Short Articles

Behavioral Flexibility and Tool Selection in a Tufted Capuchin Monkey (*Cebus apella*)

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Introduction

Capuchin monkeys use a variety of tools in many different contexts in captivity (Visalberghi, 1987, 1990, 1993; Ritchie and Fragaszy, 1988; Westergaard and Suomi, 1994; Tomasello and Call, 1997; Fragaszy *et al.*, 2004b), in semi free-ranging conditions (Ottoni and Mannu, 2001) and in the wild (Fragaszy *et al.*, 2004a; Moura and Lee, 2004; Mannu and Ottoni, 2005; but see Panger, 1998). In terms of tool variety and the multiple contexts in which tools are used, capuchins are similar to great apes in tool-using behavior (Anderson, 1996). Some argue that the ability to use tools requires the cognitive ability to establish a relationship between the object and the environment in order to implement anticipated external effects (Reynolds, 1982; Ingold, 1987). Research on tool-using behavior in non-human primates has often described tool-use performance without analyses of the underlying cognitive processes (Visalberghi and Limongelli, 1996), although noteworthy exceptions are found in the classic works of Köhler (1925) and Yerkes (1927, 1943). In terms of the relationship of cognition and intelligence to tool use, there may be little similarity between capuchins and the great apes. There is growing evidence that apes understand what they are doing when using tools (e.g. Boesch, 1992; McGrew, 1992), but this has not been shown for capuchins. To compare, in a context of tool use, the cognitive abilities of chimpanzees (or other primate species) and those of capuchin monkeys, we must look for the underlying mental program that both guides and is expressed in tool-using behavior.

In this study, we do not assume *a priori* that capuchins are less, more or equally intelligent than other primate species. Capuchins, just like chimpanzees, humans, whales or any other species, possess a particular and limited suite of cognitive capacities. Here we describe the results of an experiment that evaluated the ability of a capuchin monkey to select appropriate tools in a nut-cracking task. We also speculate on the possible factors involved in tool selection.

Materials and Methods

Subjects
A group of capuchin monkeys (*Cebus apella* sp.) were housed on a small island within a zoo setting (Parque Ecológico Municipal Eng° Cid Almeida Franco, Americana, São Paulo, Brazil). The alpha male was the experimental subject. He was an adult, wild-born and raised in captivity. He monopolized almost every new object in the small home island and prevented regular access to them by the other animals, leaving us without much choice regarding experimental subjects. It was not possible to remove the alpha male from the island. As the other monkeys had only unpredictable access to the objects, it was not possible to apply the experimental protocol to them in any regular or reliable manner. However, a juvenile male and an adult female that used tools on some occasions were included for qualitative comparisons. All three monkeys had been observed to spontaneously use tools (see below) and/or took part in other tool use experiments (Jalles-Filho *et al.*, 2001), and were thus proficient in the use of tools.

Test phase
In each trial the subject was offered one of three stones (cobbles of quartzite) of similar shape but different sizes (large: 1,565 g; medium: 915 g; small: 110 g), and one nut. Twenty trials were performed per stone (17 for the small stone). A trial began when the subject held the stone in his hands to give the first blow, and ended when the nut was broken. The time and the number of blows required to complete the task were recorded. Here, "nut" actually refers to the fruits of *Terminalia* spp. (Combretaceae), a species that is found in the zoo. Monkeys were observed to crack these fruits spontaneously with the assistance of stones naturally available on the island. This fruit has a soft external layer and, underneath it, a second fibrous and hard layer, which has to be broken in order to reach the edible seed, something the monkeys could do only with the assistance of tools. We draw attention to the fact that the test phase was not designed to give the subjects experience with the different stones. Instead, it was conceived to guide us in evaluating the magnitude of the effect of stone size on the efficiency of accomplishing the task.

Experimental phase
The same three stones of different sizes were simultaneously presented to the subject, and a single nut was offered. Criteria for the starting and ending of the trials were the same as in the test phase, unless the nut was left undisturbed for three minutes, in which case the trial ended. In each trial, the order of lateral placement of the stones was altered. A total of 50 trials were performed. Both phases were videotaped for subsequent analysis.

Qualitative analysis
The two comparison subjects were videotaped in situations of tool use identical to those performed by the experimental subject.

Results

During the test phase, there was a significant effect of stone size on the number of blows required to complete the task (Kruskal-Wallis ANOVA χ^2 (17, 2) = 36.95, p < 0.0001,

Table 1. Summary of tool-using activities in the test phase. (Trials: LS and MS, n = 20; SS, n = 17.) LS (large stone); MS (medium stone); SS (small stone).

Type of stone	Number of blows	Mean per trial (x ± SE)	Time (s)	Mean per trial (x ± SE)
Large Stone	67	3.35 ± 0.43	135.52	6.78 ± 1.12
Medium Stone	82	4.1 ± 0.34	157.91	7.9 ± 0.9
Small Stone	381	22.41 ± 1.9	739.04	43.47 ± 6.44

Monte Carlo method; see Table 1). Post-hoc tests revealed that use of the small stones required significantly more blows than the medium or large stones (Nemenyi-Dunn multiple comparisons test, for samples of unequal size, $p < 0.0001$). However, there was no significant difference in number of blows required between the large and medium stones (Mann-Whitney Test: $U = 144.0$; $p = 0.134$ – exact test, two-tailed). Since the assumption of sphericity required for a repeated measures ANOVA was violated (Mauchly's sphericity test, $w = 26.72$, $p < 0.0001$), we compared the duration data across conditions with a repeated measures MANOVA, which showed a significant difference across the different stone sizes (R (2, 15) = 18.62, $p < 0.0001$). The values associated with the small stone were again responsible for the difference (Spjøtvoll-Stoline test for unequal sample sizes, $p < 0.001$). The large and medium stones did not differ significantly in time to task completion (Student's *t*-test for independent samples, $t = -1.54$, $p > 0.05$, two-tailed). In the analysis of the experimental phase, the subject excluded the small stone as an operative tool, but did not differentiate between the other two, using the large stone during 28 trials and the medium one during the other 22 trials (two-tailed binomial test, $n = 50$, $p > 0.5$).

Discussion

When given the choice between three different stone sizes, the experimental subject rejected the small stone as a useful tool, but did not differentiate between the other two. The subject's use of the large and medium stones did not differ with regard to the number of blows or in relation to the time necessary to complete the task, and the movements executed by the subject were exactly the same in both cases. Thus, the only differential factor, in terms of metabolic expenditure and muscular cost involved, was the magnitude of the load. Note that a weight difference of 650 g (between the medium and large stones) is probably a quite considerable one given the range of adult male weights for the species (4.0–4.5 kg: Rowe, 1996). If the subject was choosing tools in order to minimize energetic costs, a preference for the medium category should be expected, but this prediction was not confirmed by the experimental data. Please note that in our analyses, there is an assumption of a difference in energetic expenditure between the medium and large stones, and an assumption that energetic efficiency, not time efficiency, is what the monkey should maximize. These assumptions are based on the conditions of the experiment, with a large weight difference between the stones, and the captive setting, where animals are usually freed from time constraints. However, until detailed measures of energetic expenditure under different conditions are carried out, our first assumption remains speculative. If there is no significant difference in energetic expenditure and/or if time is the variable being minimized, then one should expect the observed lack of preference between the medium and large stones as tools.

Bearing the above caveat in mind, the choices made by the subject (exclusion of the small stone) could be credited to an interaction between persistence of behavioral patterns and physical features of the tool. During the test phase, the individual repeatedly picked up the small stone bimanually (like he did with the other stones), a cumbersome technique that proved very ineffective. The small stone's performance as a tool was about five to six times worse than the other tools, even though it was eight and 14 times smaller than the medium and large stones respectively. One might expect that the subject would adapt his manual behaviour to best fit the tool in question (e.g., by picking it up with only one hand), but this did not happen. We speculate that, if the subject had changed his behavior, the small stone could have been a reasonable choice in terms of energetic expenditure. It is relevant that he did not change his behaviour even once over the course of 17 test trials, nor try to explore the small stone further as a potential tool over the 50 experimental trials. The two comparative subjects were also resistant to any change of established patterns of manipulative behaviour. The juvenile male engaged in a similar sequence of movements to the alpha male and, when presented with the small stone, persisted in this behavioral pattern, incurring the same difficulties as the experimental subject. The adult female employed a different technique to break the nuts. However, like the others, she never varied her movement pattern regardless of the conditions of the task. Her behavioural pattern, which was already less efficient when compared to the one exhibited by the males, made the technique absolutely ineffective with the small stone because of the reduced magnitude of the load.

These findings suggest that the choices made by the capuchins do not spring from a more detailed means-end analysis, but seemingly from gross physical limitations or restrictions only, in a context of behavioral persistence. That is, the experimental subject only rejected the very inefficient tool, but did not choose the most energetically efficient of the other two. Furthermore, the rejection seems to result from behavioural inflexibility, which made the small stone a very inefficient implement, although it seemed to have the potential to be the opposite. This reinforces previous doubts of capuchin behavioral flexibility and other cognitive capacities, as shown in Jalles-Filho *et al.* (2001). We observed the continuous reactivation of previous manipulative action patterns, with the monkeys always applying one and the same set of movements, apparently blind to the changes in the external conditions, even when a change was needed. In terms of the concept of tool mentioned above, we suggest that the mental program used by the individual to implement the operations over the environment was lacking in complexity from the outset. A sufficiently complex program would permit new elements to be incorporated, and also the selection and combination of previous elements, producing completely new arrangements of whole motor patterns.

Previous studies of tool selection or modification (partly reviewed in Fragaszy *et al.*, 2004b) have yielded mixed results when compared the present study. In all cases, there are differences in experimental design, some of them subtle, which may explain the discrepancies. For example, Antinucci and Visalberghi (1986) have shown that a capuchin monkey was able to use three different kinds of objects (a stone, a piece of wood, and a plastic container) as hammers to crack open hazelnuts and walnuts. More importantly here, they reported that the monkey showed a strong preference for the stone, followed by the wood, with near rejection of the plastic container. The authors did not analyze the time or the number of blows required by each tool to fulfil the task. They noted qualitatively that the stone was much more effective, the piece of wood less so, and the plastic container was completely ineffective. Thus, the monkeys were selecting only for effectiveness, not effectiveness *and* energetic efficiency, as in our case. Their subject, similar to ours, showed rejection of a useless tool (although he still attempted to use it a few times). However, we believe that due to its very small weight (40 g), this tool was so ineffective that no change in behavior would make it valuable, in contrast to the small stone in our study.

Visalberghi and Trinca (1989) have shown that capuchin monkeys were able to solve three conditions of a tube task in which the tools required modification before use, but that the monkeys kept performing errors throughout the course of those experiments. Note that, in order to be effective, the monkeys had to modify the tools, not their motor patterns when using them — an approach which was not possible in our test phase, since the tool could not be modified. Behaviorally, their monkeys made various different attempts, but always by performing the same general action (trying to insert something in the tube), which was absolutely useless in some cases. Thus, there was some rigidity in behavioral patterns as well, since they kept repeating motor patterns with ineffective tools.

In another tube task experiment (Visalberghi, 1993), the same capuchins selected the correct tool out of a group of four. The other three tools in this choice experiment were completely ineffective, whereas in our experimental phase the comparison was between two equally effective tools with different energetic requirements and an inefficient one that could still be used to accomplish the task. In a different experimental set-up, Cummins-Sebrae and Fragaszy (2005) showed that capuchins chose correctly positioned canes to pull out pieces of food, but they also repositioned canes to pull the food, and improved at the task with practice, thus discovering affordances of the tool according to the authors. In the vast majority of their pairings, the tools did not differ in effectiveness, only in the ease to accomplish the task and/or the familiarity of the animals with them. Also, the required change in behavior for repositioning might be regarded as involving a simpler mental operation (comprehension of a spatial relation) than the creation of whole new motor patterns that would be necessary to make the small stone an effective choice (in our case) or to understand that splinter and tapes cannot be used to push food out of a tube (as in the case of Visalberghi and Trinca, 1989).

Although very preliminary, our results may suggest crucial differences between the tool-using behavior displayed by chimpanzees (or other great ape species) and capuchin monkeys, at least regarding behavioral flexibility involving stone tools; this agrees with a growing body of literature expressing similar doubts. The possibility that capuchins are limited in their capacity to select appropriate tools, and show much less flexibility in behavior than the great apes, should at least be regarded as a working hypothesis, testable both with similar experiments (but a larger sample size), and also with different experimental paradigms, ideally contrasting the aspects which varied between and within studies (e.g. effective vs. ineffective tool; more vs. less efficient tool; requiring tool modification vs. requiring behavioral modification). Only through more experimentation we will be able to fully comprehend capuchins' range of cognitive capacities, their physical knowledge of the world, and the relation of both to their ecology.

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Distribution and Conservation Status of the Yellow-Tailed Woolly Monkey (*Oreonax flavicauda*, Humboldt 1812) in Amazonas and San Martín, Peru

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Introduction

The yellow-tailed woolly monkey (*Oreonax flavicauda*) is one of the largest and rarest Neotropical primates. First discovered in 1802 by Alexander von Humboldt (Humboldt and Bonpland, 1812), since then only a few field studies have been conducted on this species (Leo Luna, 1980, 1982; Butchart *et al.,* 1995a; DeLuycker, 2007) and it remains one of the least known of all primate species. *O. flavicauda* is restricted to a small area of pre-montane cloud forest between 1,400 and 2,500 m a.s.l. in the departments of San Martín and Amazonas in northern Peru (Leo Luna, 1980, 1982; DeLuycker, 2007). The species probably also occurs in small areas of Cajamarca, Huanuco, Loreto and La Libertad departments (Mittermeier *et al.*, 1975; Graves and O'Neil, 1980; Leo Luna, 1980, 1982, 1989; Parker and Barkley, 1981; DeLuycker, 2007; Rolando Aquino, pers. com.). *O. flavicauda* is endemic to the tropical Andes biodiversity hotspot (Myers *et al.*, 2000), and its habitat is characterised by rugged terrain of steep mountain sides and deep river gorges, with canopy