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ORIGINAL ARTICLE

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Representing tools: how two non-human primate species distinguish between the functionally relevant and irrelevant features of a tool

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Abstract Few studies have examined whether non-human tool-users understand the properties that are relevant for a tool's function. We tested cotton-top tamarins (*Saguinus oedipus*) and rhesus macaques (*Macaca mulatta*) on an expectancy violation procedure designed to assess whether these species make distinctions between the functionally relevant and irrelevant features of a tool. Subjects watched an experimenter use a tool to push a grape down a ramp, and then were presented with different displays in which the features of the original tool (shape, color, orientation) were selectively varied. Results indicated that both species looked longer when a newly shaped stick acted on the grape than when a newly colored stick performed the same action, suggesting that both species perceive shape as a more salient transformation than color. In contrast, tamarins, but not rhesus, attended to changes in the tool's orientation. We propose that some non-human primates begin with a predisposition to attend to a tool's shape and, with sufficient experience, develop a more sophisticated understanding of the features that are functionally relevant to tools.

Keywords Tools · Non-human tool-user · Expectancy violation method · Tamarins · Rhesus

Introduction

Over the past century, scientists have carefully documented the extent to which non-human animals create and use tools (for reviews see Hauser 2000; Povinelli 2000; Tomasello and Call 1997). Unfortunately, few studies have explored in detail how non-human animals represent tools, and in particular, whether they distinguish between functionally useful and useless objects based upon their design features. The few studies that have examined this problem (mostly on non-human primates) suggest that although animals may successfully use tools (Boesch-Achermann and Boesch 1993; Chappell and Kacelnik 2002; Matsuzawa 1994; McGrew 1992, 1994; Tomasello and Call 1997; Westergaard and Suomi 1995; Whiten et al. 1999), they do not necessarily understand the relevant properties of the objects they are using (Povinelli 2000; Visalberghi and Limongelli 1994; Visalberghi and Tomasello 1998; Visalberghi and Trinca 1989).

Visalberghi and her colleagues examined what capuchins (*Cebus apella*) understand about the functional properties of tools using a variety of experimental manipulations (Visalberghi and Limongelli 1994; Visalberghi and Trinca 1989). In one experiment, Visalberghi and Trinca (1989) presented capuchins with a task in which subjects were required to use a stick to obtain a food reward placed inside a clear transparent tube. Although subjects quickly solved the task with an effectively shaped stick, they failed to show an understanding of the important aspects of the task when allowed to solve the task with novel tools, some of which were ill-suited for the pushing task (e.g., a fat bundle of sticks which did not fit in the tube, sticks that were too short to reach the food reward). Although subjects eventually solved the task, they seemed to do so only through trial and error learning. Subjects would, for example, repeatedly attempt to insert a fat bundle of sticks into the narrow opening of the tube, despite the fact that it was clearly too large to fit. Because of their poor performance, Visalberghi and colleagues concluded that subjects failed to understand which features of the tool were functionally important to the task of pushing the grape out of the tube.

In an extensive series of experiments, Povinelli (2000) explored what captive chimpanzees (*Pan troglodytes*) understand about the functional properties of a variety of

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different tools. In one set of experiments, he presented chimpanzees with a means-end problem in which subjects could pull one of two rake tools to gain access to an out-of-reach food reward. He found that subjects failed to understand which of the two rakes could serve as successful pulling tools. Subjects, for example, chose rakes with inverted bases, ones that were inappropriately oriented to pull the food. Similarly, they chose rakes made of cloth, tools with ends too flimsy to drag the food. These and other experiments suggest that chimpanzees do not understand how the physical properties of a tool constrain the way it operates. Like capuchins, chimpanzees fail to focus on the physical aspects of a tool that are relevant for its function.

As part of a long term study of object knowledge in cotton-top tamarins (*Saguinus oedipus*), Hauser (1997) examined whether adult tamarins lacking experience with tools understand which properties of a tool are relevant to its functioning. Based on a procedure previously used to test human infants (see Brown 1990), an experimenter allowed a tamarin to pick one of two identical blue canes to retrieve food. The only difference between the two canes was that one had a piece of food located inside its hook while the other had a piece of food located outside its hook; given the tamarin's dexterity, pulling the cane with food inside the hook was considerably easier. Once subjects mastered this task, they were presented with a variety of new tools with different colors, shapes, textures, and sizes. Results showed that subjects attended to the functionally relevant features when deciding which new tool to choose. Subjects, for example, chose a cane of a new color over a cane of a new size. Similarly, subjects reliably chose canes of new textures over those with new shapes. These initial results suggest that tamarins consider shape and size to be critical features of tools and regard these transformations as more meaningful than other featural changes.

After completing a number of simple single-feature transformations, tamarins went on to receive test trials in which many more features were altered, some of which actually changed the functional nature of the tools. For example, subjects were asked to choose between a newly colored, newly shaped tool (e.g., a green v-shaped cane) oriented in a functionally appropriate way and a familiar looking tool oriented in a functionally inappropriate way (e.g., the original blue cane was positioned upside-down, making it inappropriate in its current orientation). Subjects consistently selected the more functional of the two options even when the features of this novel tool differed radically from the original tool. In other words, subjects attended to the functional orientation of the tool relative to the food object and selected the tool that maximized the probability of obtaining the food.

Hauser et al. (1999) also conducted a modified version of the canes task, contrasting two pieces of cloth, one with the food on or functionally connected to the pulling end of the cloth, and another off or functionally disconnected with the pulling end. As in the canes task, subjects readily tolerated color and texture changes to the pulling object, while rejecting changes in shape that affected the object's functionality. These results suggest that when choosing between two tool options, tamarins attend to more than just the tool's shape; instead, it seems that subjects are identifying the specific aspects of shape (orientation, etc.) that matter for the pulling task.

More recently, Hauser and colleagues (2002) have explored the development of tamarins' understanding of tools, using the original canes task with 4- to 8-month-old infants. Although these subjects had no experience with any freely moving and manipulable objects, they learned to use a blue cane to retrieve an out-of-reach food reward at the same rate as adults. More impressively, the pattern in which tamarin infants spontaneously generalize to new functional tools was virtually the same as that of adults. In other words, the infants readily tolerated changes to the color of the cane, but rejected canes of a new size. Similarly, they selectively chose canes of a new texture over those of a new shape if such changes negatively impacted upon functionality. Even across the more difficult changes involving multiple features, the infants reliably selected the most functionally appropriate object. These findings suggest that without any prior experience manipulating objects, young tamarins possess an early sensitivity to functionally relevant and irrelevant features of potential tools.

Although tamarins of all ages seem capable of reasoning about the functional properties of objects in the cane task, it is possible that this understanding developed after initial exposure to the original canes. Although the infants in the study by Hauser et al. (2002) had no experience manipulating objects before the study, they were able to practice manipulating the original canes across a number of sessions before the generalization conditions. It is possible then that tamarins may require experience actually *operating* a tool before they recognize which properties are important for its functioning. Alternatively, tamarins may understand which properties are relevant for a tool's functioning in the absence of direct experience with that particular tool. Do tamarins require experience operating a tool before they understand which features are appropriate and inappropriate? Or, do tamarins understand which properties are important to a tool's functioning in the absence of direct, physical experience with it?

In the following experiments, we set out to answer these questions by exploring whether experienced captive cotton-top tamarins attend to the relevant features of a tool in the absence of any direct physical experience with that tool. To do so, we used a different methodology than we have previously used to explore what tamarins understand about tools. Specifically, we used the expectancy violation method. This method, which is also known as the "looking time" paradigm, was developed for use with human infants (see Spelke 1985). It has also been successfully used with non-human primates, under both field and laboratory conditions, by different laboratories, and to assess different kinds of conceptual knowledge (Hauser 1998; Hauser and Carey 1998; Hauser et al. 1996; Munakata et al. 2001; Santos and Hauser 1999, 2002; Uller 1997; Uller et al. 2001); it has also been recently applied to studies of dogs (West and Young 2002). In looking time studies, subjects are presented with an event that is thought to violate their expectations of the physical or social world (see Hauser and Carey 1998 for review). Subjects are expected to look longer at an unexpected event that is inconsistent with their expectations than at a control event that is consistent with their expectations. This technique has become important in the field of animal cognition for at least three reasons. First, it provides a method that avoids reliance on a particular motor response or capacity, thereby making it suitable to a potentially wider range of species than techniques that require either species-typical responses (e.g., calling) or actions that are hard for some species to generate (e.g., reaching, pulling, pecking). Second, it provides a method for assessing what animals spontaneously expect about events in the environment without any training. And third, because this technique is so widely used in the field of infant cognition, it provides an excellent approach to human–non-human animal comparative research where patterns of data can be examined in the absence of potentially confounding effects of different methods or training history.

There are two important reasons to use looking time methods to test what tamarins understand about the functionally relevant properties of tools. First, unlike previous searching paradigms, the looking time paradigm allows us to explore what tamarins understand about the relevant features of a tool in the absence of direct physical experience with that tool; because looking time examines what subjects understand when they simply watch events, this paradigm allows us to ask what tamarins know about tools with which they have not yet interacted. The second reason to use looking time to explore tamarins' understanding of functional tools stems from a recent set of findings examining what non-human primates understand about objects and object motion (Hauser 2001; Santos 2003; Santos and Hauser 2002). These results suggest that the capacities that animals exhibit when tested using one methodology do not always converge with those they exhibit using a different methodology. Specifically, recent work has demonstrated that non-human primates who fail to understand a problem when tested with a searching methodology, like the one we have used to test tamarin tool-use in the past (Hauser 1997; Hauser et al. 1999, 2002), sometimes show an understanding of the same problem when tested with a looking time method (see Santos and Hauser 2002). For these reasons, it is argued, we must explore the same cognitive capacity with different methods.

We also wished to examine the role of environmental experience in tamarins' understanding of tools. All animals in our colony have now had experience manipulating objects to gain access to food. Consequently, it is necessary to examine what an experimentally naive population understands about tools they have not yet manipulated and to see whether or not they too attend to the properties that are most important to a tool's function. To explore this possibility, we examined whether an inexperienced population of rhesus macaques (*Macaca mulatta*) spontaneously attends to the relevant features of a tool. The population of rhesus monkeys we tested on the island of Cayo Santiago, Puerto Rico (see Rawlins and Kessler 1987) are semi-free-ranging and have far less experience with artifacts than do our captive tamarins. More specifically, the only direct experience these monkeys have with artifact-like objects is opening a lid to obtain food chow from a small dispenser (see Hauser et al. 1991); they do, of course, have a wide variety of opportunities to manipulate more natural objects (e.g., branches, leaves, coconuts), but none of these involve using one object to act upon another.

In the following three experiments, we allowed both tamarin and rhesus subjects to passively observe a human actor manipulate a tool. We then changed different features of this tool and examined which changes elicited the greatest increases in looking time, corresponding to an unexpected outcome. In the following experiments, we first familiarized subjects to an actor using a small L-shaped stick to displace a grape. Subsequently, we selectively changed the tool's shape and color and observed which of these two featural changes resulted in significant changes in looking time over the baseline, habituation trials. We reasoned that if subjects recognize that shape is more important to a tool's function than color, then individuals should look longer at a differently shaped tool than a differently colored tool performing the same action.

Experiment 1

Method

Subjects

Cotton-top tamarins (*Saguinus oedipus*) are an arboreal New World monkey species endemic to the Colombian rainforests. Individual subjects were born in captivity at the New England Primate Research Center in Southborough, Mass. and subsequently housed in a single room at the Primate Cognitive Neuroscience Lab at Harvard University. All subjects are adults and have had experience in experiments involving both object manipulation (Hauser 1997; Hood et al. 1998; Santos et al. 1999) and passive viewing of objects and events (Hauser and Carey 1998; Hauser 1998; Uller et al. 2001) prior to training. Nine monkeys (EM, EN, ES, ID, PB, RB, SH, SP, UB) were run in this experiment. Subject DD was tested, but his data could not be used due to inattention. Several other monkeys in our colony (AC, JG, MR, RW) could not be tested due to pregnancy or sickness. Three of the participants (EM, SP, UB) had been previously tested in a tool experiment (Hauser 1997; Hauser et al. 1999) and all animals had been previously run in other expectancy violation studies involving both living and non-living objects (Hauser 1998; Santos 1997; Santos and Hauser 1999), but no tools.

Apparatus

We tested subjects inside a Plexiglas testing chamber (45 cm × 40 cm × 60 cm). Subjects have had substantial exposure to this chamber having sat comfortably inside this area for long periods of time (e.g., 30 min), due to previous experiments. We placed the apparatus approximately 50 cm in front of the testing chamber. The objects used in this experiment were sticks made from purple and pink Sculpey clay (Fig. 1). We used two stick shapes: a shape that was functional with respect to the task (an L-shape, 25 cm high, 10 cm base) and a non-functional shape (an L-shape with a stubby base, 25 cm high, 2 cm base). These sticks were used to push a grape (approximately 3 cm in diameter) across a white foamcore stage. The stage consisted of two connected portions: a tall upper platform (15 cm tall × 30 cm long × 15 cm wide) and a ramp (15 cm long) which led down into a lower platform. Along the midline of the upper platform and ramp was a small groove (2 cm wide, 0.5 cm deep) that constrained the grape's path down the ramp after being pushed. A flatter groove near the back of the stage constrained the path of the tool. A portion of the platform and ramp could be occluded using a black foamcore screen (15 cm tall × 30 cm long) which could be inserted into the stage. A video camera placed to the side of the apparatus recorded subject's looking for the duration of the session. Because of the camera's position, the video record only captured the subject and not the experimenter and the apparatus, thereby allowing for coding of looking time blind to condition.

Procedure

We presented each subject with three habituation trials and two test trials (see Fig. 1). The purpose of the habituation trials was to provide subjects with experience of the tool and its actions. In each of these trials, subjects watched the following series of events: The experimenter placed the grape onto the upper platform, then showed the subject the functional tool (e.g., purple L-shaped tool) and placed it at the far end of the upper platform. As the subject watched, the experimenter slid the tool across the upper platform of the stage and then hit the grape with the tool, knocking the grape down the ramp and into the lower platform. Once the grape hit the lower platform, the experimenter called "start" and the subject's looking time was recorded for the next 10 s. This habituation trial was

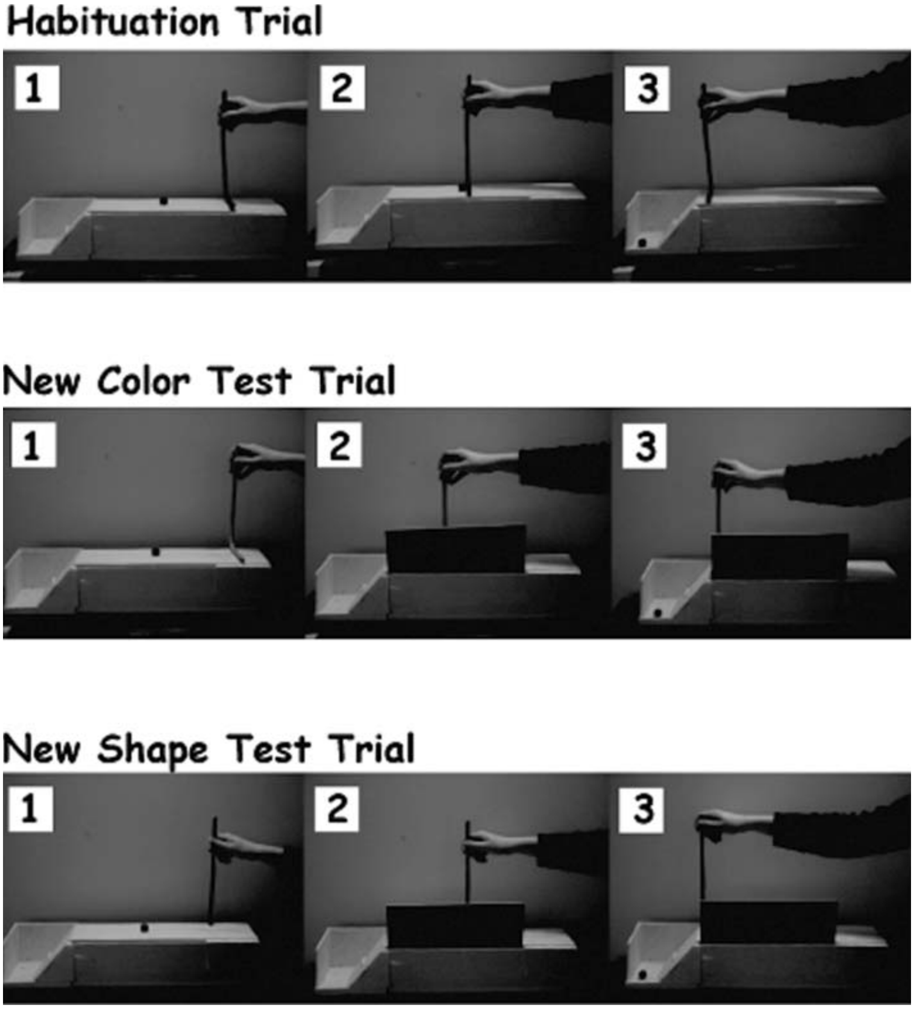


Fig. 1 Habituation and test trials of experiment 1

repeated three times; prior studies have demonstrated that looking times generally decrease over the course of three trials, indicating some level of familiarity (see Santos 1997; Santos and Hauser 1999). Subjects who failed to look at the critical moment the grape was hit or who looked away from the display for over 30 s during presentation were considered inattentive and dropped from the experiment.

After viewing all three habituation trials, subjects were given two test trials: a *new shape* condition and a *new color* condition. In each of these tests, subjects watched as a novel tool acted on the grape. As in the habituation trials, subjects first watched as the experimenter placed the grape onto the upper platform. In the new color condition, the experimenter placed a tool with the same shape but new color (e.g., pink L-shaped tool) onto the far end of the upper platform. The experimenter then inserted the black foamcore screen into the stage to occlude the subject's view of the platform. After inserting the screen, the experimenter slid the tool across the upper platform of the stage and behind the screen. The subject then saw the grape roll down the ramp and into the lower platform. In the new shape condition, the experimenter placed the tool with the new shape but same color (e.g., purple stubby-based tool) onto the far end of the upper platform. The experimenter inserted the black screen into the stage and slid the tool across the upper platform of the stage and behind the screen. The subject then observed the grape roll down the ramp and onto the lower platform. Based on the distance between the base of the tool and the grape, this event should be perceived as unexpected. The newly shaped tool is too short to actually push the grape at its middle position in the groove. Therefore, this event looked unexpected from the perspective of a human observer. In order to keep both test trials consistent, however, neither the new colored tool nor the new shaped tool actually pushed the grape behind the screen; in both test conditions, the experimenter moved the grape manually behind the screen to appear as though it had been pushed. Therefore, the grape moved from behind the screen instantaneously in both test conditions. At the moment the grape hit the lower platform, the experimenter called "start" and the subject's looking was recorded for the following 10 s. As in the habituation trials, subjects who failed to look at the critical moment the grape was hit were dropped from the experiment. Similarly, subjects who looked away from the display for over 30 s during presentation were considered inattentive and dropped from the experiment. The order of the test trials (new shape first or new color first) and the color of the object familiarized (purple or pink) were counterbalanced across subjects.

Videotape scoring

Video records of each trial were transferred to a Power Macintosh G3 using a Radius Video Vision digitizing board and were then analyzed with Adobe Premiere 4.2 software. Two coders scored these digitized sequences (see Hauser 1998; Santos and Hauser 1999; and Uller et al. 2001 for more detailed descriptions of coding tamarin looking time). Because the camera did not record the actions of the tool or the apparatus, both coders were blind to the experimental condition. In addition, one of the coders (CTM) did not participate in testing the subjects and therefore had no knowledge of the conditions that subjects received. Both coders examined looking during each frame (30 frames=1 s) of the 10 s looking period that followed each trial. A "look" for the purposes of these experiments refers to a period of 5 frames or longer during which both the subject's head and eyes were oriented towards the stage (approximately 50° of the subject's visual angle). Inter-observer reliability between the two coders across ten trials was r=0.98.

Subjects

Subjects were adult rhesus monkeys (*Macaca mulatta*) from the Cayo Santiago population (Rawlins and Kessler 1987). The Cayo Santiago field site is run and maintained by the Caribbean Primate Research Center and the University of Puerto Rico, School of Medicine. At the time of experimentation, the population consisted of 1,100 individuals divided into approximately ten social groups. Subjects in this population are well habituated to human observers and can easily be identified because of their chest and leg tattoos. Several experiments have already successfully tested monkeys in this population using the expectancy violation procedure (Hauser and Carey 1998; Hauser et al. 1996; Munakata et al. 2001; Santos and Hauser 2002; Uller 1997). The island is provisioned with Purina monkey chow at three feeding stations. The chow represents approximately 50% of the monkey's diet which is further supplemented by foraging on leaves, flowers, and mineral-rich soil. Water is provided ad libitum throughout the day at a number of sources. Twenty-four monkeys were run in this experiment; data from 21 other subjects could not be used due to subject inattention (i.e., the subject walked away during the presentation), interference from other animals (i.e., another animal approached mid-session), and/or experimental error.

Procedure

We located subjects opportunistically by searching the island for individuals either separated from other group members or in areas of relatively low density; we avoided testing individuals engaged in social interactions or foraging. Two experimenters were involved in running the experiment. One experimenter, kneeling down approximately 1.5 m in front of the animal, operated the foamcore stage and presented the stimuli to the subject. The second experimenter operated the video camera from above the stage and recorded the subject's looking; the video record thus captured the subject but neither the experimenter's display apparatus or his actions. Before testing, the experimenters noted the subject's identity and checked to be sure that the subject was not previously tested in the experiment. All other aspects of the procedure were as described for cotton-top tamarins.

Coding

We coded rhesus looking as in previous experiments (Hauser et al. 1996; Munakata et al. 2001; Santos and Hauser 2002). More specifically, a look for the purpose of coding referred to a period where the subjects' eyes were oriented towards the display. In most cases, the display took up about 30° of the subject's visual angle. Two experimenters coded all trials. As with the tamarins, both coders were blind to the experimental trial number and condition. All other aspects of coding were similar to that described for tamarins.

Results

All subjects appeared to habituate across the first three trials. Subjects looked reliably less on the third habituation trial than the first [*t* (31)=4.29, *P*=0.0002]. We performed a repeated measures ANOVA on the test trial data with species (rhesus or tamarin) as a between subjects factor and condition (shape change or color change) as a within subject factor. We found a main effect of species [*F* (1,30)=11.72, *P*=0.0018]. Across all trials, rhesus monkeys looked significantly longer than the tamarins. More importantly, we observed a main effect of condition [*F* (1,30)=6.17, *P*=0.02]. Subjects looked significantly longer at the shape change condition than the color change condition (see Fig. 2). Non-parametric tests confirmed this result. Across both species, a significant number of individuals looked longer at the shape change condition than the color change condition (Wilcoxon signed rank, *Z*=2.97, *P*=0.0029). There was no interaction between species and condition [*F* (1,30)=1.15, *P*=0.29], suggesting that there was no difference between the pattern of looking across the two species. Both rhesus and tamarins looked longer at the shape change condition than the color change condition.

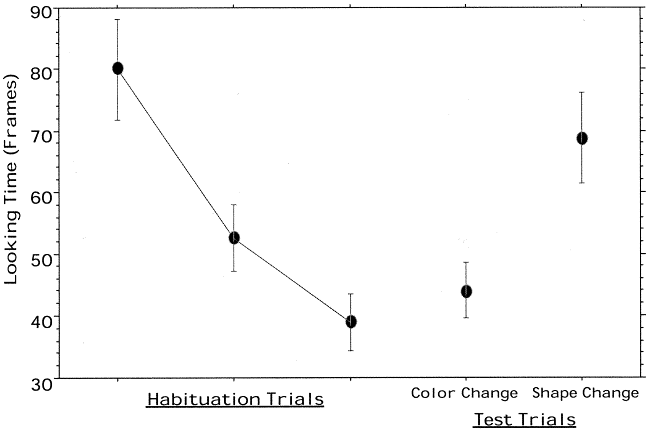


Fig. 2 Mean (±SE) duration of looking in frames (30 frames=1 s) across habituation and test conditions of experiment 1 for both species

Discussion

After being familiarized to a tool acting on a grape, both tamarins and rhesus looked longer at a change in the tool's shape than at a change in the tool's color. This suggests that after being familiarized with one object acting on the grape, both primate species perceived a shape change as more salient than a color change. Specifically, our looking time data imply that tamarins and rhesus see a shape change as functionally relevant with respect to displacing the grape, but classify a color change as functionally irrelevant or perceptually less salient. This result provides further support for studies of tool use in tamarins (Hauser 1997; Hauser et al. 1999, 2002) in which individuals, both adult and infant, attend to shape over color when choosing which of two possible tools to use to obtain an out-of-reach food pellet. In addition, these data also suggest that tamarins and rhesus monkeys are capable of attending to the important functional properties of tools even before they have actually acted on the object. That is, they appear to understand that shape is an important component of a tool's function even before they have had direct experience manipulating the tool. The similarity in the performance of the two groups is interesting in light of the fact that rhesus macaques have far less experience with artifact-like objects than our captive tamarins.

Due to the design of our habituation procedure, subjects were not familiarized with the test stimuli before seeing them act on the grape. Subjects may, therefore, have had an initial baseline preference for the newly shaped tool over the newly colored tool and this may have contributed to the increase in looking to the newly shaped tool. To explore this alternative hypothesis, we ran another version of the same expectancy violation experiment. In this experiment, however, we employed a familiarization design (see Hauser et al. 1996; Munakata et al. 2001; Santos and Hauser 2002) instead of the habituation procedure. Before running the test trial, in which an actor used one of two tools to displace a grape, we first familiarized subjects to the two canes. If subjects' performance in experiment 1 was due to a baseline preference for the new shape, then subjects should also show the same baseline preference in these familiarization trials. Alternatively, if subjects looked longer at the non-functional new shape test condition because they considered this event unexpected, then subjects should show no preference for the non-functional tool in the familiarizations but still show the same pattern of looking across test trials.

Experiment 2

Method

Subjects

Eleven cotton-top tamarins (AC, EM, EN, ES, ID, JG, RB, RW, SH, SP, UB) were run in this experiment. Data from one monkey was dropped due to inattention (DD). Two other monkeys could not be tested due to sickness (MR) or misbehavior (PB). Approximately 10 months had elapsed between testing for experiment 1 and experiment 2.

Procedure

We presented subjects with three familiarization trials and two test trials using the same apparatus and stimuli as experiment 1 (see Fig. 3). The first two of these trials served to familiarize the subject with the two featural changes they would witness in the two test trials. In neither trial did subjects witness the experimenter perform any actions on the grape. They were, however, allowed to observe the original tool with a new color but same shape (*new color familiarization*) or with a new shape but the same color (*new shape familiarization*). In these trials, the experimenter placed the grape in the middle of the upper platform. We then presented subjects with a tool with one feature altered – either color or shape. The tool then slid up to the grape, stopping approximately 0.5 cm before touching the grape. The experimenter then called “start” and the duration of the subject’s looking at the display was recorded for the following 10 s. All subjects were first given these two familiarization trials (in a counterbalanced order) followed by the *action familiarization*.

In the action familiarization, subjects watched the event used to habituate subjects in experiment 1. Specifically, the experimenter placed the grape onto the upper platform, showed the subject the functional tool and placed it at the far end of the upper platform. The experimenter then slid the tool across the upper platform of the stage and hit the grape with the tool, knocking the grape down the ramp and into the lower platform. At the moment the grape hit the lower platform, the experimenter called “start” and the subject’s looking time was recorded for the next 10 s.

After viewing all three familiarization trials, subjects were given two test trials, the *new shape* condition and the *new color* condition, as in experiment 1. The order of the test trials (new shape first or new color first) and the color of the object familiarized (purple or pink) were counterbalanced across subjects.

Subjects

We tested 24 rhesus macaques. None of the subjects had previously participated in experiment 1. Data from 39 other monkeys could not be used due to subject inattention, interference, and/or experimental error. Approximately 1 week had elapsed between testing for experiments 1 and 2.

Procedure

We presented rhesus subjects with the same familiarization and test trials as the tamarins. The actual testing procedure was identical to that of experiment 1 for the rhesus macaques.

Results

There was no difference in looking time between the two types of familiarization trials [*t* (34)=16, *P*=0.87]. Subjects looked equally at the new color familiarization (*M*= 67.29 frames) and the new shape familiarization (*M*= 66.17 frames). We performed a repeated measures ANOVA on the test trial data with species (tamarin or rhesus) as a between subject factor and condition (shape test trial or color test trial) as a within subjects factor. There was no main effect of species [*F* (1,33)=0.183, *P*=0.67]. There was, however, a main effect of condition [*F* (1,33)=5.2, *P*=0.029]. Subjects looked reliably longer at the new shape test trial than the new color test trial (see Fig. 4). Non-parametric tests confirmed this finding. Twenty-four out of 35 subjects looked longer at the new shape test condition than the new color test condition (Wilcoxon signed rank, *Z*=2.91, *P*=0.0036). In addition, there was no interaction between species and condition [*F* (1,33)=1.2, *P*=0.28] suggesting that both species demonstrated longer looking at the new shape test trial than the new color test trial.

Discussion

Experiment 2 replicated the main result of experiment 1; both captive tamarins and free-ranging rhesus macaques looked reliably longer on the test trial involving a shape change than on a test condition involving a color change. More importantly, however, subjects looked equally on the new shape and new color familiarization trials. This suggests that the pattern of results observed in experiment 1 is not due to a baseline preference for the newly shaped tool. Instead, results suggest that subjects looked longer at the new shape test trial because this represents a more significant featural alteration than does color with respect to the tool’s capacity to displace the grape.

Why do subjects find the new shape test trial unexpected, more interesting to look at? One possibility is that subjects may have attended more to the new shape condition because they considered the act of the short cane pushing the grape to be physically impossible. In other words, they may have attended to the *functional properties* of the cane and recognized that the new cane was not long enough to push the grape down the ramp. As such, when

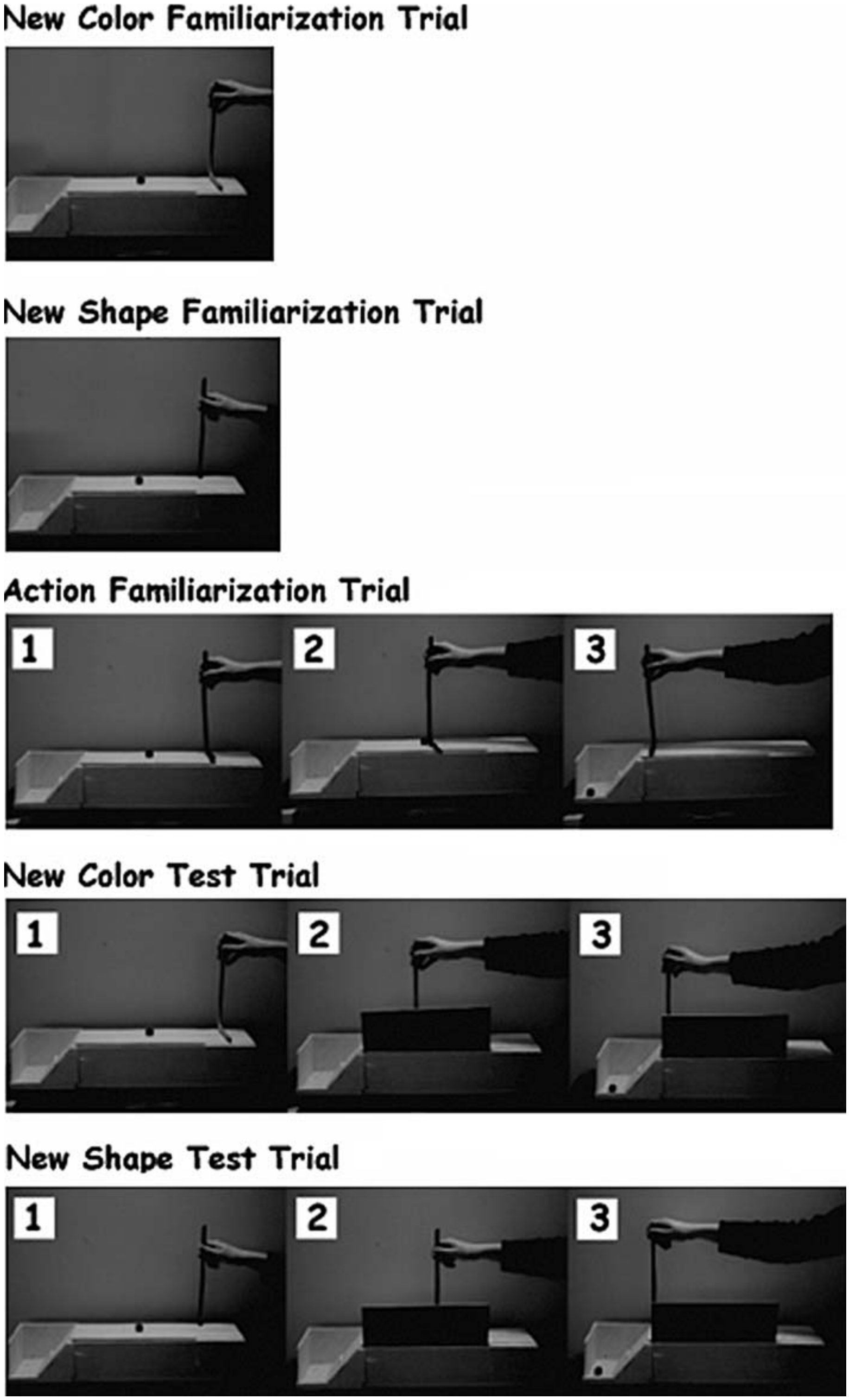


Fig. 3 Familiarization and test trials of experiment 2

the non-functional cane pushed the grape down the ramp, their expectations were violated. Alternatively, subjects may have looked longer at the shape change because, for this particular object, a shape change is inherently more salient than a color change, independent of its function.

Experiment 3 was designed to test between these two alternative hypotheses. The procedure was a familiarization paradigm identical to that of experiment 2, except that instead of changing the shape of the tool during the new shape condition, the same object was simply inverted, changing its orientation. Although there is no shape change caused by inverting the L-shaped tool, there is a change in its functional properties; the upside-down L-shaped tool is no better at pushing the grape than the non-functional

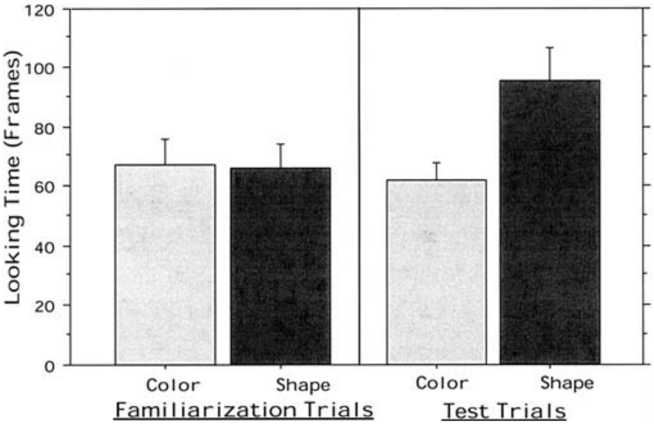


Fig. 4 Mean (±SE) duration of looking in frames (30 frames=1 s) across familiarization and test conditions of experiment 2 for both species

stubby-based tool; this manipulation mirrors experiments 3 and 4 of Hauser (1997) in which tamarins picked a novel, functionally appropriate tool over the original and familiar blue cane oriented upside down, and thus functionally inappropriate for the task at hand. If subjects in experiments 1 and 2 looked longer at the shape change because they were attending to the functional properties of the tool, then they should show a similar pattern in this experiment; namely, they should look longer at the upside-down L-shaped tool condition than at the color-change condition. However, if subjects' performance in experiment 1 was due to the fact that they were merely detecting shape changes (as opposed to function changes), then they should look equally at the orientation and color-change test conditions.

Experiment 3

Method

Subjects

Twelve cotton-top tamarins (AC, EM, EN, ES, ID, JG, MR, RB, RW, SH, SP, UB) participated in this experiment; all subjects except MR had participated in experiment 2. Data from one subject (DD) were excluded due to inattention during test conditions and one subject (PB) was not run due to misbehavior. Experiments 2 and 3 were separated by 4 days.

Procedure

The procedure and coding of experiment 3 was exactly the same as for experiment 2 except that the new shape familiarization and test trial conditions were replaced with *new orientation* conditions in which an upside-down L-shaped tool was used (see Fig. 5).

Subjects

Thirty rhesus monkeys from the Cayo Santiago population participated. None of these individuals had been tested in experiments 1 or 2. The data of 16 other animals were excluded from the final dataset due to subject inattention, interference from other animals, and/or experimental error.

Procedure

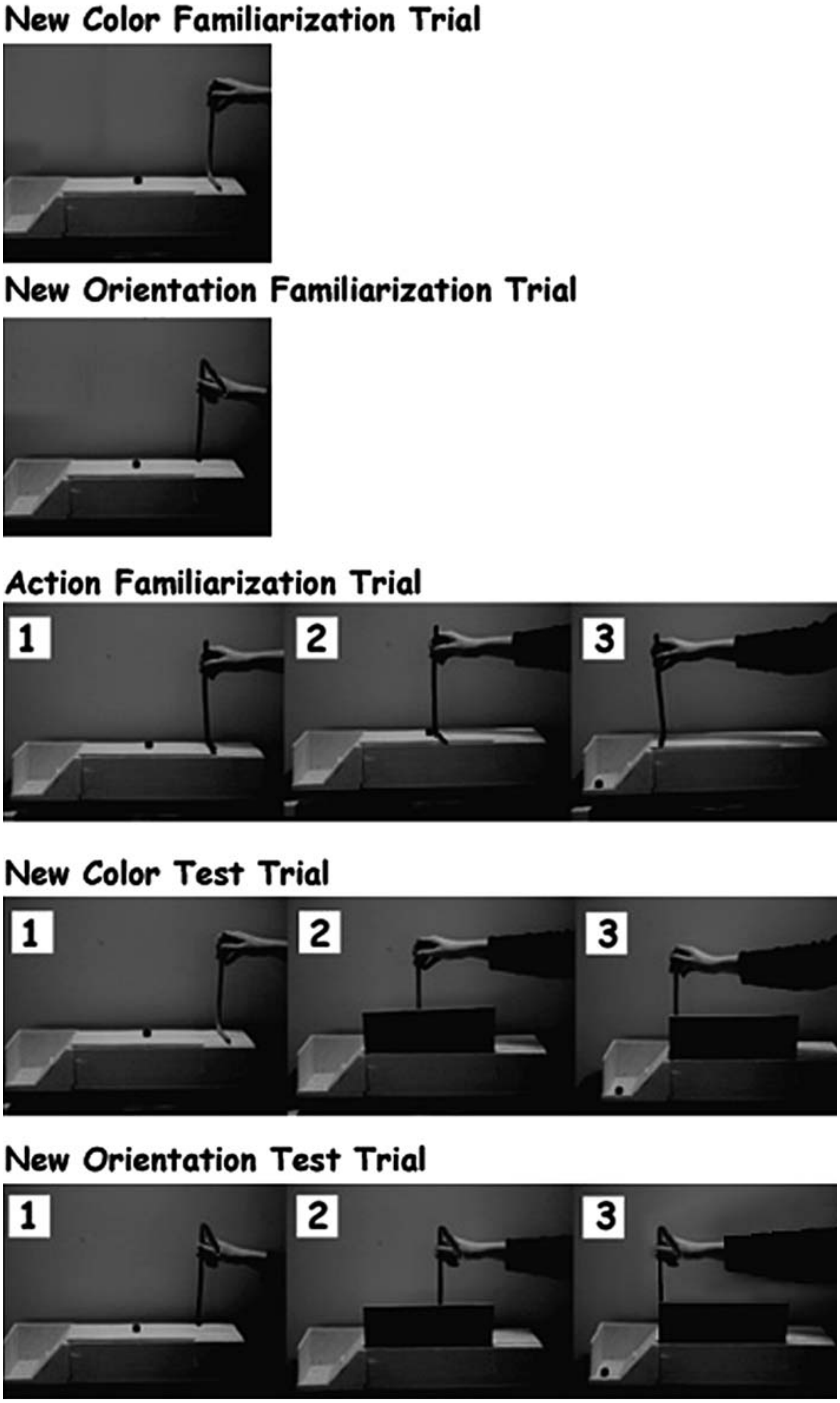
The test conditions for rhesus subjects were as described for tamarins and the procedure modeled that used in the previous experiments.

Results

There was no difference in looking time across familiarization trials [*t* (41) =0. 76, *P*=0.45]. Subjects looked equally at the new color familiarization (*M*=102.52 frames) and the new orientation familiarization trials (*M*=93.88 frames) (Fig. 6). We performed a repeated measures ANOVA on the test trial data with species (tamarin or rhesus) as a between subjects factor and condition (new orientation test trial or new color test trial) as a within subjects factor. This analysis revealed no main effect of species [*F* (1,40)=0.17, *P*=0.69]. Subjects looked longer at the new orientation test trial than the new color test trial, but this difference was not significant [*F* (1,40)=2.77, *P*=0.10]; there was a non-significant interaction of species and condition [*F* (1,40)=3.15, *P*=0.08]. Follow-up t-tests revealed that while tamarin subjects looked longer at the new orientation condition than the new color condition [*t* (11)=3.36, *P*=0.0063], rhesus subjects showed no difference in looking across the different test conditions [*t* (29)=-0.092, *P*=0.93]. Non-parametric statistics supported this pattern as well. While 10 out of 12 tamarins looked longer at the new orientation condition (Wilcoxon signed rank, *Z*=2.43, *P*=0.02), only 17 out of 30 rhesus did the same (*Z*=-0.45, *P*=0.65).

To further explore this interaction, we combined the data from experiment 3 with that of experiment 2. We entered both into a repeated measures ANOVA with experiment (shape change or orientation change) and species (tamarin or rhesus) as between subject factors and condition (new function test or new color test) as a within subject factor. There were no main effects of experiment [*F* (1, 73)=1.0, *P*=0.31], and there was no main effect of species [*F* (1, 73)=0.34, *P*=0.56], suggesting that tamarins and rhesus monkeys do not differ in their overall duration of looking across all conditions. There was, however, an overall main effect of condition [*F* (1, 73)=7.97, *P*= 0.0061]. Collapsing across experiment and species, subjects tended to look longer at the shape/orientation-change test trials than the color-change test trials. The only statistically significant interaction was the three-way interaction between experiment, species, and condition [*F* (1, 73)=4.03,

Fig. 5 Familiarization and test trials of experiment 3



P=0.048]. Although the difference between looking on the new shape/orientation condition and the new color condition differed across experiments for the rhesus monkeys, it did not differ across the two experiments for the tamarins (Fig. 7). In other words, rhesus monkeys demonstrate a different pattern across the two experiments than tamarins, detecting the function change violation only when it was associated with an actual shape change as opposed to an orientation change. Tamarins, in contrast, show the same pattern across both the shape and orientation change violations.

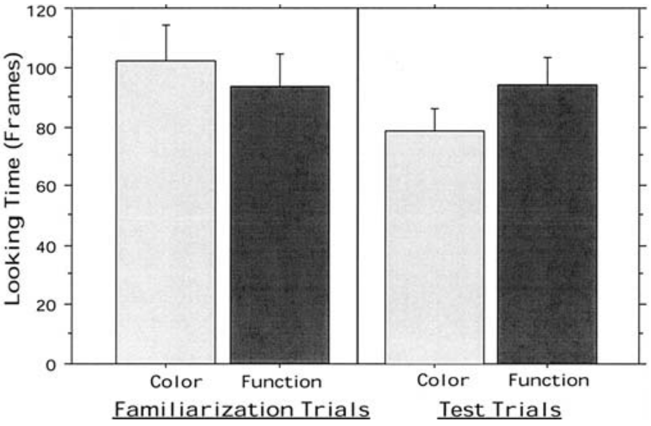


Fig. 6 Mean (±SE) duration of looking in frames (30 frames=1 s) across familiarization and test conditions of experiment 3 for both species

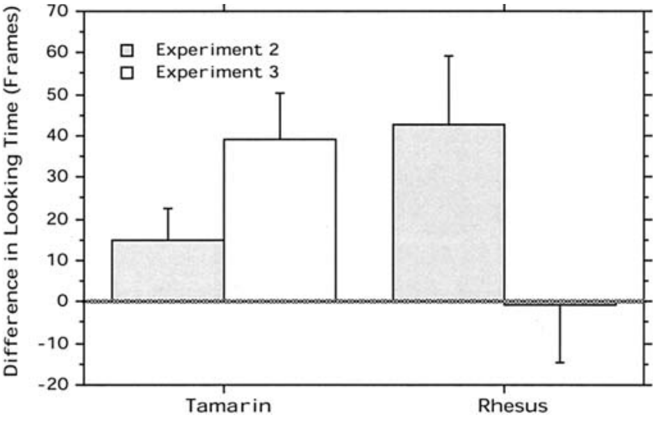


Fig. 7 Mean (±SE) difference in looking time (function-change test minus color-change test) across experiment and species

Conclusions

As in experiments 1 and 2, tamarins looked longer at the non-functional tool acting on the grape than a newly colored, but functional tool. This suggests that after watching a tool act on an object, subjects do not expect the same tool to perform the same action with a non-functional orientation. In addition, this result indicates that during experiments 1 and 2, tamarins attended to more than the tool's shape; in both experiments, they attended to the functional relationship between the tool and the grape.

This result is consistent with the findings of Hauser (1997) and Hauser et al. (2002) which suggested that tamarins reliably choose the most functional tool even when its properties are different from the tools with which they had previously been trained. However, unlike Hauser's previous tool studies, subjects in this experiment had no direct experience with these tools before generalization. Although the subjects in these experiments have had experience with flat cane-like tools used to pull objects (see Hauser 1997; Hauser et al. 1999), they have had no experience with L-shaped pushing tools like those used in these experiments. These results suggest that at least one population of tamarins has some understanding of how a tool functions even in the absence of physical experience with that particular tool. These results also extend the range of actions that a tool can take on, ranging from pulling a cloth or cane, to pushing a stick.

Unlike tamarins, however, rhesus monkeys show no difference in looking time to a familiar but inverted tool acting on a grape than to a newly colored tool acting on the grape. Apparently, rhesus perceive the inverted tool as a functionally possible one with respect to displacing the grape down the ramp. Most importantly, this result suggests that in experiments 1 and 2, rhesus were not attending to the functional features of the newly shaped cane. Instead, it seems that they were more interested in a change in the object's shape than in a change in its color. Consequently, it appears that tamarins and rhesus attend to slightly different aspects of the tool in these experiments. While rhesus appear to attend only to the tool's overall shape, tamarins attend to more specific aspects of the tool, namely the length of its base in relation to the position of the grape. As such, this pattern of results suggests that of the two species tested, only tamarins, who have had experience acting on other artifact-like objects, are capable of attending to the specific aspects of the tool that are relevant to its subsequent actions.

It is important to note that although rhesus do not attend to the particular features of the tool that are relevant for this specific task, they do selectively attend to overall shape over color in experiments 1 and 2. This result raises the question of why rhesus attend to changes in shape in this experiment even though they do not detect the specific functional relationship between the tool and the grape? One possibility is that rhesus have a general, heretofore unexplained tendency to look longer at shape changes than at color changes. This explanation seems unlikely given other results from the same Cayo Santiago rhesus population (Santos et al. 2001; Santos et al. 2002). In a recent series of experiments, Santos et al. (2001) examined the properties that rhesus monkeys attend to when categorizing novel food objects. In these experiments, an experimenter ate a novel object in front of a test subject (e.g., a green sphere made of Play-Doh clay). After this presentation, subjects were given a choice of two objects whose features differed in one dimension from the originally eaten object (e.g., a green cube versus a pink sphere). Results suggest that rhesus selectively attend to the property of color when choosing between possible food objects, always choosing the similarly colored object over the similarly shaped object. Santos and colleagues also found that rhesus did not respond to a novel food's shape change even when all other features were held constant. Specifically, subjects who witnessed an experimenter eating a green sphere and were given a choice between a green square and a green sphere choose randomly. Finally, if an experimenter places a green sphere in her ear or rolls it around on the ground, and then offers subjects a choice between a green square and an orange sphere, no preference is found, suggesting that the color biases observed have something specifically to do with eating. As such, it seems that when choosing between food objects rhesus monkeys seem to ignore coarse-grained changes in a food's shape. These results suggest that rhesus monkeys' attention to shape as demonstrated in experiments 1 and 2 is not a consistent bias. For rhesus monkeys, shape changes are not equally salient for all domains of objects; for one domain – food objects – rhesus selectively attend to color over shape. We argue that a general shape bias cannot explain rhesus monkeys' selective attention to shape in these experiments. Instead, we believe that rhesus attend to a change in a tool's shape because they are biased to detect the functionally relevant feature of shape when perceiving the actions of a tool.

In contrast with rhesus macaques, tamarins' capabilities seem to extend beyond a simple selective attention to shape. Our results indicate that tamarins attend to more than just a tool's shape; they seem to pay attention to the relationship between the base of the tool and the location of the grape. This pattern of performance raises the question of why tamarins have a more sophisticated understanding of the functional properties of tools than rhesus macaques. We see two possibilities for this difference. One possibility is that tamarin subjects gained a better understanding of the task because they had more experience with this experiment. Although none of the rhesus were tested on more than one experiment, most of our tamarin subjects were tested on all three experiments. It is possible, then, that the additional exposure to the pushing tool allowed them to gain a better understanding of the task. A second explanation, however, is that rhesus macaques as a species inherently lack the capacity to understand sophisticated functional relations. To date, there is little evidence that rhesus macaques use tools in the wild and few studies have explored tool-using abilities of captive rhesus monkeys (see Tomasello and Call 1997). As such, rhesus may simply lack the ability to comprehend the function of objects as tools. The third possibility for the difference we observe appeals to an experiential difference between captive and natural-living populations. Our tamarins' understanding of the specific functional properties of the pushing tool is likely to be related to their experience with other artifact-like objects in their daily lives. It is possible, then, that more naturally reared tamarins start out with an understanding that is much like that of rhesus monkeys under natural conditions. As a function of manipulating other tools during laboratory experiments (and therefore attending to both global shape and orientation), they may eventually refine their understanding of the relevant properties of objects and subsequently master which specific aspects of shape are relevant to a tool's functionality in a particular task. This hypothesis makes the prediction that rhesus macaques given additional experience with other artifact-like objects would, like tamarins, be able to learn more about the relationship between shape and functionality. It also predicts that naïve tamarins who lack direct experience with tools would perform similarly to the Cayo Santiago macaques on this task, attending to global changes in a tool's shape but not to more subtle changes in a tool's function.

In conclusion, we have provided evidence that both cotton-top tamarins and rhesus macaques selectively attend to a tool's shape when passively observing it function. These data suggest that both tool-experienced and tool-inexperienced primates are biased to attend to global shape when representing functional objects. This initial bias to attend to global shape may pave the way for further learning about a tool's function, perhaps yielding a deeper understanding of the properties that matter for a tool's operation. It is possible, then, that such a rich understanding of tools is restricted to humans and other highly experienced non-human primates.

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References

Boesch-Achermann H, Boesch C (1993) Tool use in wild chimpanzees: new light from dark forests. Curr DirPsychol Sci 2: 18–21

Brown A (1990) Domain-specific principles affect learning and transfer in children. Cogn Sci 14:107–133

Chappell J, Kacelnik A (2002) Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). Anim Cogn 5:71–78

Hauser MD (1997) Artifactual kinds and functional design features: what a primate understands without language. Cognition 64:285–308

Hauser MD (1998) A nonhuman primate's expectations about object motion and destination: the importance of self-propelled movement and animacy. Dev Sci 1:31–38

Hauser MD (2000) Wild minds: what animals really think. Holt, New York

Hauser MD (2001) Searching for food in the wild: a nonhuman primate's expectations about invisible displacement. Dev Sci 4:84 – 93

Hauser MD, Carey S (1998) Building a cognitive creature from a set of primitives: evolutionary and developmental insights. In: Cummins D, Allen C (eds) The evolution of mind.. Oxford University Press, Oxford, pp 51–106

Hauser MD, Perry S, Manson J, Ball H, Williams M, Pearson E, Berard J (1991) It's all in the hands of the beholder: new data on handedness in a free-ranging population of rhesus macaques. Behav Brain Sci 14:342–344

Hauser MD, MacNeilage P, Ware M (1996) Numerical representations in primates. Proc Natl Acad Sci 93:1514–1517

Hauser MD, Kralik J, Botto-Mahan C (1999) Problem solving and functional design features: experiments on cotton-top tamarins (*Saguinus oedipus*). Anim Behav 57:565–582

Hauser MD, Pearson HM, Seelig D (2002) Ontogeny of tool-use in cotton-top tamarins (*Saguinus oedipus*): innate recognition of functionally relevant features. Anim Behav 64:299–311

Hood BM, Hauser MD, Anderson L, Santos L (1998) Gravity biases in a nonhuman primate? Dev Sci 1:35–41

Matsuzawa T (1994) Field experiments on use of stone tools by chimpanzees in the wild. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) Chimpanzee cultures. Harvard University Press, Cambridge, Mass., pp 351–370

McGrew WC (1992) Chimpanzee material culture: implications for human evolution. Cambridge University Press, Cambridge

McGrew WC (1994) Tools compared: the material of culture. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG (eds) Chimpanzee cultures.Harvard University Press, Cambridge, Mass., pp 25–40

Munakata Y, Santos LR, Spelke ES, Hauser MD, O'Reilly RC (2001) Visual representation in the wild: how rhesus monkeys parse objects. J Cogn Neurosci 13:44–58

Povinelli DJ (2000) Folk physics for apes. Oxford University Press, Oxford

Rawlins RG, Kessler MG (1987) The Cayo Santiago Macaques: history, behavior, and biology. SUNY Press, Albany

Santos LR (1997) Precursors to a theory of mind: insights from a nonhuman primate. Unpublished honors thesis, Harvard University, Cambridge, MA

Santos LR (2003) "Core knowledges": a dissociation between looking and searching in a non-human primate. Dev Sci (in press)

Santos LR, Hauser MD (1999) How monkeys see the eyes: cotton-top tamarins' reaction to changes in visual attention and action. Anim Cogn 2:131–139

Santos LR, Hauser MD (2002) A nonhuman primate's understanding of solidity: dissociations between seeing and acting. Dev Sci 5:F1-F7

Santos LR, Ericson BN, Hauser MD (1999) Constraints on problem solving and inhibition: object retrieval in cotton-top tamarins (*Saguinus oedipus oedipus*). J Comp Psychol 113: 186–193

Santos LR, Hauser MD, Spelke ES (2001) Recognition and categorization of biologically significant objects by rhesus macaques (*Macaca mulatta*): the domain of food. Cognition 82:127–155

Santos LR, Sulkowski GM, Spaepen GM, Hauser MD (2002) Object individuation using property/kind information in rhesus macaques (*Macaca mulatta*). Cognition 83:241–264

Spelke ES (1985) Preferential-looking methods as tools for the study of cognition in infancy. In: Gottlieb G, Krasnegor NA (eds.) Measurement of audition and vision in the first year of postnatal life: a methodological overview. Ablex, Stamford, Conn., pp 323–363

Spelke ES (1991) Physical knowledge in infancy: reflections on Piaget's theory. In: Carey S, Gelman R (eds) The epigenesis of mind: essays on biology and cognition. Erlbaum, Hillsdale, NJ, pp 37–61

Tomasello M, Call J (1997) Primate cognition. Oxford University Press, Oxford

Uller MC (1997) Origins of numerical concepts: a comparative study of human infants and nonhuman primates. Doctoral dissertation, Massachusetts Institute of Technology. Diss Abstr Int Sect B Sci Eng 58:3-B

Uller C, Xu F, Carey S, Hauser MD (1997) Is language needed for constructing sortal concepts? A study with nonhuman primates. In: Hughes E (ed.) Proceedings of the 21st Annual Boston University Conference on Language Development, pp 665–677

Uller C, Hauser MD, Carey S (2001) Spontaneous representation of number in cotton-top tamarins (*Saguinus oedipus*). J Comp Psychol 115:248–257

Visalberghi E, Limongelli L (1994) Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella)*. J Comp Psychol 108:15–22

Visalberghi E, Tomasello M (1998) Primate causal understanding in the physical and psychological domains. Behav Process 42:189–203

Visalberghi E, Trinca L (1989) Tool use in capuchin monkeys: distinguishing between performance and understanding. Primates 30:511–521

West RE, Young RJ (2002) Do domestic dogs show any evidence of being able to count? Anim Cogn 5:183–18

Westergaard GC, Suomi SJ (1995) The stone tools of capuchins (*Cebus apella*). Int JPrimatol 16:1017–1024

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. Nature 399:682–685