibly oriented tools. Like tamarins (Hauser, 1997; Hauser, Pearson, & Seelig, 2002) and capuchins (Cummins-Sebree & Fragaszy, 2001), lemurs recognize which orientations will be more suitable for a simple straight-back pull and selectively choose those orientations over ones that need more manipulation.

Our second aim was to explore whether subjects would spontaneously attempt to manipulate the convertible tools into a more effective orientation. Despite their preference for possible tools, our subjects did occasionally pull convertible tools, thereby allowing us to assess whether they tried to change the orientation of these tools. In contrast to tamarins' performance, lemurs did sometimes manipulate the orientation of a convertible tool such that they were able to gain access to the food reward. Lemurs successfully used convertible tools to gain access to the food reward on about 8.3% of trials. The tendency to manipulate objects was also quite common across individuals; all but 1 lemur successfully obtained food with the convertible tool. In this respect, lemurs performed exactly like tool-using capuchins, who obtained food on 8% of the convertible tool trials (Cummins-Sebree & Fragaszy, 2001). This result is somewhat surprising in light of the fact that lemurs are far less manipulative than capuchin monkeys.

Given our subjects' ability to successfully manipulate convertible tools, we decided to present subjects with one final test. In Experiment 4, we again presented subjects with a series of novel tools. This time, however, we presented subjects with ineffectively oriented tools that were perceptually similar to the lime-green cane-shaped tool that subjects were originally trained on. As in Hauser (1997), our goal was to pit familiar but incorrectly positioned tools against novel but functionally positioned tools.

Experiment 4

Method

Subjects. We tested the 5 subjects that completed Experiment 3.

Design. Again replicating the conditions of Hauser (1997), Experiment 4 introduced subjects to novel possible and convertible tools (see Figure 8 for a depiction of all pairwise comparisons). These new tools included an orange cane, an orange cane with a small ridge at the base, a cane with an upper triangle shape, an H-shaped tool with a small ridge at the top, and a green cane that could be stood vertically such that it needed to be flipped on its side to be used correctly. In this study, some familiar tools were placed into novel convertible positions such that when pulled straight back, they no longer delivered the food item as they had previously. For example, the purple ring-shaped tool from Experiment 3 was placed such that the food reward was just outside the ring, rather than inside. To successfully use the tool, subjects would have to lift the ring up over the grape and pull straight back. In another trial, the original cane-shaped tool was set up so that it was rotated 45° from its original position, requiring that subjects move it sideways while pulling back to get the food item. In this way, novel
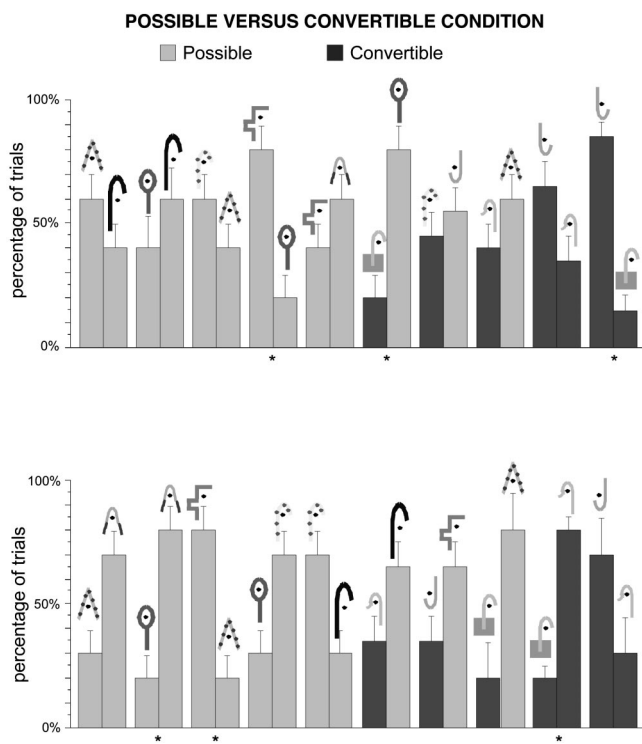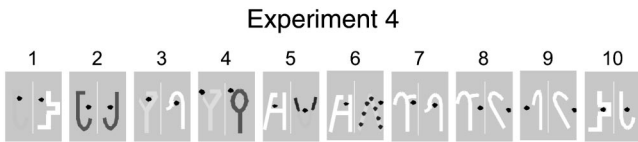
Experiment 4

Figure 8. A depiction of the tool combinations used in Experiment 4.

tools in possible positions were pitted against familiar tools in convertible positions. If perceptual familiarity was the driving force behind the subjects' choices, then they should pick the familiar tools in convertible orientations. If, however, subjects were instead paying attention to how the tool was oriented, then we would expect them to pick the possible rather than convertible tools or to manipulate the convertible tools into possible orientations before pulling.

We again presented subjects with 20 trials in each session, with the presentation order of each pairwise comparison randomized across the session. Again, each subject received two sessions, for a total of 40 trials.

Results

Subjects successfully generalized to novel pulling tools, choosing to pull both novel and familiar tools (see Figure 9). In this experiment, however, subjects did not show a statistically significant preference for possible over convertible tools ($Ms = 52\%$ vs. 48%), $t(4) = 0.39$, *ns*. As such, it seemed that subjects were pulling convertible tools more than in the previous study. We then explored whether this was due to the effect of familiarity. Subjects did not show a preference for familiar over unfamiliar tools ($Ms = 53\%$ vs. 47%), $t(4) = 1.41$, *ns*. We then explored whether subjects successfully obtained food when they pulled the convertible tools. All together, subjects successfully retrieved food on only 14 of the 148 trials ($M = 9.5\%$ of trials) in which they pulled a convertible tool. Subjects were able to successfully convert six of the different

convertible tool exemplars. Again, all subjects except Guinness were able to convert this kind of tool at least once.

Discussion

The results of Experiment 4 provided another demonstration that our lemur subjects were capable of generalizing to novel-looking tools and will attempt to use these novel tools to obtain the food. The specific goal of Experiment 4, however, was to examine the role of familiarity in our subjects' choice of tools. To explore this, we presented subjects with a choice between novel-looking tools positioned in possible orientations and familiar tools (i.e., tools that subjects had previously used successfully to obtain the food) in convertible orientations. We find it interesting that lemurs showed no preference for familiar over unfamiliar tools. This result suggests that subjects chose between the two tools by using more than just their perceptual familiarity with previously reinforced tools.

It is also interesting to note, however, that in contrast to their performance in Experiment 3, subjects in Experiment 4 did not show a preference for the possible over the convertible tools; although subjects did pull the possible tool on the majority of trials, this result did not reach statistical significance. This failure to discriminate possible and convertible tools makes some sense in light of the fact that subjects attempted to reposition more of the convertible tool exemplars than they had in the previous experiment. Subjects in Experiment 4 attempted to convert six of the different convertible tools, in contrast to the single tool they attempted to reposition in Experiment 3. Moreover, in contrast to the performance of tamarins in previous studies, our lemur subjects were successful in obtaining the food with convertible tools on almost 10% of the attempts. As such, subjects may not have shown the preference for possible over convertible tools in part because
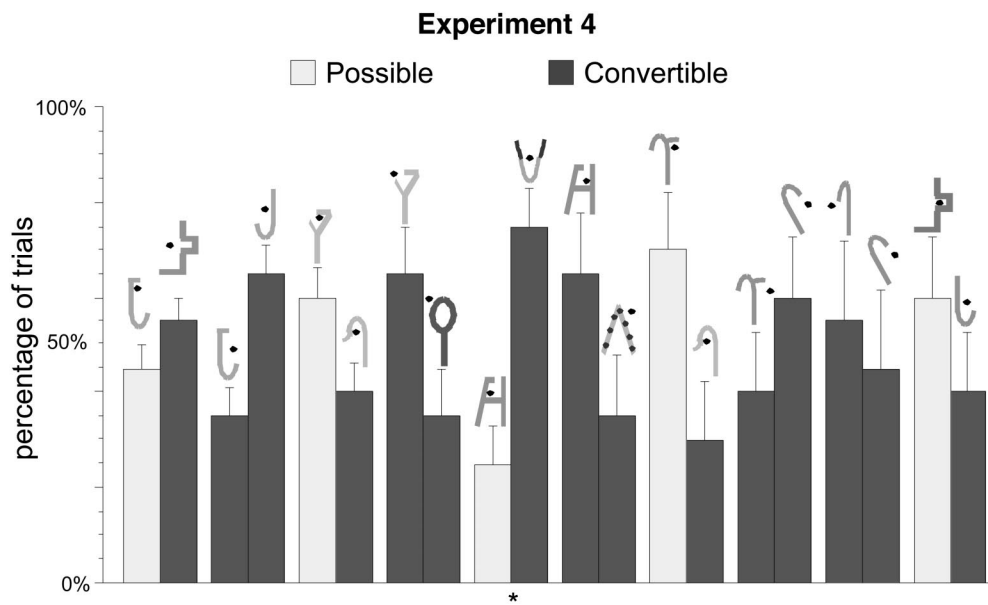

Figure 9. Mean percentage of trials ($\pm$ *SE*) in which subjects chose each tool in Experiment 4. Asterisks indicate significant comparisons.

they were sometimes able to obtain the food with the convertible tools.

General Discussion

The aim of this study was to explore how two lemur species reason about simple pulling tools. To do so, we presented ring-tailed and brown lemurs with a task involving the use of simple pulling tools to gain access to an out-of-reach food reward. This task was chosen for two reasons. First, the cane-pulling task has previously been used by a number of labs investigating what other primate species know about tools (e.g., Cummins-Sebree & Fragaszy, 2001; Fujita et al., 2003; Hauser, 1997; Spaulding & Hauser, 2005; Santos, Pearson, et al., in press). Second, the pulling task is simple enough to be used to explore tool use in subjects like lemurs that possess relatively little manual dexterity (e.g., tamarins: Hauser, 1997). Our first major result is that lemurs, like other primates, can learn to use simple pulling tools with relatively little training. This is, to our knowledge, the first demonstration of successful tool use in a prosimian primate. It is interesting that although lemurs have never been observed using tools in the wild, the results of Experiment 1 suggest that lemurs can learn to use pulling tools as quickly as other more dexterous primates; lemurs learned the initial training task at about the same rate as capuchin subjects (e.g., Cummins-Sebree & Fragaszy, 2001; Fujita et al., 2003), who are far more manipulative than our subjects.

Our second major finding is that lemurs, like other primates, spontaneously attend to some of the features that are causally relevant for a successful pulling tool. In Experiment 2, our lemur subjects spontaneously attended to the size of the pulling tool that they used, preferring a wider sized tool that was easier to grip than the thinner sized tool with which they had been trained. This pattern of data differs from the specific results seen in other primate species but makes sense given the gripping pattern of our lemur subjects; because the lemur thumb is more ventrally placed, it is better than other primate hands at gripping wider objects. Our subjects' special attention to the width of the tool therefore provides evidence that lemurs do attend to the aspects of a tool that matter for their ability to use it properly. Moreover, these results also suggest that lemurs will choose between two potential tools not on the basis of perceptual familiarity, but instead on the basis of features that are relevant to the tool's functionality; subjects rejected the tool on which they were originally trained (the thinner tool) and instead chose a novel but more functionally appropriate wider tool. Our subjects' attention to functionality over familiarity was also observed in Experiment 4; here, subjects were just as likely to choose familiar tools as unfamiliar tools. Taken together, these findings suggest that lemurs, like other primates, seem to have some knowledge of the features that are required for functional pulling tools. It is intriguing that they seem to possess this knowledge despite the fact that they rarely use tools in the wild.

Finally, we have shown that lemurs solve the tool problem in a somewhat more flexible way than do other primates (e.g., tamarin monkeys). Specifically, in the final two experiments, lemurs sometimes changed the position of tools that were inappropriately oriented and repositioned them into effective orientations. All but 1 subject showed this behavior on at least one trial. In addition, subjects that did convert tools demonstrated this behavior for a number of the different tool exemplars. In this way, lemurs per-form the cane-pulling task differently than tamarins, marmosets, and vervet monkeys, but quite similar to naturally tool-using capuchin monkeys. This result is somewhat surprising because capuchins are far more manipulative than lemurs and other pros-imian primates. Although capuchins spend a great deal of time manipulating objects in the wild and captivity, lemurs rarely in-teract with external objects and never have been observed using tools. As such, our results paint a somewhat surprising picture of lemurs' capabilities in the domain of tool use and suggest the need for more research on their physical cognitive abilities more generally.

Our overall pattern of results, which suggests that lemurs solve the cane-pulling task like other tool-using primates, poses a puzzle for the view that differences in primates' natural tool use reflect differences at the level of conceptual ability. Our results, instead, provide support to an alternative account—namely, that many primates share an ability to reason about the functional properties of different objects, irrespective of whether they exhibit tool use in their natural behavioral repertoire (see also Hauser, 1997; Hauser, Pearson, & Seelig, 2002; Spaulding and Hauser, 2005). These data fit with a growing view that both tool-using and non-tool-using primates share a suite of domain-specific—possibly innate (e.g., Hauser, Pearson, & Seelig, 2002)—mechanisms for reasoning about physical objects and that performance in simple pulling tasks may tap into these abilities.

The fact that prosimian and anthropoid primates seem to share the capacity to reason about the functional properties of objects makes the question posed in the introduction—the question of variation in primate tool use—all the more puzzling. If species from across the primate order seem to share a basic understanding of the functional properties of objects, then why is it that only some of them naturally use objects as tools? Although the present data do not solve this puzzle, they point to the importance of future comparative work in evaluating hypothetical answers to this puz-zle. Moreover, they provide an example of how important it is for comparative psychologists to develop tasks that can be applied across distantly related species. Only in this way will scientists carefully be able to distinguish between failures at the level of conceptual competence and failures at the level of performance.

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