Task-specific temporal organization of percussive movements in wild bearded capuchin monkeys

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Tool-assisted percussion is an ancient feature of human technology. Tool-assisted percussion is not uniquely human; chimpanzees, *Pan troglodytes*, longtailed macaques, *Macaca fascicularis aurea,* and capuchin monkeys (*Sapajus* spp.) use stone tools to crack open encased foods. The knowledge of how these nonhuman primates use percussion tools helps us to understand how extinct hominins might have used percussion tools. Wild bearded capuchin monkeys, *Sapajus libidinosus,* crack palm nuts of different species by placing them on rock outcroppings, boulders and logs (anvils) and striking them with stone hammers. In the present study, we examined whether and how these monkeys modulate the kinematic parameters of individual strikes and the organization of successive strikes to accommodate the physical properties of a nut. To this end, we observed seven monkeys as they cracked two species of nuts that differ in their structure and resistance to fracture. They cracked the less resistant tucum (*Astrocaryum* spp.) nut by striking it repeatedly with moderate force (that is, by not exceeding a threshold) and modulating the kinematic parameters of each strike on the basis of the condition of the nut (that is, the development of a fracture) following the preceding strike. In contrast, they cracked the more resistant piaçava (*Orbignya* spp.) nut by striking it with the maximum force that they could generate without modulating the kinematic parameters of their strikes until that nut cracked. These results demonstrate that the task-specific temporal organization of percussive movements necessary for knapping stones is within the capability of extant nonhuman primates.

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Tool-assisted percussion (here, percussion refers loosely to 'a forceful, muscle-driven striking of one body against another'; Marchant & McGrew, 2005, page 342) is an ancient feature of human technology. The earliest archaeological evidence of the use of percussion tools by extinct hominins is the stone artefacts belonging to the Lomekwian (3.3 million years ago) (Harmand et al., 2015) and Oldowan Industrial Complexes (2.6–2.5 million years ago) (Semaw et al., 1997). Many authors have suggested that tool-assisted percussion in hominins has its precursor in extractive foraging as seen in extant nonhuman primates, as the latter often involves the direct percussion of objects on substrates and, occasionally, the use of wood and stones in their natural form as anvil-and-hammer tools (Boesch & Boesch-Achermann, 2000; Byrne, 2005; Marchant & McGrew, 2005; Matsuzawa, 2001; Sugiyama & Koman, 1979). For example, wild chimpanzees, *Pan troglodytes*

(Boesch & Boesch, 1981; Hannah & McGrew, 1987; Whitesides, 1985), longtailed macaques, *Macaca fascicularis aurea* (Gumert & Malaivijitnond, 2012; Malaivijitnond et al., 2007) and capuchin monkeys (*Sapajus* spp.) (Canale, Guidorizzi, Kierulff, & Gatto, 2009; Ferreira, Emidio, & Jerusalinsky, 2010; Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004; Mangalam & Fragaszy, 2015; Moura & Lee, 2004; Ottoni & Mannu, 2001; Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011) use anvil-and-hammer tools to crack open encased foods. A question follows from these examples: what distinguishes the percussion skills of extant nonhuman primates and extinct hominins with regard to cracking nuts and knapping stones, respectively?

Biomechanics provides a framework for understanding the skilful use of a tool by describing the kinetic, kinematic and spatiotemporal properties of tool-use movements (Latash, Turvey, & Bernstein, 1996). The organization of movements in vertebrates is grounded in their musculoskeletal system and perceptual processes; the features of the body, task and environment collectively impose constraints on the development of movements (Newell,

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1986). The physical structure and physiological make-up of the body impose morphological and/or anatomical constraints. For example, when cracking nuts, chimpanzees mostly hold stone hammers with one hand, but because of their relatively smaller size, capuchin monkeys hold hammers of comparable mass with both hands (Visalberghi, Sirianni, Fragaszy, & Boesch, 2015). The ergonomic and goal-related features of the task impose task constraints. For example, to crack a nut, one needs to control the following three functional parameters simultaneously: (1) the point of percussion, (2) the angle of percussion and (3) the kinetic energy that initiates a fracture (Bril et al., 2012) (Fig. 1a). To knap a stone, one needs to control the following five functional parameters simultaneously: (1) the exterior platform angle, (2) the platform depth, (3) the point of percussion, (4) the angle of the blow relative to the platform and (5) the kinetic energy that initiates a fracture (Bril et al., 2012; Dibble & Rezek, 2009; Nonaka, Bril, & Rein, 2010) (Fig. 1b). Various extraneous factors that may affect the task performance impose environmental constraints. For example, it is easier to initiate and control a conchoidal fracture in isotropic stones than in anisotropic stones, because isotropic stones lack cleavage planes or other inclusions that inhibit the free passage of energy (Whittaker, 1994). Thus, goal-directed movements vary depending on what constraints the features of the body, task and environment impose upon them (Sporns & Edelman, 1993).

Skilfully knapping a stone requires different skills and a different perception of the affordances of the task compared to successfully cracking a nut. For example, inducing a conchoidal fracture when knapping a stone requires precise control over the orientation of the core and the trajectory of the hammer (Bril et al., 2012; Dibble & Rezek, 2009; Nonaka et al., 2010). However, this precision is not required to crack a nut (Bril et al., 2012). One hypothesis is that the differences among nonhuman primates and extinct hominins are a matter of degree, and not categorical; nonhuman primates may be less capable of temporal integration of movements than were extinct hominins and may not be able to control simultaneously as many physical parameters of the task as knapping demands but, nevertheless, show indicators of these skills (Bril, Parry, & Dietrich, 2015). Empirical results on nonhuman primates support this hypothesis. For example, when cracking a macadamia nut, *Macadamia integrifolia,* or a Brazil nut, *Bertholletia excels*, chimpanzees modulate the kinematic parameters of their strikes to adapt to stones of different masses (Bril, Dietrich, Foucart, Fuwa, & Hirata, 2009; Foucart et al., 2005), and when cracking a tucum nut, wild bearded capuchin monkeys, *Sapajus libidinosus* (previously known as *Cebus libidinosus*; Alfaro, Silva, & Rylands, 2012), modulate the

kinematic parameters of each strike on the basis of the condition of the nut following the preceding strike (Mangalam & Fragaszy, 2015). The evidence supporting this hypothesis forces us to rethink the emergence and continuity of percussion skills among nonhuman primates and hominins.

In the present study, we examined whether and how wild bearded capuchin monkeys modulate the kinematic parameters of individual strikes and the organization of successive strikes to accommodate the properties of a nut. To this end, we observed the monkeys as they cracked two species of nuts that differ in their structure and resistance to fracture. The most common species of nuts that the monkeys at Fazenda Boa Vista, Brazil (our study site) crack habitually differ considerably in their resistance to fracture: (1) catulé (*Attalea* spp.; mean ± SD peak-force-at-failure = 5.15 ± 0.26 kN, $N = 18$); (2) tucum (*Astrocaryum* spp.; 5.57 ± 0.25 kN, $N = 12$); (3) catulí (*Attalea* spp.; 8.19 ± 0.35 kN; $N = 20$); and (4) piaçava (*Orbignya* spp.; 11.50 ± 0.48 kN, $N = 35$; Visalberghi et al., 2008). These nuts are considerably more resistant to fracture than the orally processed food provided to nonhuman primates in captivity (Williams, Wright, Truong, Daubert, & Vinyard, 2005) and the species of nuts that humans commonly crack, such as almonds, *Prunus dulcis* (peak-force-at-failure: ca. $0.05-0.5$ kN depending on the variety and moisture content; Aktas, Polat, & Atay, 2007) and walnuts, *Juglans regia* (ca. 0.5 kN; Sharifian & Derafshi, 2008). We compared how these monkeys crack tucum and piaçava nuts, which, besides lying at the extremes of the spectrum of resistance to fracture, also differ structurally.

An intact tucum nut has two distinct layers, a soft outer hull (the exocarp and the mesocarp) and a hard inner shell (the endocarp) (mean ± SD thickness: 4.12 ± 0.14 mm, $N = 12$) encapsulating a relatively soft kernel (the endosperm); the hull can be easily detached from the inner shell manually or by using the mouth once it is breached (Visalberghi et al., 2008; Fig. 2a, Supplementary Movie S1). It follows 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, and, likewise, completely cracking a partially cracked shell should require less force than cracking an intact shell; and (3) when there is no perceptible change in the physical condition of the nut, another more forceful strike should follow (see Fig. 3a). Accordingly, these monkeys crack a tucum nut by striking it repeatedly with moderate force (that is, by not exceeding a threshold) and modulating the kinematic parameters of each strike on the basis of the condition of the nut (that is, the development of a fracture) following the preceding strike (Mangalam & Fragaszy, 2015). In
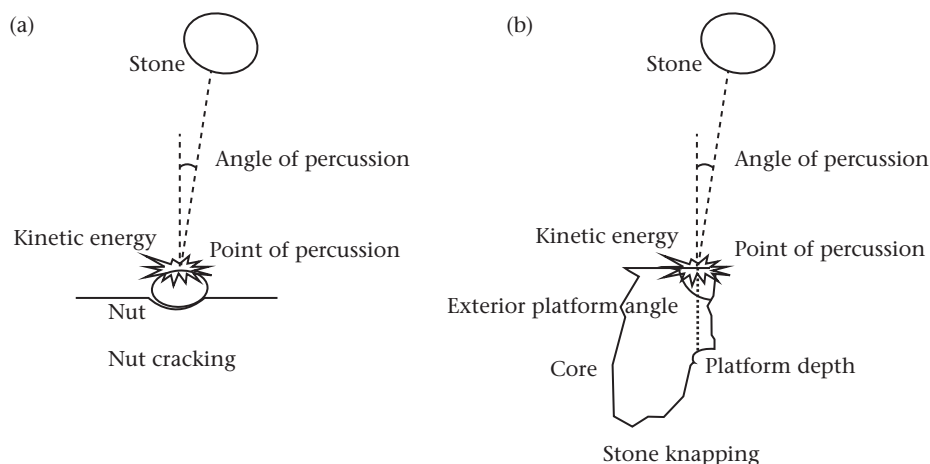

Figure 1. Functional parameters of the two percussion tasks: (a) nut cracking; (b) stone knapping.

Figure 2. The two species of nuts: (a) tucum: intact; hull breached partially; hull breached completely; shell cracked partially; shell cracked completely; (b) piaçava: intact; whole nut cracked partially; whole nut cracked completely (exposing multiple locules, encapsulating one kernel each); segment cracked partially; segment cracked completely.

contrast, a piaçava nut has a highly resistant shell (the endocarp; thickness = 7.66 ± 0.30 mm, N = 35) and is a composite of several locules, each encapsulating one kernel (the endosperm; mean ± SD number of locules = 3.00 ± 0.18, N = 35) (Fig. 2b, Supplementary Movie S2) compared to only one kernel for a tucum nut (Visalberghi et al., 2008). Piaçava nuts also have an outer hull, which is removed prior to cracking either by the monkeys themselves or more commonly by grazing cattle. We reasoned that (1) completely
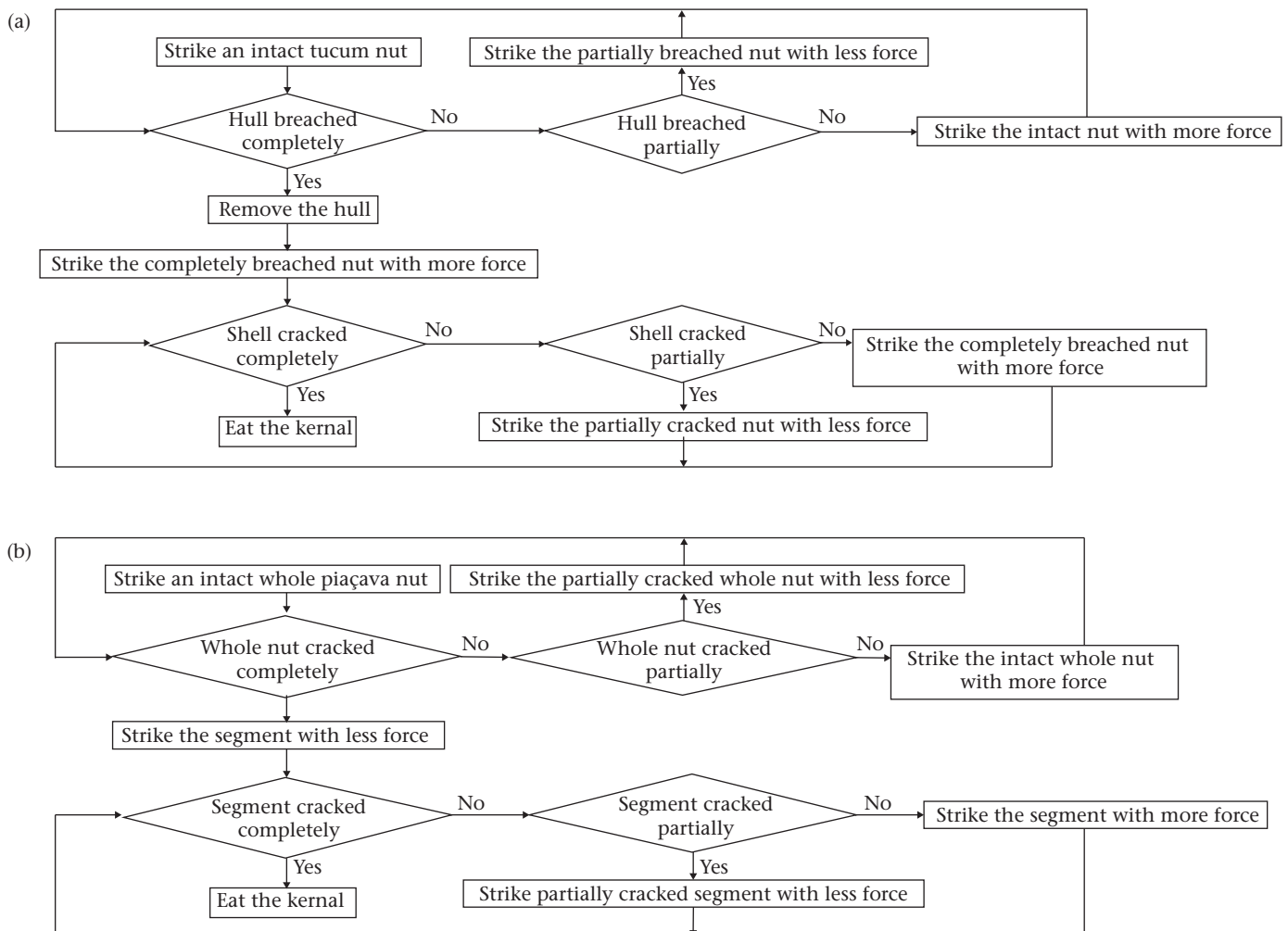

Figure 3. Flow charts illustrating the algorithms that we hypothesized that the monkeys would follow when cracking (a) a tucum nut and (b) a piaçava nut.

cracking a partially cracked whole piaçava nut (that is, a nut that already has fracture(s)) should require less force than cracking an intact whole nut, and, likewise, completely cracking a partially cracked segment (here, 'segment' refers to a portion of a piaçava nut with at least one locule) of a nut should require less force than cracking an intact segment of a nut; (2) cracking a segment of a nut should require equal or (presumably) less force than cracking a partially cracked whole nut; and (3) when there is no perceptible change in the physical condition of the nut, another equally or more forceful strike should follow (Fig. 3b). However, because of its locular structure and very high resistance to fracture, it might not be feasible to induce and propagate a fracture in an intact whole piaçava nut by striking it less forcefully, even multiple times. Therefore, we expected that the monkeys would crack a piaçava nut by striking it with the maximum force that they could generate without modulating the kinematic parameters of their strikes until that nut cracked.

METHODS

Ethics Statement

The Institutional Animal Care and Use Committee (IACUC no. A2012 02-012Y3 A0) at the University of Georgia (Athens, GA, U.S.A.) approved the present experiments.

Subjects and Study Site

The subjects were seven wild bearded capuchin monkeys (males: three adults, one subadult and one juvenile; females: two adults) (see Results, Table 1) inhabiting the EthoCebus study site at Fazenda Boa Vista in the southern Parnaíba Basin (9°39′S, 45°25′W), Piauí, Brazil. The log anvil and stone hammers that the monkeys used were available at the study site and both tucum and piaçava palms were abundant throughout the home range of these monkeys. We collected the nuts for the present study locally.

Experimental Procedure

Monkeys at Fazenda Boa Vista use quartzite stones of an average mass of about 1.1 kg (Visalberghi et al., 2007). However, because monkeys with body mass of less than 3 kg do not attempt to crack a piaçava nut using stones of mass less than about 1 kg (Liu, Fragaszy, & Visalberghi, submitted for publication), we provided the monkeys with 0.455 kg, 0.539 kg, 1.042 kg and 1.000 kg stones to crack the tucum nuts and a 1.500 kg stone to crack the piaçava nuts. The hulls of the piaçava nuts were already removed when we provided them to the monkeys. Both species of nuts were at the same stage of maturity at which Visalberghi et al. (2008) used them to test their physical properties. We placed a stone (0.455 kg, 0.539 kg, 1.042 kg, 1.000 kg or 1.500 kg) next to a log anvil and provided the focal monkey with a whole tucum or piaçava nut, and set up a Canon™ XF100 camcorder approximately 11.5 m away from and perpendicular to the anvil. We videorecorded the monkey from the sagittal plane of view as it cracked the nut, recording multiple nut-cracking sequences for each monkey. For kinematic analysis, at the start of each day, we videorecorded a 1×1 m square frame marked with reflective tape at 20 cm intervals by placing it directly above the anvil pit in which the monkeys placed the nuts.

Data Extraction

A nut-cracking sequence comprises several strikes, with each strike comprising the following three phases: (1) a preparatory prelift 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). We used an open source video analysis and modelling tool, Tracker (downloaded from http://physlets.org/tracker/) to measure the following two kinematic parameters of each strike: (1) the height of the stone from the surface of the anvil at the zenith point (amplitude) and (2) the velocity of the stone at the moment it hit the nut (impact velocity) (see Supplementary Movies S3 and S4). We used the values of these two parameters to determine a third work parameter of each strike: the proportionate work done by the monkey on the stone, using the formula: proportionate work done = (kinetic energy of the stone at the moment it hit the nut − potential energy of the stone at the zenith point)/potential energy of the stone at the zenith point. We determined the physical condition of the nut following each strike by the sound of impact between the stone and the nut and by looking at the physical condition of the nut following impact. To test our coding for interobserver reliability, we compared the repeated coding of 12 strikes by the same observer and by two different observers; there was no difference between the repeated coding by the same observer (amplitude: mean ± SD absolute difference = 0.007 ± 0.008 m; dependent samples t test: $t_{11} = 1.173$, $P = 0.266$; impact velocity: 0.133 ± 0.122 m/s; $t_{11} = 0.345$, $P = 0.737$) and by the two different observers (amplitude: mean ± SD absolute difference = 0.008 ± 0.006 m; dependent samples t test: $t_{11} = 0.897$, $P = 0.389$; impact velocity: 0.289 ± 0.631 m/s; $t_{11} = 1.100$, $P = 0.295$).

Statistical Analysis

We used Fisher's exact tests to compare the proportion of the tucum and piaçava nuts that each monkey cracked successfully. We used Mann−Whitney's U tests to compare the number of strikes that each monkey took to crack a tucum and a piaçava nut. We used

Table 1
Comparison of the proportion of the tucum and piaçava nuts that each monkey cracked and the number of strikes that it took to crack a tucum nut completely and to crack a piaçava nut into two or more segments

Individual	Sex	Age class	Body mass (kg)	Proportion of the nuts cracked			Number of strikes to crack a nut				
				T	P	P	T Versus P	U	N₁	N₂	P
Mansinho	M	A	3.44	12/12	9/9	1.000	T=P	27.0	12	9	0.096[b]
Jatobá	M	A	4.20	10/11	9/10	1.000	T>P	6.5	10	9	**0.001**
Teimoso	M	A	3.54	25/26	5/6	0.345	T>P	26.0	25	5	**0.039**
Catu	M	SA	2.73	11/11	4/5	0.313	T>P	4.5	11	4	**0.021**
Coco[a]	M	J	1.88	10/17	0/2	—	—	—	—	—	—
Piaçava	F	A	1.73	9/10	4/5	1.000	T=P	12.5	9	4	0.392
Dita[a]	F	A	2.04	12/13	2/2	1.000	—	—	—	—	—

M: male; F: female; A: adult; SA: subadult; J: juvenile; T: tucum; P: piaçava. Significant P values are shown in bold.
[a] Insufficient data.
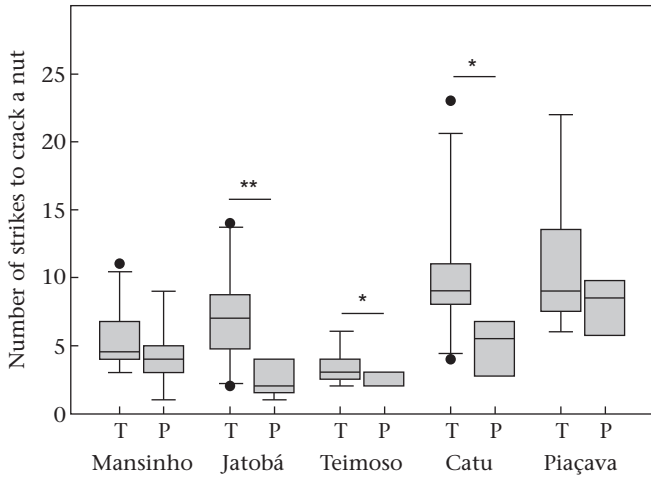[b] After removing an outlier at $P < 0.05$.

Figure 4. Comparison of the number of strikes that each monkey took to crack a tucum (T) nut and a piaçava (P) nut. Error bars indicate SEs. *$P < 0.05$; **$P < 0.005$.

independent samples t tests to compare for each monkey the two kinetic parameters of the strikes (amplitude and impact velocity) when cracking the tucum and piaçava nuts for the first strike of each sequence and for all strikes of each sequence. We used Wilcoxon signed-ranks tests to compare the number of strikes across all tucum and piaçava nuts in which the monkeys modulated or did not modulate the kinematic parameters on the basis of the condition of a nut following the preceding strike. We performed statistical analyses using SPSS 23 (IBM, Armonk, NY, U.S.A.) and used two-tailed tests at the significance level of $\alpha = 0.05$ (we used nonparametric tests for the data that did not meet the assumptions of normality and equality of variance).

RESULTS

Table 1 describes the proportion of the tucum and piaçava nuts that each monkey cracked and the number of strikes that it took to crack a tucum nut completely and to crack a piaçava nut into two or more segments. On the whole, it took the monkeys fewer strikes to crack an intact piaçava nut into two or more segments than to crack a tucum nut completely (Fig. 4, Table 1).

The velocity of the stone at the moment it hits the nut (impact velocity) determines the force of a strike (impact force). Also, a monkey can increase the impact velocity (and thus the impact force) beyond what the potential energy of the stone at the zenith point would predict, by raising the stone higher or exerting more force on the stone when lowering it (that is, by putting work into the stone). When cracking a tucum nut, the monkeys modulated the kinematic parameters of each strike on the basis of the condition of the nut following the preceding strike, according to the four possible outcomes of the strike (hull breached partially, hull breached completely, shell cracked partially or no perceptible change in the condition of the nut; Table 2, Supplementary Movies S3 and S4). In contrast, when cracking a piaçava nut, the monkeys modulated both kinematic parameters of their strikes following only one of the four possible outcomes; when a whole nut was cracked partially, the monkeys reduced the amplitude and impact velocity of the subsequent strike (Table 3). They did not modulate their strikes when a whole nut cracked completely or when there was no perceptible change in the physical condition of the nut. When a segment of a nut cracked partially, the monkeys decreased the amplitude of the subsequent strike but did not alter the impact velocity of the strike.

Five monkeys cracked at least three tucum nuts and three piaçava nuts; three of these monkeys raised a heavy stone (1.500 kg) higher in the first strike of each sequence when cracking a piaçava nut compared to a lighter stone (0.455, 0.439, 1.042 or 1.100 kg) when cracking a tucum nut (Fig. 5a, Table 4), and two of these monkeys raised a heavy stone higher across all strikes of each sequence compared to a light stone (Fig. 5b, Table 4). Each monkey lowered both the heavy and light stones with equal velocity in the first strike of each sequence (Fig. 5c, Table 4), but across all strikes of each sequence, they lowered the heavy stone when cracking a piaçava nut with a slower velocity compared to a light stone when cracking a tucum nut (Fig. 5d, Table 4). Whereas the monkeys put positive work into a light stone when cracking a tucum nut (mean ± SE proportionate work done: Mansinho: 0.434 ± 0.277, $N = 65$; Jatoba: 0.474 ± 0.353, $N = 82$; Teimoso: 0.227 ± 0.270, $N = 145$; Catu: 0.251 ± 0.309, $N = 123$; Piaçava: 0.244 ± 0.215, $N = 103$), they put almost zero or negative work into the heavy stone when striking a piaçava nut (Mansinho: -0.063 ± 0.174, $N = 60$; Jatoba: 0.030 ± 0.308, $N = 32$; Teimoso: -0.076 ± 0.271, $N = 24$; Catu: -0.120 ± 0.213, $N = 26$; Piaçava: -0.087 ± 0.164, $N = 49$).

Table 2
The number of strikes in which each monkey modulated or did not modulate the kinematic parameters on the basis of the condition of a tucum nut following the preceding strike

Individual	Hull breached partially (Expectation: Decrease)				Hull breached completely (Expectation: Increase)				Shell cracked partially (Expectation: Decrease)				No effect (Expectation: Increase)			
	Amplitude ($Z=-2.207$, $N=7$, $P=$**0.027**)		Impact velocity ($Z=-2.214$, $N=7$, $P=$**0.027**)		Amplitude ($Z=-0.846$, $N=7$, $P=0.398$)		Impact velocity ($Z=-2.207$, $N=7$, $P=$**0.027**)		Amplitude ($Z=-2.375$, $N=7$, $P=$**0.018**)		Impact velocity ($Z=-2.371$, $N=7$, $P=$**0.018**)		Amplitude ($Z=-2.371$, $N=7$, $P<$**0.018**)		Impact velocity ($Z=-2.366$, $N=7$, $P=$**0.018**)	
	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
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
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

D: decreased; ND: not decreased; I: increased; NI: not increased. Significant P values are shown in bold.

Table 3
The number of strikes in which each monkey modulated or did not modulate the kinematic parameters on the basis of the condition of a piaçava nut following the preceding strike

Individual	Whole nut cracked partially (Expectation: Decrease)				Whole nut cracked completely (Expectation: Decrease)				Segment cracked partially (Expectation: Decrease)				No effect (Expectation: Increase)			
	Amplitude ($Z=-2.214$, $N=6$, **$P=0.027$**)		Impact velocity ($Z=-2.214$, $N=6$, **$P=0.027$**)		Amplitude ($Z=0.378$, $N=6$, $P=0.705$)		Impact velocity ($Z=-1.294$, $N=6$, $P=0.196$)		Amplitude ($Z=-2.271$, $N=6$, **$P=0.023$**)		Impact velocity ($Z=-1.190$, $N=6$, $P=0.234$)		Amplitude ($Z=-1.709$, $N=7$, $P=0.088$)		Impact velocity ($Z=-0.966$, $N=7$, $P=0.334$)	
	D	ND	D	ND	D	ND	D	ND	D	ND	D	ND	I	NI	I	NI
Mansinho	9	1	8	2	2	4	1	5	3	1	3	1	12	16	14	14
Jatobá	5	2	5	2	2	0	2	0	1	0	0	1	6	4	6	4
Teimoso	5	1	5	1	1	1	0	2	1	0	0	1	4	2	3	3
Catu	3	0	3	0	1	0	1	0	1	0	1	0	10	6	10	6
Coco	–	–	–	–	–	–	–	–	–	–	–	–	12	6	10	6
Piaçava	3	1	3	1	1	1	0	2	1	0	1	0	19	13	15	17
Dita	2	0	2	0	0	2	0	2	2	0	2	0	7	3	4	6

D: decreased; ND: not decreased; I: increased; NI: not increased. Significant *P* values are shown in bold.

DISCUSSION

Wild bearded capuchin monkeys modulated the kinematic parameters of individual strikes and the organization of successive strikes according to the type and condition of a nut. When cracking a nut with a more resistant shell encapsulating a soft kernel, an optimal strike should be forceful enough just to crack the shell while leaving the kernel intact, because a more forceful strike is likely to smash the kernel, and a less forceful strike is likely to be ineffective. Striking such a nut repeatedly induces microfractures in its shell; this ultimately causes fatigue failure of the nut. A moderately forceful strike is enough to crack a nut that already has
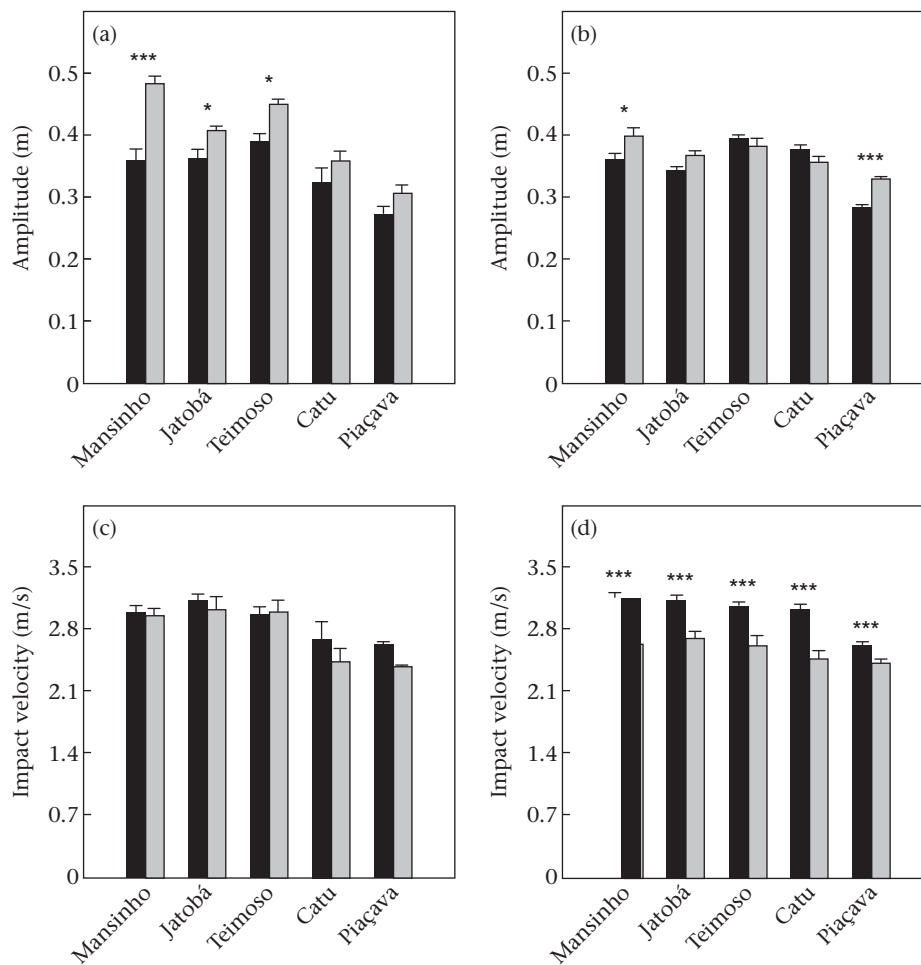

Figure 5. Comparison of the kinematic parameters of the strikes that each monkey took to crack a tucum nut (black bars) and a piaçava nut (grey bars). The amplitude of (a) the first strike of each sequence and (b) all strikes of each sequence. The impact velocity of (c) the first strike of each sequence and (d) all strikes of each sequence. Error bars indicate SEs. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

Table 4
Comparison of the kinematic parameters of the strikes that each monkey took to crack a tucum nut and a piaçava nut

Individual	Amplitude				Impact velocity		
	T versus P	*t*	*df*	*P*	T versus P	*t*	*P*
First strike of each sequence							
Mansinho	T<P	5.080	19	**<0.001**	T=P	0.341	0.737
Jatobá	T<P	2.630	19	**0.016**	T=P	0.660	0.517
Teimoso	T<P	2.217	30	**0.034**	T=P	0.360	0.722
Catu	T=P	0.821	18	0.423	T=P	0.731	0.474
Coco[a]	–	–	–	–	–	–	–
Piaçava	T=P	1.703	13	0.112	T=P	0.519	0.613
Dita[a]	–	–	–	–	–	–	–
All strikes of each sequence							
Mansinho	T<P	2.298	123	**0.023**	T>P	5.328	**<0.001**
Jatobá	T=P	2.362	118	0.098	T>P	4.467	**<0.001**
Teimoso	T=P	0.836	167	0.404	T>P	3.984	**<0.001**
Catu	T=P	1.339	147	0.183	T>P	4.541	**<0.001**
Coco[a]	–	–	–	–	–	–	–
Piaçava	T<P	6.035	150	**<0.001**	T>P	3.398	**<0.001**
Dita[a]	–	–	–	–	–	–	–

T: tucum; P: piaçava. Significant *P* values are shown in bold.
[a] Insufficient data.

fracture(s). For example, Koya (2006) demonstrated, both theoretically and experimentally, that striking an oil palm, *Elaeis guineensis,* nut (peak-force-at-failure 0.2–3.7 kN, depending on the size and moisture content of the nut; Manuwa, 2007) repeatedly, less forcefully reduces the rate of damage to the kernel of the nut. However, the locules presumably interrupt the passage of energy, so it might not be feasible to induce and propagate a fracture in a piaçava nut even after striking it less forcefully many times. Therefore, the monkeys cracked each piaçava nut by striking it repeatedly with the maximum force they could generate (without compromising on the angle and point of percussion) until that nut cracked.

It seems counterintuitive that although the monkeys had to use the maximum force possible to crack a piacava nut, they did not exert positive work into the heavy (1.5 kg) stone when lowering it to increase its impact velocity, but instead exerted negative work into it, thus reducing the impact velocity of the stone. The following two hypotheses explain this anomaly: (1) the monkeys may decrease the velocity of a heavy stone while lowering it to maintain the lateral stability of the body while maintaining a bipedal posture or to control the angle and point of percussion; and/or (2) the monkeys may be more likely prevent injury to themselves when lowering the stone more slowly, because they can better control the trajectory of the stone after it hits the nut, compared to when lowering the stone at greater velocity. These hypotheses need further investigation.

One could argue that the use of stones of different mass may also explain how the monkeys cracked a piaçava and tucum nut differently. However, the monkeys used strikes of a greater amplitude when striking a piaçava nut with a heavy stone (1.500 kg) compared to when striking a tucum nut with a light stone (0.455, 0.539, 1.042 or 1.000 kg). Also, they did not modulate the amplitude of the strike when cracking a piaçava nut except when the shell of the nut cracked partially. Both these results suggest that how the monkeys cracked a tucum or piaçava nut is not merely the outcome of the physical constraints imposed by the stone mass. Previously, two monkeys of the same group (both highly proficient at cracking nuts) used strikes of a greater amplitude when cracking a piaçava nut that was of a larger diameter and, therefore, more resistant to fracture compared to a nut that was of smaller diameter and, therefore, less resistant to fracture (Liu et al., submitted for publication).

Optimizing movements on the basis of the energetic constraints of a task characterizes the skilful use of a tool. The present study demonstrates that capuchin monkeys modulate their strikes on the basis of the type and condition of a nut. In a previous study, the captive chimpanzees modulated their strikes based on the mass of the stones and the resistance of the nuts, and experience enhanced the range and precision of their modulation (Bril et al., 2009; Foucart et al., 2005). These adjustments to percussive movements to produce an optimal amount of force are characteristic of skilful stone knapping by humans (Bril, Rein, Nonaka, Wenban-Smith, & Dietrich, 2010; Nonaka et al., 2010; Rein, Nonaka, & Bril, 2014). All three taxa, capuchin monkeys, chimpanzees and humans, are capable of modulating the kinematic parameters of individual percussive movements.

A body of literature suggests that task-specific temporal organization of percussive movements, as evident by the tools of the Oldowan Industrial Complex, is a skill that is peculiar to hominins (Ambrose, 2001; Delagnes & Roche, 2005; Roche et al., 1999; de la Torre, Mora, Domınguez-Rodrigo, de Luque, & Alcalá, 2003). However, the monkeys in the present study exhibited this skill, suggesting that, as in many other domains, such as precise manipulation (Marzke, 1997; Marzke & Marzke, 2000; Tocheri, Orr, Jacofsky, & Marzke, 2008) and bipedal locomotion (Hunt, 1994; Schmitt, 2003; Thorpe, Holder, & Crompton, 2007), the differences in percussion skills among nonhuman primates and extinct hominins are a matter of degree instead of categorical. Accordingly, we can ask questions about the task-specific temporal organization of percussive movements at different timescales. For example, at a longer timescale, we can ask how extinct hominins progressed technologically from using a stone to crack something to eat at that moment (which nonhuman primates, including chimpanzees, longtailed macaques and capuchin monkeys can do) to knapping a stone to use it for some other purpose now or later, (which nonhuman primates cannot do; see, for example, studies on efforts to induce Kanzi, a bonobo, *Pan paniscus,* to knap a stone: Schick et al., 1999; Toth, Schick, Savage-Rumbaugh, Sevcik, & Rumbaugh, 1993; and studies on efforts to induce bonobos and orang-utans, *Pongo pygmaeus,* to select, transport and save appropriate tools for future use: Mulachy & Call, 2015). Also, at a shorter timescale, we can ask how an individual organizes consecutive percussive movements based on the dynamics between the body and the rapidly changing requirements of the percussion task. The present study examines this phenomenon among capuchin monkeys, and previous studies have examined this phenomenon extensively among the glass bead knappers from Khambat, Gujarat, India (Biryukova & Bril, 2008; Bril, Roux, & Dietrich, 2005; Nonaka & Bril, 2012; Rein et al., 2014; Roux, Bril, & Dietrich, 1995) and humans cracking nuts using stones (Bril et al., 2015).

Two questions follow from the above arguments: what are the morphological and anatomical correlates of percussion, and why is it important to describe them? We argue that how individuals use their body to execute percussive movements determines the extent to which they can modulate them, as some morphological and anatomical features allow a greater range of movements and more precise control over these movements compared to other morphological and anatomical features. For example, young children predominantly use their elbow and shoulder joints while hammering (Kahrs, Jung, & Lockman, 2014), and adults move their wrist, elbow and shoulder joints to a comparable degree (Côté, Raymond, Mathieu, Feldman, & Levin, 2005). The use of the wrist joint leads to more precise control over percussive movements compared to the use of the elbow and shoulder joints (Kahrs et al., 2014). In short, the relative contribution of different joints contributes to the dexterity of percussive movements.

An individual can modulate the force of a strike by modulating the amplitude of the strike, or putting positive or negative work on the stone when lowering it, or both. The morphological and anatomical features of a species may support the modulation of one of these two parameters to a greater extent than the other. For example, bearded capuchin monkeys, chimpanzees and humans execute percussive movements with one hand or both hands when assuming sitting as well as standing postures. However, because of several morphological and anatomical differences (see, for example, Fleagle, 2013, for some of these differences), the three species may execute percussive movements across different combinations of joints to achieve the same composite task performance. Comparative assessment of the morphological and anatomical correlates of percussion among extant nonhuman primates that use percussion tools and humans would advance the study of the evolution of stone knapping.

Acknowledgments

Supplementary Material

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