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Report

Selection of Effective Stone Tools by Wild Bearded Capuchin Monkeys

Elisabetta Visalberghi,[1,*] Elsa Addessi,[1] Valentina Truppa,[1,2] Noemi Spagnoletti,[1,3] Eduardo Ottoni,[4] Patricia Izar,[4] and Dorothy Fragaszy[5]
[1]Unit of Cognitive Primatology and Primate Center
Institute of Cognitive Sciences and Technologies
CNR, Via Aldrovandi 16B
00197 Rome
Italy
[2]Department of General Psychology
University of Padua
Via Venezia 8
35131 Padua
Italy
[3]Department of Animal and Human Biology
Sapienza Università di Roma
Viale dell'Università 32
00185 Rome
Italy
[4]Department of Experimental Psychology
University of São Paulo
Av. Mello Moraes 1721
São Paulo
CEP 05508-030
Brazil
[5]Psychology Department
University of Georgia
Athens, GA 30602
USA

Summary

Appreciation of objects' affordances and planning is a hallmark of human technology. Archeological evidence suggests that Pliocene hominins selected raw material for tool making [1, 2]. Stone pounding has been considered a precursor to tool making [3, 4], and tool use by living primates provides insight into the origins of material selection by human ancestors. No study has experimentally investigated selectivity of stone tools in wild animals, although chimpanzees appear to select stones according to properties of different nut species [5, 6]. We recently discovered that wild capuchins with terrestrial habits [7] use hammers to crack open nuts on anvils [8–10]. As for chimpanzees, examination of anvil sites suggests stone selectivity [11], but indirect evidence cannot prove it. Here, we demonstrate that capuchins, which last shared a common ancestor with humans 35 million years ago, faced with stones differing in functional features (friability and weight) choose, transport, and use the effective stone to crack nuts. Moreover, when weight cannot be judged by visual attributes, capuchins act to gain information to guide their selection. Thus, planning actions and intentional selection of tools is within the ken of monkeys and similar to the tool activities of hominins and apes.

*Correspondence: elisabetta.visalberghi@istc.cnr.it

Results and Discussion

Tool selectivity should be experimentally tested by repeatedly providing an individual with sets of tools varying in specific properties in order to rule out the possibility that processes other than active selection are involved (i.e., tool fidelity [10]). We assessed whether wild capuchins (*Cebus libidinosus*) living in Boa Vista (Piauí, Brazil) select hammers of material and weight appropriate to crack open nuts not otherwise accessible. To this purpose, we presented to eight capuchins choices between two (or among three) stones differing in functional features. To crack palm nuts, stones should be heavy and sturdy enough to overcome the resistance of the nut; for example, quartzite stones lighter than 150–200 g or weathered sandstones are not functional even for an adult human because they are too light or too fragile, respectively.

In the first two conditions, subjects chose between natural stones, similar to those that they usually encounter in their habitat, differing in friability ("Friability" condition, sandstone versus siltstone) or in size and weight ("Size and Weight" condition, small versus large quartzite stones). No other stones were available in the area. Nuts were provisioned to the subjects. In both of the above conditions, all subjects touched first, transported, and used the functional stone significantly more often than expected by chance (Table 1 and Figure 1).

Usually, weight is correlated with size, and humans use size to predict weight, especially if objects appear to be of the same material [12]. In the next three conditions, subjects chose between novel artificial stones (of the same color and material) whose weight (i.e., a functional, "invisible" feature) did not correlate with size. Capuchins had to choose between stones of the same size and different weight ("Same Size-Different Weight" condition), between a light and large stone and a heavy and small stone ("Conflicting Size and Weight" condition), and among a light and large stone, a light and small stone, and a heavy and large stone ("Three Stones Size and Weight" condition).

In the Same Size-Different Weight and Three Stones Size and Weight conditions, weight could not be properly detected by sight but could be perceived by manipulating the object (see below). In both conditions, no subject touched the functional stone first more often than expected by chance; nevertheless, all subjects (except for one in the Same Size-Different Weight condition) transported and used the functional tool more often than expected by chance (Figures 1 and 2 and Table 1). In the Conflicting Size and Weight condition, in which the heavier stone was smaller, half of the subjects touched the functional stone first more often than expected by chance. However, when the light tool was the first to be touched or moved, capuchins did not transport it but always proceeded to touch or move the other stone. All subjects transported and used the heavier stone significantly more often than expected by chance (Figure 1 and Table 1).

Capuchins always used the stone that they chose first and never modified their initial choice after the first strike(s). They did not crack the nut in 10.3% of the trials (39 trials out of 377). When unsuccessful, they used the nonfunctional tool in

Table 1. Main Results

Subject	Total Number of Trials	First Touched	p	Transported	p	Used	p	Success	p
Friability: Siltstone versus sandstone									
Chicao	10	10[a]	<0.001	10[a]	<0.001	10	<0.001	9	<0.01
Dengoso	10	10[a]	<0.001	10[a]	<0.001	10	<0.001	8	0.044
Teimoso	10	10[a]	<0.001	10[a]	<0.001	10	<0.001	10[a]	<0.001
Chuchu	10	10[a]	<0.001	10[a]	<0.001	10	<0.001	10[a]	<0.001
Tucum	10	9[a]	<0.01	9[a]	<0.01	10	<0.01	6[a]	0.20 ns
Dita	10	9[a]	<0.01	10[a]	<0.001	10	<0.01	9[a]	<0.01
Jatoba	10	10[a]	<0.001	10[a]	<0.001	10	<0.001	10[a]	<0.001
Mansinho	10	10[a]	<0.001	10[a]	<0.001	10	<0.001	10[a]	<0.001
Size and Weight: Big quartzite versus small quartzite									
Chicao	10	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001	8[a]	0.044
Dengoso	10	8	0.044	9	<0.01	9	<0.01	10	<0.001
Teimoso	10	9[a]	<0.01	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001
Chuchu	10	8[a]	0.044	8[a]	0.044	8[a]	0.044	9[a]	<0.01
Tucum	10	10[a]	<0.001	9[a]	<0.01	9[a]	<0.01	8[a]	0.044
Dita	10	8[a]	0.044	8[a]	0.044	8[a]	0.044	9[a]	<0.01
Jatoba	10	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001
Mansinho	10	8[a]	0.044	8[a]	0.044	8[a]	0.044	9[a]	<0.01
Same Size-Different Weight									
Chicao	10	7[a]	0.12 ns	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001
Dengoso	10	6[a]	0.20 ns	10[a]	<0.001	10[a]	<0.001	9[a]	<0.01
Teimoso	10	6[a]	0.20 ns	9[a]	<0.01	9[a]	<0.01	8[a]	0.044
Chuchu	10	7[a]	0.12 ns	8[a]	0.044	8[a]	0.044	8[a]	0.044
Tucum	10	5	0.25 ns	9	<0.01	9	<0.01	8	0.044
Dita	6	5[a]	0.09 ns	6[a]	0.02	6[a]	0.02	6[a]	0.02
Jatoba	10	5	0.25 ns	5	0.25 ns	5	0.25 ns	4	0.20 ns
Mansinho	10	6	0.20 ns	8[a]	0.044	8[a]	0.044	8[a]	0.044
Conflicting Size and Weight									
Chicao	10	9[a]	<0.01	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001
Dengoso	10	9	<0.01	10[a]	<0.001	10[a]	<0.001	9[a]	<0.01
Teimoso	10	8	0.044	10[a]	<0.001	10[a]	<0.001	9[a]	<0.01
Chuchu	10	7[a]	0.12 ns	10[a]	<0.001	10[a]	<0.001	8[a]	0.044
Tucum	10	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001	8[a]	0.044
Dita	7	6[a]	0.055	7[a]	<0.01	7[a]	<0.01	7[a]	<0.01
Jatoba	10	6[a]	0.20 ns	10[a]	<0.001	10[a]	<0.001	9[a]	<0.01
Mansinho	10	7	0.12 ns	10[a]	<0.001	10[a]	<0.001	9[a]	<0.01
Three Stones Size and Weight									
Chicao	10	4	0.23 ns	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001
Dengoso	10	3	0.26 ns	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001
Teimoso	4	0	0.20 ns	4[a]	0.012	4[a]	0.012	4[a]	0.012
Chuchu	10	5	0.14 ns	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001
Tucum	10	4	0.23 ns	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001
Jatoba	10	2[a]	0.20 ns	10[a]	<0.001	10[a]	<0.001	9[a]	<0.001
Mansinho	10	3	0.26 ns	10[a]	<0.001	10[a]	<0.001	10[a]	<0.001

The number of trials in which each subject first touched the functional stone, transported it to the anvil, used it, and cracked the nut open (success) in the five experimental conditions and corresponding significance level according to the Binomial test (two tailed, $\alpha = 0.05$).
[a] Indicates that the behavior occurred in trial 1. Two subjects did not participate in all trials (Dita completed seven trials in the Conflicting Size and Weight condition, and Teimoso completed four trials in the Three Stones Size and Weight condition).

5 trials and the functional one in 25 trials. In a few trials, they did not use the chosen tool (seven nonfunctional, two functional) because they abandoned it, either spontaneously or when higher-ranking individuals approached.

Overall, wild capuchins chose the functional tool on the basis of material and of weight, even when weight could not be judged by vision, and, in all conditions, most subjects transported and used the designated functional tool on the first trial (Table 1). Moreover, latencies to transport indicate that the decision-making process was rapid and similar across conditions, even in the conflicting condition in which weight was dissociated from size.

Whenever visual cues were available and reliable, as with the natural stones, capuchins always touched the functional stone first, suggesting that they discriminated the stones by sight. In contrast, when visual cues were not predictive or conflicting, as with the artificial stones, individuals gained information about the weight of the experimental stones by moving, lifting, and/or tapping them. Tapping is an exploratory behavior commonly used by capuchins to localize hidden food sources and to recognize whether nuts are full or empty [13–16].

Capuchins tapped the artificial stones to generate acoustic or haptic information. From this information, they could infer the weight of the stones if they recruited their knowledge of the different sounds or different haptic sensations produced by more and less dense objects. In the Same Size-Different Weight condition, tapping occurred in 11.8% of the trials (five subjects out of eight); in the Conflicting Size and Weight

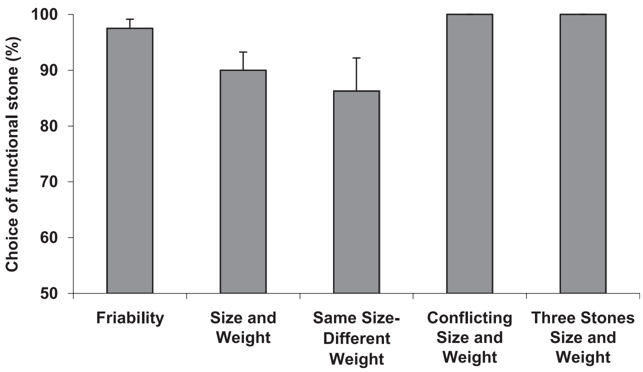

Figure 1. Average Percentage of Choice of the Functional Stone and Standard Error in the Five Experimental Conditions

condition, in 26.0% of the trials (five subjects out of eight); and in the Three Stones Size and Weight condition, in 48.4% of the trials (five subjects out of eight). Conversely, in the conditions with natural stones, in which visual cues were available, no subject performed tapping behavior on either stone.

Switches, i.e., touching and/or lifting a stone without transporting it and then moving to the other stone(s), indicate the exploration of the affordances of the stones and reflect the individual's decision-making process. In all of the conditions with artificial stones, capuchins performed significantly more correct switches (from a nonfunctional stone to a functional one) than incorrect ones (from a functional stone to a nonfunctional one) (Same Size-Different Weight: Wilcoxon Signed Ranks test: $T = 0$, $N = 7$; $p = 0.018$; Conflicting Size and Weight: Wilcoxon Signed Ranks test: $T = 0$, $N = 7$; $p = 0.018$; Three Stones Size and Weight: Wilcoxon Signed Ranks test: $T = 0$, $N = 7$; $p = 0.018$) (Figure 3). In both conditions with natural stones, the above analysis could not be carried out because too few switches occurred (one correct in the Friability condition and four correct and two incorrect in the Size and Weight condition).

Conclusions

In sum, wild capuchins consistently and immediately selected functional tools, regardless of the condition intricacies, outperforming captive capuchins tested in tool tasks [17, 18]. In light of these findings, we must reconsider the manner in which we evaluate cognition in captive primates. Wild capuchins' recognition of the affordances of objects relied on their lifelong experience with a wide variety of nuts and stones. In captive nonhuman primates, training involving a larger and more varied set of stimuli allows better generalization of abstract concepts [19]. Similarly, in young children, recognition of the affordances of objects develops during exploration and play, and such knowledge supports the use of objects in goal-directed activity [20]. Moreover, repetitive effective use of a tool induces a plastic modification of the body representation in the brain [21]. Finally, it is through experience that modern humans acquire practical knowledge of stone properties to use as criteria for selecting raw material for flaking [22], and, presumably, this was the case for human ancestors as well. Thus, because experience affects cognitive development, a more accurate appreciation of intelligence in a nonhuman species requires either carefully designed field experiments [23] or systematic exposure of captive individuals to a wide variety of challenges [24, 25]. In conclusion, planning actions in order to select stones of functional material and weight is within the ken of wild monkeys living in ecological conditions promoting the use of pounding tools [7] and not distinctive of the tool activities of hominin and apes. The present findings, along with many striking analogies between capuchins and humans in encephalization index, ontogeny, omnivorous diet, and manipulative skills [18], make capuchins a compelling model to identify independently evolved traits, to track the evolutionary roots of stone tool use, and to

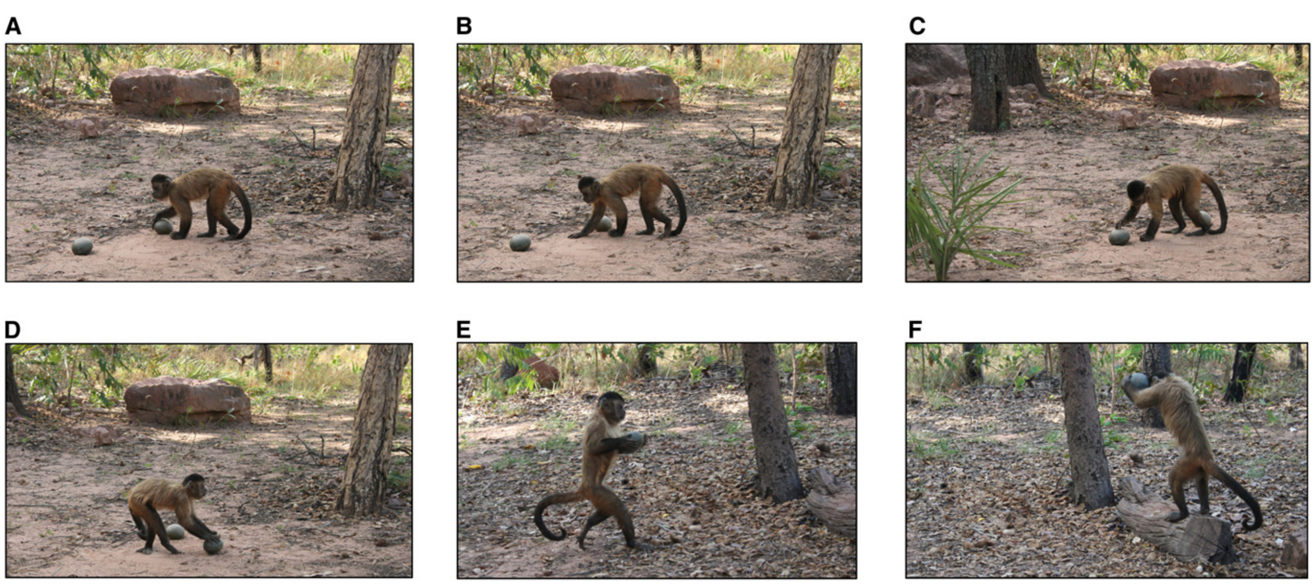

Figure 2. Mansinho, an Adult Male, in Trial 8 of the Size and Weight Condition

In this trial, the light stone is on the right, and the heavy one is on the left. The monkey goes to the light stone and contacts it (A), switches to the other stone (B), contacts the heavy stone (C), lifts it (D), transports the stone to the log anvil (E), and pounds the nut in a bipedal stance with this hammer until it cracks open (F) (photos by Elisabetta Visalberghi).

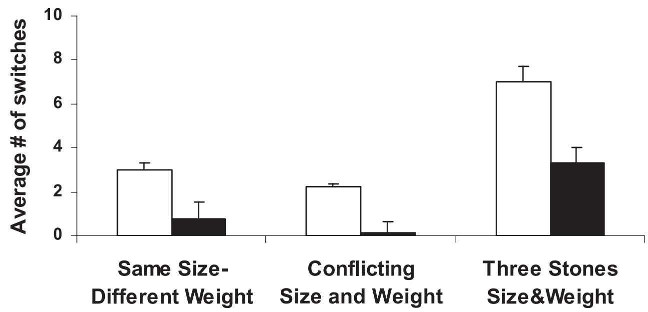

Figure 3. Average Number of Switches per Subject and Standard Error

White bars indicate correct switches (from a nonfunctional stone to a functional one), and black bars indicate incorrect switches (from a functional stone to a nonfunctional one) performed over all trials in the Same Size-Different Weight, Conflicting Size and Weight, and Three Stones Size and Weight conditions. Results concerning the conditions with natural stones are not reported because too few switches occurred.

understand which features of a species' ecology lead to these rare adaptations.

Experimental Procedures

Eight capuchins that routinely use tools to crack open palm nuts were tested in an area frequently visited (Figure S1 available online), from which we removed all stone hammers. In each trial, there were one functional stone and one or two nonfunctional stone(s) to choose from (Table S1). Testing occurred opportunistically, and a trial started when the subject was provided with a nut. Subjects received ten trials in each condition.

In the Friability condition, we used eight pairs of natural stones, each consisting of one weathered sandstone (nonfunctional) and one siltstone (functional) of similar weight. In the Size and Weight condition, we used eight pairs of natural stones, each consisting of two quartzite stones of different size and weight. In the Same Size-Different Weight condition, we used 12 pairs of artificial stones differing only in weight. In the Conflicting Size and Weight condition, we used 12 pairs of artificial stones differing only in size and weight. In this condition, size did not predict weight because the functional stone was small and heavy, whereas the nonfunctional stone was light and large. Finally, in the Three Stones Size and Weight condition, a triplet of stones differing only in size and weight was used. The functional stone was a heavy and large quartzite, whereas large and light and large and small artificial stones were nonfunctional.

We scored the first stone touched, transported (choice), and used to strike the nut; success; tapping behavior (i.e., gently and repeatedly beating an object with finger nails); number of switches between stones; anvil used; latency to transport (time elapsed between first contact and onset of transport); and average distance and height above ground of the anvil used from the choice location.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and Results, two figures, one table, and five movies and can be found with this article online at www.current-biology.com/supplemental/S0960-9822(08)01624-2.

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