

Current Biology

Wild Bearded Capuchin Monkeys Crack Nuts Dexterously

Highlights

- Wild bearded capuchin monkeys repeatedly strike tucum nuts with moderate force
- They modulate the kinematic parameters of each strike while cracking a single tucum nut
- They do so on the basis of the condition of the nut following the preceding strike
- Dynamically optimizing movements this way is a dexterous accomplishment

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In Brief

Mangalam and Fragaszy show that wild bearded capuchin monkeys crack tucum nuts dexterously, maintaining the kinetic force of each strike within a zone while modulating the kinetic parameters of the current strike on the basis of the condition of the nut following the preceding strike.



Wild Bearded Capuchin Monkeys Crack Nuts Dexterously

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SUMMARY

Dexterous tool use has been crucial in the evolution of hominid percussive technology [1–3]. According to Newell [4], “dexterity” is the ability of an organism to make goal-directed corrections in movements to optimize effort. Dexterous movements are smooth and effective and accomplish the same goal with less energy than less dexterous movements. Dexterity develops during the later phases of refining a motor skill as the actor becomes sensitive to the outcome of the preceding movement, or to its modulation. In the present study, we examined how wild bearded capuchin monkeys, *Sapajus libidinosus*, at Fazenda Boa Vista in Piauí, Brazil, that routinely crack palm nuts using stones by placing them on rock outcrops, boulders, and logs (collectively termed anvils) [5] modulate the kinematic parameters of the strikes while processing a single tucum, *Astrocaryum campestre* nut. The monkeys cracked the nuts by repeatedly striking them with moderate force (i.e., not exceeding a threshold), rather than by striking them more forcefully once, and modulated the kinematic parameters of the current strike on the basis of the condition of the nut following the preceding strike (i.e., the development of any fracture or crack). Repeatedly striking the nuts with moderate force is energetically more efficient than forcefully striking them once and reduces the likelihood of smashing the kernel. Determining the changing energetic constraints of the task and dynamically optimizing movements using those as criteria are dexterous accomplishments. We discuss the implications of the present findings.

RESULTS AND DISCUSSION

We observed 14 wild bearded capuchin monkeys cracking the tucum nuts (mean \pm SD peak force at failure = 5.57 ± 0.25 kN, $n = 12$; [6]). Cracking a tucum nut requires several strikes; each strike can be divided into three phases: (1) a preparatory pre-lift phase (holding and manipulating the stone), (2) an upward phase (elevating the stone to a zenith point), and (3) a downward phase (lowering the stone to hit the nut). For each strike, we determined the two crucial kinematic parameters: (1) the height

of the stone from the nut at the zenith point and (2) the maximum velocity of the stone during the downward phase of the strike. Whereas the height of the stone at the zenith point is related to its maximum velocity during the downward phase of the strike, the latter can also be modulated by adding work into the stone; the force of impact depends on the velocity of the stone. An intact tucum nut (Figure 1A) has two distinct layers, a soft outer hull (i.e., the exocarp and the mesocarp) (Figures 1B and 1C) and a hard inner shell (i.e., the endocarp) encapsulating a relatively soft kernel (i.e., the endosperm) (Figures 1D and 1E); the outer hull can be easily detached manually from the inner shell once it is breached. Following the structure of the tucum nut, we hypothesized that: (1) breaching the hull should require less force than cracking the shell. (2) Completely breaching a partially breached hull should require less force than breaching an intact hull; likewise, completely cracking a partially cracked shell should require less force than cracking an intact shell. (3) No perceptible change in the physical condition of the nut following a strike should require another more forceful strike (Figure 2).

Typically, the monkeys took (1) two strikes to breach the hull (and after that, they removed the hull manually or with their teeth), (2) two strikes to crack the shell, and (3) one or more ineffective strikes with no perceptible change in the condition of the nut while breaching the hull and/or while cracking the shell (Table 1; see Movies S1 and S2). An analysis of the change in the values of the kinematic parameters (i.e., the height of the stone from the nut at the zenith point and the maximum velocity of the stone during the downward phase of the strike) between consecutive strikes within a single nut-cracking sequence indicated that the monkeys modulated them on the basis of the condition of the nut following the preceding strike (i.e., the development of any fracture or crack) while cracking a single tucum nut (for an illustration, refer to the graphs plotting the height and the velocity of the stone against time in Movies S3 and S4, respectively). Statistical comparison of the number of strikes in which the monkeys modulated or did not modulate the kinematic parameters of the strikes on the basis of the condition of the nut following the preceding strike, as illustrated in Figure 2, using paired samples *t* test, revealed that the monkeys modulated more strikes than expected by chance (Table 2). A significant proportion of the monkeys modulated the kinematic parameters in the majority of strikes at each stage of nut cracking, except after the hull was breached completely (Table 2). This anomaly raises the question of whether the monkeys perceive “breaching the hull” and “cracking the shell” as two different tasks, but evaluating this hypothesis needs further experimentation. Table S1 provides an overview of the scale of modulation; it describes the mean \pm SD values of the modulation of the kinematic

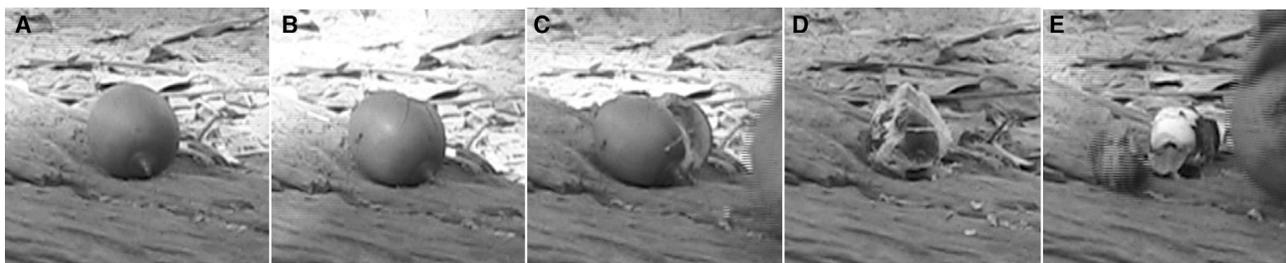


Figure 1. A Tucum Nut in Different Conditions

- (A) Intact.
- (B) Hull breached partially.
- (C) Hull breached completely (and removed).
- (D) Shell cracked partially.
- (E) Shell cracked completely.

parameters along with the values of the kinematic parameters of the preceding strike for each monkey.

In summary, the monkeys cracked the nuts by repeatedly striking them with moderate force (i.e., not exceeding a threshold), rather than by striking them more forcefully once, and modulated the kinematic parameters of the current strike on the basis of the condition of the nut following the preceding strike (i.e., the development of any fracture or crack). Cracking nuts like the tucum, which have a hard shell encapsulating a soft kernel, requires optimal force. The strike should be forceful enough just to crack the shell but leave the kernel intact because the force exceeding a maximum threshold value would smash the kernel, and not exceeding a minimum threshold value would be ineffective. Koya [7] demonstrated theoretically as well as experimentally that repeatedly striking the oil palm, *Elaeis guineensis* nuts (which are thick shelled, but not as resistant to cracking as the tucum nuts used in the present study; peak force at failure: 0.2–3.7 kN depending on the size and moisture content of the nut [8]), with moderate force (1) is energetically more efficient than striking them forcefully once, as the energy of several “mini” strikes sum up to less than that of a single forceful strike, and (2) reduces the likelihood of smashing the soft kernel.

Moderately forceful strikes induce micro-fractures in the shell, which ultimately cause fatigue failure. The last crack grows more rapidly from the existing cracks, with much lower force than would be required to develop this crack de novo. Thus, if the force is not reduced while cracking a shell with existing cracks, the impact is likely to smash the kernel.

It can be argued that the monkeys cracked the tucum nuts by repeatedly striking them with moderate force, rather than by striking them more forcefully once, because they could not lift the stones higher or lower them with greater velocity. However, the fact that they modulated the kinematic parameters of the strikes strongly undermines this argument. Had the monkeys faced musculoskeletal limits in raising the stones higher or in lowering them with greater velocity, they would not have modulated the strikes but rather would have struck the nuts with the maximum force they could generate, without any modulation, until the nuts cracked. An individual can modulate the strike force by modulating the height to which it raises the stone and/or by putting work into the stone while lowering it. The latter strategy allows achieving the required value of the composite end variable (i.e., the strike force) under variable conditions; experience contributes to this ability in chimpanzees [9] and humans [10].

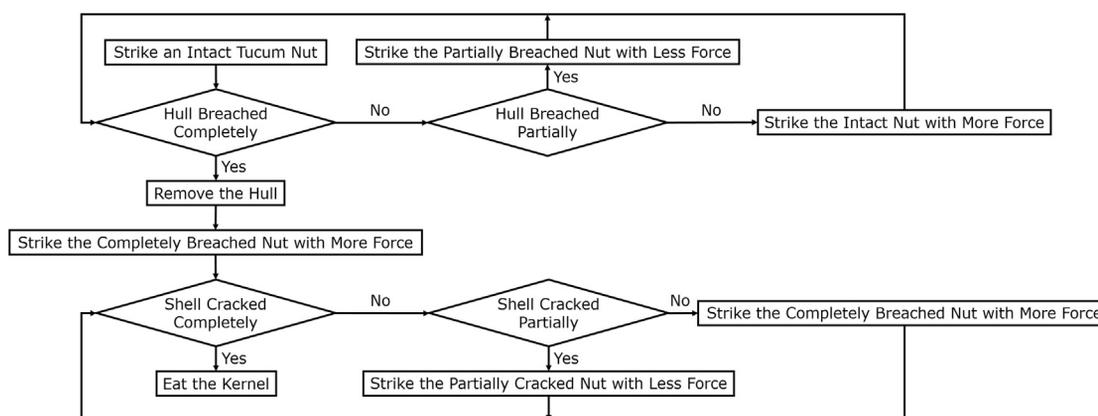


Figure 2. Flow Chart Illustrating the Model We Hypothesized the Monkeys Would Follow

The flow chart illustrating the model we hypothesized the monkeys would follow while cracking a single tucum nut to modulate the kinematic parameters of the current strike on the basis of the condition of the nut following the preceding strike.

Table 1. The Median—Interquartile Range—Number of Strikes to Crack the Tucum Nuts for Each Monkey

Individual	Sex	Age Class	Body Mass (kg)	Successes/ Attempts	Overall	Breach the Hull		Crack the Shell	
						Effective	Ineffective	Effective	Ineffective
Mansinho	M	A	3.44	12/12	4.5 (4–6.25)	2 (2–2)	0 (0–1)	1 (1–2)	0.5 (0–1.25)
Jatobá	M	A	4.20	10/11	7 (5.25–8)	2 (2–2.75)	0 (0–1)	2 (2–2)	1.5 (0–5.25)
Teimoso	M	A	3.54	25/26	5 (3–7)	1 (1–2)	0 (0–1)	2 (2–2)	0 (0–2)
Tomate	M	SA	2.53	30/30	4.5 (3–6)	1 (1–2)	0 (0–1)	1 (1–2)	0 (0–2.75)
Catu	M	SA	2.73	15/15	8 (5–9.5)	1 (1–2)	1 (0–2)	2 (1–2)	3 (0–5.5)
Coco	M	J	1.88	10/17	9.5 (7.25–14.75)	2 (1–3)	0 (0–1)	2 (2–2)	6 (2–10.5)
Presente	M	J	1.67	0/5	–	–	–	–	–
Cachassa	M	J	1.29	2/3	19.5 (13.25–32)	1.5 (1.25–2)	9 (5.5–16)	2.5 (2.25–3)	7 (3.5–14)
Piaçava	F	A	1.73	9/10	9 (8–12)	2 (2–2)	2 (2–3)	2 (2–2)	4 (2–5)
Dita	F	A	2.04	12/13	6.5 (4.5–12.5)	2 (1.75–3)	1 (0–1)	2 (1.75–2)	1.5 (0–6)
Doree	F	A	1.69	10/12	5 (5–10)	2 (0.5–2)	1 (1–2.75)	2 (1–2)	2 (0.25–4.75)
Chuchu	F	A	2.00	17/18	8 (6–11)	2 (1–3)	1 (0–2)	2 (1–2)	3 (1–5)
Pamonha	F	J	1.73	3/4	4 (3.5–6.5)	1 (1–1.5)	0 (0–0)	1 (1–1)	2 (1–4.5)
Pasoca	F	J	1.81	1/5	6 (6–6)	1 (1–1)	4 (4–4)	1 (1–1)	0 (0–0)

M, male; F, female; A, adult; SA, subadult; J, juvenile.

The present finding that wild bearded capuchin monkeys are capable of modulating the kinematic parameters of individual percussive movements as driven by the changing requirements of the task is similar in important ways to what is observed in humans cracking nuts with stone hammers. (1) The !Kung of the Kalahari crack the mongongo, *Schinziophyton rautanenii* nuts (which, like the tucum nuts, have two distinct layers: a soft outer hull and a hard inner shell encapsulating the kernel, but are harder) [11], and (2) Nigerian farmers crack the oil palm nuts ([12], p. 471) by placing the nuts between two stones and varying the applied force over consecutive strikes. Cracking nuts requires asymmetrical, cooperative, and bimanual actions and control over the trajectory and kinetic energy of percussive movements and the point of percussion, which also are the requirements for knapping stones. On the basis of these similarities, nut cracking has been proposed to be a likely precursor to the evolution of the more “complex” activity of knapping [13–15]. However, there are important differences between the two percussive tasks. In addition to the demands for control described above for cracking nuts, stone knapping also requires the simultaneous control of the reciprocal orientation of the stone and the trajectory of the strike, both of which vary across blows [14, 16–19].

The analysis of percussive tasks in nonhuman primate species (here, nut cracking) has progressed from their description [5, 20] to the complexity of actions [21–23] and the choice and adaptation of tools [24–28] but has not yet progressed far concerning the adaptation of individual percussive movements. A preliminary attempt to understand the adaptation of movements to the properties of tools and nuts in one chimpanzee failed to reveal whether it adapted the movements (i.e., varied strike force) to the characteristics of the tasks (anvils with and without cavity; different types of nuts), although it deployed slightly more energy while cracking nuts on a flat-surface anvil than on an indented anvil [29]. In a follow-up study, five chimpanzees modulated the strike force when using stones of different mass, and

the experienced individuals showed an enhanced range and precision of modulation [9]. Both these studies incorporated variation in the percussive movements across sets of tools. They do not, therefore, represent the kind of challenges that are characteristic of stone knapping. The structure of the tucum nuts continually changes during percussion, thereby changing the challenge associated with the task of cracking them. This provided us an opportunity to examine the real-time modulation of percussive movements.

Following Bril et al. [9], we advocate that the present findings compel us to shift the focus of research on hominid percussive evolution from the human specificity of tool use per se to the species-specific differences in the control of individual movements as driven by the changing requirements of the task. Determining the changing energetic constraints of the task and dynamically optimizing movements using those as criteria are dexterous accomplishments. The question that immediately follows the present findings is how does an individual develop and utilize this kind of dexterity? Only when individual movements and movement synergies constituting the techniques and skills underlying the two activities—cracking nuts and knapping stones—are elaborated can one study these activities as integrated wholes. Then, the comparison of these movements and movement synergies might elucidate the differences in the associated cognitive processes and/or biomechanical constraints between nonhuman primates and the hominids who first knapped stones.

EXPERIMENTAL PROCEDURES

We studied 14 individually recognized wild bearded capuchin monkeys (males: 3 adults, 2 subadults, and 3 juveniles; females: 4 adults and 2 juveniles) at Fazenda Boa Vista in the southern Parnaíba Basin (9°39'S, 45°25'W) in Piauí, Brazil (Table 1) (see [30] for a detailed description of the study site).

We video recorded the monkeys cracking tucum nuts on a log anvil using quartzite stones (mass: 0.455, 0.539, 1.042, or 1.100 kg) at 30 frames per second. We placed a Canon XF100 camcorder ~11.5 m away from the anvil,

Table 2. The Number of Strikes in Which the Monkeys Modulated or Did Not Modulate the Kinematic Parameters on the Basis of the Condition of the Nut following the Preceding Strike, as Illustrated in Figure 2

Individual	Hull Breached Partially (Expectation: Decrease)				Hull Breached Completely (Expectation: Increase)				Shell Cracked Partially (Expectation: Decrease)				No Effect (Expectation: Increase)			
	H		V		H		V		H		V		H		V	
	D	ND	D	ND	I	NI	I	NI	D	ND	D	ND	I	NI	I	NI
Mansinho	8	5	11	2	3	5	6	2	7	1	8	0	17	7	14	6
Jatobá	9	7	10	6	6	3	6	3	9	2	8	3	24	12	21	15
Teimoso	14	10	12	12	14	6	16	4	18	3	21	0	33	21	31	13
Tomate	10	3	11	2	14	13	16	11	15	3	14	4	40	19	39	20
Catu	7	7	8	6	5	7	7	5	9	1	7	3	45	27	44	28
Coco	10	7	9	8	6	6	6	6	8	1	7	2	58	38	57	29
Presente	4	2	6	0	2	2	1	3	–	–	–	–	39	21	36	24
Cachassa	1	1	0	2	1	0	1	0	2	1	2	1	23	11	17	17
Piaçava	9	1	7	3	3	6	6	3	8	2	8	2	42	21	40	23
Dita	12	3	8	7	10	2	9	3	10	1	9	2	39	30	40	29
Doree	4	3	5	2	6	2	7	1	6	0	6	0	37	25	35	27
Chuchu	11	6	11	6	10	5	7	8	11	1	10	2	50	37	53	34
Pamonha	1	1	1	1	2	2	3	1	–	–	–	–	25	17	21	21
Pasoca	–	–	–	–	–	–	–	–	–	–	–	–	19	8	19	8
Test Results																
Paired samples t test ^a	$(t_{2,12} = -3.975,$ $p = 0.002^{**})$		$(t_{2,12} = -3.341,$ $p = 0.005^*)$		$(t_{2,12} = -1.767,$ $p = 0.102)$		$(t_{2,12} = -3.117,$ $p = 0.009^*)$		$(t_{2,10} = -7.195,$ $p < 0.001^{***})$		$(t_{2,10} = -4.785,$ $p = 0.001^{***})$		$(t_{2,13} = -11.576,$ $p = 0.001^{***})$		$(t_{2,13} = -5.942,$ $p = 0.001^{***})$	
Binomial test ^b	$p = 0.092$		$p = 0.023^*$		$p = 1.000$		$p = 0.092$		$p = 0.001^{**}$		$p = 0.001^{**}$		$p < 0.001^{***}$		$p = 0.013^*$	

H, the height of the stone from the nut at the zenith point; V, the maximum velocity of the stone during the downward phase of the strike; D, decreased; ND, not decreased; I, increased; NI, not increased.

^aResults of the paired samples t tests comparing the number of strikes in which the monkeys modulated or did not modulate the kinematic parameters.

^bResults of the binomial test examining the proportion of monkeys that modulated the kinematic parameters in the majority of strikes.

capturing the sagittal plane views (field of view ~ 1.5 m) of the monkeys cracking nuts. Before the monkeys used anvils, we video recorded a 1 m \times 1 m square frame, which was marked with reflective tape, in the center of the anvil immediately above the pit in which the monkeys placed the nut in each strike, to add a reference scale. All experimental procedures were approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Georgia, Athens, USA.

A nut-cracking sequence comprises several strikes; each strike was divided into (1) a preparatory pre-lift phase (holding and manipulating the stone), (2) an upward phase (elevating the stone to a zenith point), and (3) a downward phase (lowering the stone to hit the nut) (see [31]). We used an open source video analysis and modeling tool, "Tracker" (downloaded from <https://www.cabrillo.edu/~dbrown/tracker/>), to determine the two crucial kinematic parameters of the strikes: (1) the height of the stone from the nut at the zenith point to the nearest centimeter and (2) the maximum velocity of the stone during the downward phase to the nearest centimeter per second. To this end, we documented the position of the bottom of the stone in each frame with the visible center of the nut as the origin of the axis of the frame (see *Movies S3* and *S4*).

We tested our coding for inter-observer reliability by comparing repeated codings of 12 striking movements by the same observer and by two different observers. The coded values did not differ between repeated coding by the same observer (height: mean \pm SD absolute difference = 0.007 \pm 0.008 m, paired samples *t* test: $t = -1.173$, $n = 12$, $p = 0.266$; velocity: 0.133 \pm 0.122 m/s, $t = -0.345$, $n = 12$, $p = 0.737$) and by the two different observers (height: 0.008 \pm 0.006 m, $t = 0.897$, $n = 12$, $p = 0.389$; velocity: 0.289 \pm 0.631 m/s, $t = -1.100$, $n = 12$, $p = 0.295$).

SUPPLEMENTAL INFORMATION

Supplemental Information includes one table and four movies and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.03.035>.

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