THE BIOMECHANICS OF MULTI-JOINT POSTURE AND MOVEMENT CONTROL IN WILD BEARDED CAPUCHIN MONKEYS USING STONE HAMMERS

by

MADHUR MANGALAM

(Under the Direction of Dorothy M. Fragaszy)

ABSTRACT

The appearance of stone-assisted tooling and bipedalism is a milestone in human evolution. However, because of the fragmentary nature of the fossil record and challenges in reconstructing behavior in fossils, changes in posture and motor control that accompanied the evolution of this behavior have remained elusive. Quadrupedal nonhuman primates that adopt a bipedal stance while using stone hammers to process hard food provide a unique comparative reference point to investigate specific aspects of such changes. In my dissertation research, I investigated the multi-joint posture and movement control in a population of wild bearded capuchin monkeys, *Sapajus libidinosus* using anvil-and-hammer tools in bipedal stance. Some populations of *Sapajus* crack open palm nuts using stone hammers during routine foraging. In the first and second studies, I found that the monkeys modulate the kinematic parameters of individual strikes and the organization of successive strikes to accommodate the nut's resistance-to-fracture. In the third study, I found that the monkeys keep the strike's amplitude and the hammer's velocity at impact constant with respect to hammer mass. However, in doing so, the hammer's kinetic energy at impact—which determines the propagation of a fracture/crack in a nut and is the key parameter that humans control while knapping stones to manufacture stone tools—varies across hammers of different mass. In the fourth study, I found that the monkeys use joint synergies to stabilize the hammer trajectory while cracking nuts in bipedal stance. Together these findings show that although inadequate to manufacture stone tools like humans do, these monkeys solve the challenge of postural and movement control by controlling hammer’s velocity at impact instead of hammer’s kinetic energy at impact, and structure motor variability strategically. They highlight the importance of studying the evolution of bipedal striking, and more generally, research on tooling in nonhuman animals, using method of biomechanics and human movement science.

INDEX WORDS: manual dexterity; nut cracking; percussion; *Sapajus libidinosus*; stone knapping; tooling

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Dual-Degree B.S.-M.S., Indian Institute of Science Education and Research (IISER) Pune, 2012

A Dissertation Submitted to the Graduate Faculty of the University of Georgia in Partial
Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2018

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December 2018

DEDICATION

I dedicate this dissertation to my father Umesh Chandra and my mother Mamta Agarwal, with love and eternal appreciation.

ACKNOWLEDGEMENTS

I would like to gratefully acknowledge the guidance, support and encouragement of my doctoral advisor, Dr. Dorothy M. Fragaszy, and the members of my committee, Dr. Karl M. Newell and Dr. Dean Sabatinelli, during my time at the University of Georgia, as well as students of Dr. Karl M. Newell, for their continued mentorship and collaboration, and for fueling my budding interests in comparative biomechanics.

I thank Patricia Izar and Elisabetta Visalberghi for shared direction of the EthoCebus project at Fazenda Boa Vista, of which this study is one product. I also thank Fonseca de Oliveira family for logistical help and permission to conduct research at Fazenda Boa Vista. Finally, I would like to thank Ashley Myers, James Y. Hammers, and Lindsey K. R. Roles for assistance with kinematic coding of videos.

This dissertation would not have been possible without funding from the University of Georgia and the National Geographic Society.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Percussive tooling [wherein *percussion* refers loosely to “a forceful, muscle-driven striking of one body against another” Marchant and McGrew (2005, p. 342)] is an ancient feature of human technology. The stone artefacts belonging to the Lomekwian Complex dating 3.3 million years (Harmand et al., 2015) and Oldowan Industrial Complexes dating 2.6–2.5 million years (Semaw et al., 1997) provide the earliest archaeological evidence of percussive tooling in ancestral hominins. Several authors have suggested that the evolution of percussive tooling in ancestral 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), long-tailed 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; Moura & Lee, 2004; Ottoni & Mannu, 2001; Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011) use anvil-and-hammer tools to crack open encased foods. Thus, it is useful to study percussive tooling and other bipedal activities, as well as bipedal locomotion, in these species while seeking insights into motor strategies that may have accompanied the evolution of bipedal striking in hominins. The ancestors of chimpanzees and capuchin monkeys diverged from hominids long before hominins adopted bipedal locomotion (if not before they began percussive tooling) and thus do not represent a progressive step in the evolution of bipedal striking in ancestral hominins. Yet, they offer a unique, independently-evolved comparative reference point to clarify specific aspects of the evolution of bipedal striking, such as how an occasionally bipedal species can solve the biomechanical challenges of posture and movement control while using massive hammers, that have remained elusive until now.

Unusually among primates, bearded capuchin monkeys, *Sapajus libidinosus*, routinely walk bipedally on the ground (Biondi, 2010). The monkeys in my study population at Fazenda Boa Vista (FBV), Piauí, Brazil, often use massive hammers, often ≥ 50% of an adult female's body mass, for processing highly resistant nuts (Fig. 1.1) (Mangalam, Izar, Visalberghi, & Fragaszy, 2016; Visalberghi et al., 2009). I estimate that other nonhuman primates that use stone hammers typically use proportionally lighter hammers (chimpanzees: < 20% of body mass (Visalberghi, Sirianni, Fragaszy, & Boesch, 2015); long-tailed macaques: < 10% of body mass (Gumert, Kluck, & Malaivijitnond, 2009). Capuchin monkeys at FBV carry hammers to anvils bipedally (Duarte, Hanna, Sanches, Liu, & Fragaszy, 2012) and stand bipedally while using hammers (Liu et al., 2009). These monkeys must solve significant biomechanical challenges of posture and movement control while using massive hammers and thus are ideal for investigating the changes in the motor control strategies that accompanied the evolution of bipedal striking in ancestral hominins.

The constraints-led perspective on the development of coordination for movement in action (Newell, 1986; Newell & Jordan, 2007) provides a framework for investigating the motor control strategies used to solve the biomechanical challenges of postural and movement control. This perspective takes the premise that a confluence of features of the organism, environment, and task are the sources of constraints imposed on the development of coordination. The physical structure and physiological make-up of the body impose morphological and anatomical, perceptuomotor, and affective constraints. Various extraneous factors that may affect the actor's performance impose environmental constraints. Finally, the ergonomic and goal-related features of the task dictate how the constraints imposed by the body and the environment interact to shape coordination. A given pattern of coordination can be explained in terms of these constraints. Alternatively, when some constraints are manipulated, the resulting changes in patterns of coordination can also highlight how these constraints shape the coordination of movement in a task.

The goals of my dissertation research were twofold: first, to investigate how wild bearded capuchin monkeys control stone hammers to meet the energetic demands of the nut-cracking task; second, to identify the motor control strategies they use to solve the challenges associated with standing bipedally while using massive hammers. I captured the striking movements of monkeys in their natural habitat at Fazenda Boa Vista (FBV), Piauí, Brazil, as they crack nuts using stone hammers. I conducted the biomechanical analysis of multi-joint posture and movement control to examine how constraints from different sources influence patterns of coordination. The nut-cracking behavior in bearded capuchin monkeys can be analyzed in terms of constraints on striking movements (Fig. 1.2). The sources of organismal constraints include body mass, limb length, the range of motion of segments about the joints, and sensitivity to variation in the movement of the hammer. The putative sources of environmental constraints include hammer mass, the friability of the substrate on which the monkeys stand, and the compliance of the anvil. Finally, the putative sources of task constraints include the force required to initiate a fracture in the nut, which might be controlled by modulating the point and angle of contact, choosing a lighter or heavier hammer, and by modulating the hammer's kinetic energy at impact once the hammer is chosen. By manipulating some of these constraints, one can study the development of coordination of striking movements in these monkeys.

I manipulated several putative sources of constraints on the monkeys' striking movements. First, I included both juvenile and adult monkeys to examine the influence of body mass (a source of organismic constraint) on the coordination of movement. The most common species of nuts that the monkeys at FBV habitually process differ considerably in their resistance-to-fracture: (1) catule (*Attalea* spp.: mean ± s.d. 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). Each of these nuts is considerably harder than the orally processed food provisioned to nonhuman primates in captivity (Williams, Wright, Truong, Daubert, & Vinyard, 2005) and the nuts that humans commonly process with the hand or the mouth, such as almonds, *Prunus dulcis* (peak-force-at-failure: ca. 0.5 kN) (Aktas, Polat, & Atay, 2007), and walnuts, *Juglans regia* (ca. 0.5 kN) (Sharifian & Derafshi, 2008). I manipulated the task constraints by providing the monkeys with the tucum and piaçava nuts, which, in addition to lying at the extremes of the spectrum of resistance to fracture, also differ structurally. Finally, I manipulated the environmental constraints by providing the monkeys with hammers of different masses. I analyzed the resulting changes in patterns of coordination to elucidate how these constraints shape the monkeys' striking movements.

A Note on the Structure of My Thesis

My dissertation research consists of four distinct studies each which I describe below in brief. I devote four chapters of this thesis (Chapters 2–5) to describing each study in full detail. Finally, I discuss the general conclusions and implications of all my findings in Chapter 6.

Study 1 (Chapter 2)

In the first study, I investigated whether wild bearded capuchin monkeys modulate the kinematic parameters of consecutive strikes nut as per the [changing] energetic requirements of the task.

An intact tucum nut consists of soft exocarp and mesocarp (which together constitute the hull) that encapsulate a hard endocarp (the shell) that encapsulates a soft endosperm; the hull can be easily detached from the endocarp manually or by using the mouth once it is breached

(Visalberghi et al., 2008). Accordingly, (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; and (3) if there is no perceptible change in the physical condition of the nut, then a more forceful strike should follow. I thus anticipated that while processing a tucum nut, the monkeys would modulate successive strikes in accordance with the physical condition of the nut.

The kinematic analysis of strikes revealed that the monkeys process a tucum nut by striking it repeatedly with moderate force (i.e., by not exceeding a threshold), and modulate the kinematic parameters of each strike on the basis of the physical condition of the nut (i.e., the development of a fracture) following the preceding strike. Repeatedly striking the nuts with moderate force is energetically more efficient than forcefully striking them once and reduces the likelihood of smashing a soft kernel. Determining the energetic constraints of the task and dynamically optimizing movements using those as criteria are dexterous accomplishments.

Study 2 (Chapter 3)

In the second study, I 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. I provided monkeys with tucum and piaçava nuts, which, in addition to lying at the extremes of the spectrum of resistance to fracture, also differ structurally. I examined whether and how monkeys use different strategies to process the two species of nuts.

In contrast to a tucum nut (which the monkeys processed in Study 1), an intact piaçava nut is extremely resistant to fracture, has a thicker endocarp (the shell), and consists of several locules, each encapsulating an endosperm (the kernel) (Visalberghi et al., 2008). An intact piaçava nut also has an exocarp and an edible mesocarp that the monkeys themselves remove before cracking, or more commonly at our site, grazing cattle remove them. Accordingly, (1) completely cracking a partially cracked whole piaçava nut (i.e., a nut that already has fracture(s)) should require less force than cracking an intact whole nut; likewise, cracking a partially cracked segment (i.e., 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) if there is no perceptible change in the physical condition of the nut, then a more forceful strike should follow. However, because of its very high resistance to fracture and locular structure, 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. However, given the above differences between hardness and structure of tucum and piaçava nuts, I anticipated 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 completely cracks open.

I found that the monkeys aptly accommodate the physical properties of the nut into the kinematic parameters of each strike and the organization of successive strikes. They crack open the less resistant tucum nut by striking it repeatedly with moderate force (i.e., by not exceeding a threshold), and modulate the kinematic parameters of each strike on the basis of the physical condition of the nut (i.e., the development of a fracture) following the preceding strike. In contrast, they crack open the more resistant piaçava nut by striking it with the maximum force that they can generate without modulating the kinematic parameters of their strikes until that nut cracks.

Study 3 (Chapter 4)

In the third study, I analyzed the patterns of coordination in multi-joint movement in relation to the control of stone hammers in wild bearded capuchin monkeys.

The biomechanical analysis of multi-joint movement revealed that the monkeys predominantly rely on the movement of their hindlimbs (hip and knee) and their torso (lumbar) to lift and lower a hammer, and to a limited extent, on the movement of their forelimbs (shoulder) to lift a hammer. They alter patterns of coordination of movement to accommodate changes in hammer mass to keep the strike's amplitude and the hammer's velocity at impact constant. In doing so, the hammer's kinetic energy at impact—which determines the propagation of a fracture in a nut and also is the key parameter that knappers control while manufacturing stone tools—varies with hammer mass.

Study 4 (Chapter 5)

In Study 4, I identified the motor strategies wild bearded capuchin monkeys use to control the hammer's trajectory while using massive hammers. I hypothesized that if the requirement of standing bipedally poses a significant postural challenge, then to control the hammer trajectory, monkeys would more closely control joint variability in the lower body compared with the upper body. To test this hypothesis, I used an uncontrolled manifold (UCM) analysis to determine whether and how monkeys control joint variability differently in the lower and upper bodies to reduce variability in the hammer trajectory.

The UCM analysis allows studying how variability in the degrees of freedom (DoFs) at the joint level influences variability in the putatively controlled variable (Latash, Scholz, & Schöner, 2007; Scholz & Schöner, 1999; Schöner, 1995). In the context of the nut-cracking task, this putatively controlled variable is the hammer's position. The concept of the UCM analysis is most clearly understood in terms of muscle synergies: multiple muscles work as functional units such that the central nervous system (CNS) jointly and proportionally activates all muscles in the synergy. As demands of a task change, so does the CNS control that in turn changes the muscle synergies. By extending the notion of muscle synergies to groups of muscles that span multiple joints, the coordination of multiple DoFs can be understood. The UCM analysis proceeds by partitioning variability in the putatively controlled variable into two subspaces: controlled and uncontrolled. While variability in the controlled subspace influences the controlled variable, variability in the uncontrolled subspace leaves the controlled variable unchanged. A greater magnitude of variability in the uncontrolled subspace compared to the controlled subspace implies the use of a joint synergy. Accordingly, the ratio of uncontrolled to controlled variability reflects the strength of the synergy: stronger or weaker.

When considering a strike in monkeys' sagittal plane of view, each strike involves motion about seven body joints—foot, knee, hip, lumbar, shoulder, elbow, and wrist (or eight angles including the angle between the feet and the ground)—to control the hammer's position in the horizontal and vertical (Mangalam, Pacheco, Izar, Visalberghi, & Fragaszy, 2017). That is, the movement space of a strike is a six-dimensional uncontrolled manifold. I thus anticipated that the monkeys would use strong joint synergies to exploit this redundancy in the movement space of a strike to reduce variability in the hammer's trajectory. In study 3, I found that spatiotemporal coordination between any two joints is greater for a heavier hammer compared to a lighter hammer (Mangalam, Pacheco, Izar, Visalberghi, & Fragaszy, 2018). Accordingly, I expected that the strength of synergy would reduce with increase in hammer mass.

Capuchin monkeys predominantly rely on the movement of their hindlimbs (hip and knee) and their torso (lumbar) to lift and lower a hammer, and to a limited extent, on the movement of their forelimbs (shoulder) to lift a hammer (Mangalam et al., 2017). I thus anticipated that the monkeys would differently structure motor variability across the DoFs of the lower and upper bodies. I predicted that the monkeys would control variability in motion about the lower body joints more stringently compared with the upper body and thus the controlled variability would be predominantly concentrated in the lower body, whereas the uncontrolled variability, in the upper body.

The UCM analysis revealed that the challenge of standing bipedally dictates the structure of motor variability in bearded capuchin monkeys using hammers. The uncontrolled variability [which did not influence the hammer's trajectory and, therefore, is referred to as "uncontrolled"] was predominantly concentrated in the upper body. The controlled variability [which influences the hammer's trajectory and, therefore, is referred to as "controlled"] was predominantly concentrated in the lower body. Thus, the hammer's trajectory was highly sensitive to variability in the motion of the lower body joints, and only to a limited extent, to variability in the motion of the upper body joints. No such distinction was apparent in the trunk and the pelvis, as comparable magnitudes of controlled and uncontrolled variabilities characterized the motion of both these joints.

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Figure 1.1. A wild bearded capuchin monkey, *Sapajus libidinosus*, is striking an intact piaçava nut with a quartzite stone hammer. Photo courtesy of Noemi Spagnoletti.

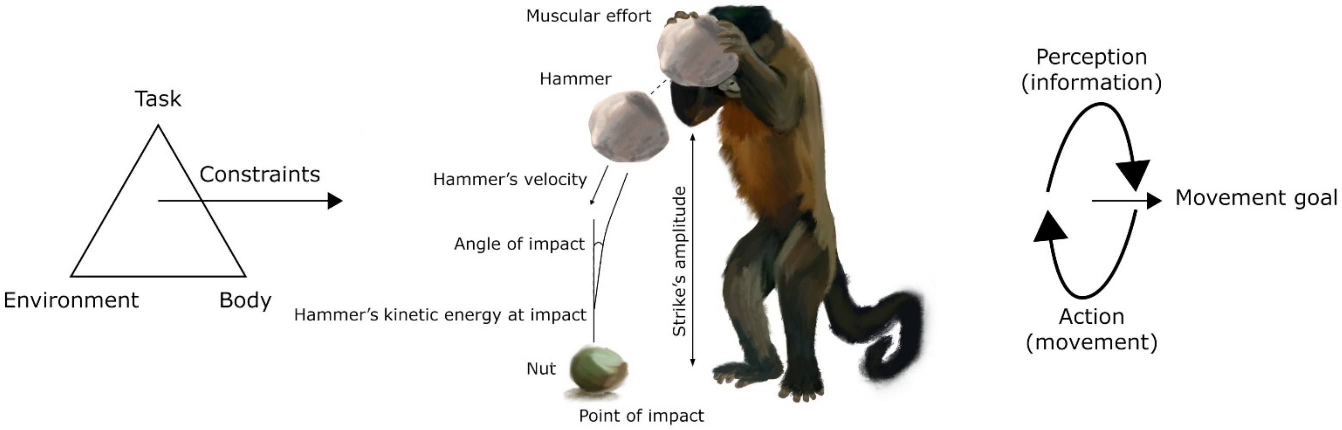

Figure 1.2. Schematic illustration of the constraints-led perspective on the development of coordination for movement in action (Newell, 1986), using as an example a bearded capuchin monkey striking a nut with a stone hammer. Drawings courtesy of Antonio Jose Osuna Mascaró.

CHAPTER 2

WILD BEARDED CAPUCHIN MONKEYS CRACK NUTS DEXTEROUSLY[1]

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[1] Mangalam, M. and Fragaszy, D. M. Accepted by *Current Biology*.

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Abstract

Dexterous tool use has been crucial in the evolution of hominid percussive technology (Ambrose, 2001; Byrne, 2005a; Matsuzawa, 2001). According to Newell (1986), ‘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 (Piauí, Brazil), that routinely crack palm nuts using stones by placing them on rock outcrops, boulders, and logs (collectively termed anvils) (D. Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004), 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/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 current findings.

Keywords: bearded capuchin monkey; control and coordination; dexterity; nut-cracking; percussion; *Sapajus libidinosus*; tool use

Results and Discussion

We observed 14 wild bearded capuchin monkeys cracking the tucum nuts [mean ± s.d. peak-force-at-failure = 5.57 ± 0.25 kN, *n* = 12 (E. Visalberghi et al., 2008)]. 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 (Fig. 2.1a) has two distinct layers, a soft outer hull (i.e., the exocarp and the mesocarp) (Fig. 2.1b, c), and a hard inner shell (i.e., the endocarp) encapsulating a relatively soft kernel (i.e., the endosperm) (Fig. 2.1d, e); 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: (a) breaching the hull should require less force than cracking the shell. (b) 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. (c) No perceptible change in the physical condition of the nut following a strike should require another more forceful strike (Fig. 2.2).

Typically, the monkeys took (a) two strikes to breach the hull (and after that, they removed the hull manually, or with their teeth), (b) two strikes to crack the shell, and (c) 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 2.1). 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/crack) while cracking a single tucum nut). Statistical comparison of the number of strikes in which the monkeys modulate 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 2.2, using paired samples t-test revealed that the monkeys modulated more strikes than expected by chance (Table 2.2). 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 2.2). This anomaly raises the question whether the monkeys perceive 'breaching the hull' and 'cracking the shell' as two different tasks; but evaluating this hypothesis needs further experimentation. Table 2.3 provides an overview of the scale of modulation; it describes the mean ± s.d. values of the modulation of the kinematic 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/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 (2006) 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 to 3.7 kN depending on the size and moisture content of the nut (Manuwa, 2007)] with moderate force (a) 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 (b) 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 (Bril, Dietrich, Foucart, Fuwa, & Hirata, 2009) and humans (Bril, Rein, Nonaka, Wenban-Smith, & Dietrich, 2010).

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. (a) 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) (Bock, 2005) and, (b) Nigerian farmers crack the oil palm nuts by placing the nuts between two stones and varying the applied force over consecutive strikes (Luedtke, 1992). 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 (Bril et al., 2012; Byrne, 2005b; Marchant & McGrew, 2005). 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 which vary across blows (Biryukova & Bril, 2008; Bril et al., 2010; Bril et al., 2012; Nonaka, Bril, & Rein, 2010; Rein, Nonaka, & Bril, 2014).

The analysis of percussive tasks in nonhuman primate species (here, nut-cracking) has progressed from their description (Boesch & Boesch, 1981; Fragaszy et al., 2004) to the complexity of actions (Boesch & Boesch, 1993; De Resende, Ottoni, & Fragaszy, 2008; Hirata, Morimura, & Houki, 2009) and the choice and adaptation of tools (Christophe Boesch & Hedwige, 1982; Fragaszy et al., 2010; Liu et al., 2011; Visalberghi et al., 2009), 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 if it adapted the movements (i.e., varied strike force) to the characteristics of the tasks (anvils with and without cavity; different types of nuts), though it deployed slightly more energy while cracking nuts on a flat-surface anvil than on an indented anvil (Foucart et al., 2005). 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 (Bril et al., 2009). 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. (2009), 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.

Methods

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 2.1) (see Spagnoletti et al. (2011) 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 fps. We placed a CanonTM XF100 camcorder ~ 11.5 m away from the anvil, 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 1×1 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.

A nut-cracking sequence comprised several strikes, each strike divided into (a) a preparatory pre-lift phase (holding and manipulating the stone), (b) an upward phase (elevating the stone to a zenith point), and (c) a downward phase (lowering the stone to hit the nut) [see Liu, et al. (2009)]. 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/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.

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 ± s.d. abs. difference = 0.007 ± 0.008 m, paired samples t-test: $t = -1.173$, $n = 12$, $p = 0.266$; velocity: 0.133 ± 0.122 m/s, $t = -0.345$, $n = 12$, $p = 0.737$), and by the two different observers (height: 0.008 ± 0.006 m, $t = 0.897$, $n = 12$, $p = 0.389$; velocity: 0.289 ± 0.631 m/s, $t = -1.100$, $n = 12$, $p = 0.295$).

Acknowledgements

We thank the Family Fonseca de Oliveira for logistical support and assistance in Boa Vista; Caroline E. Jones, Elisabetta Visalberghi, Hannah Mosley, Michael Haslam, Patrícia Izar, Victoria Tobolsky, and other EthoCebus colleagues for help with video-recording the monkeys cracking nuts, the Brazilian Institute of Environment and Renewable Natural Resources for permitting us to work in Brazil, and the European Research Council, the National Geographic Society, and the University of Georgia, Athens, USA for supporting the present study.

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Table 2.1

Median (IQR) 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.

Table 2.2

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

Monkey	**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
Paired samples t-test[†]	$t_{2,12}$	– 3.975		– 3.341		– 1.767		– 3.117		– 7.195		– 4.785		– 11.576		– 5.942	
	p	0.002**		0.005**		0.102		0.009*		< 0.001***		0.001**		0.001**		0.001**	
Binomial test[‡]	p	0.092		0.023*		1.000		0.092		0.001**		0.001**		0.001***		0.013*	

'H:' Height of the stone from the nut at the zenith point; 'V:' Maximum velocity of the stone during the downward phase of the strike

'D:' Decreased; 'ND:' Not decreased; 'I:' Increased; 'NI:' Not increased

[†] Results of paired samples t-tests comparing the number of strikes in which the monkeys modulate or did not modulate the kinematic parameters

[‡] Results of binomial tests examining the proportion of monkeys that modulated the kinematic parameters in the majority of strikes

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

Table 2.3

Mean ± s.d. Values of the Modulation of the Kinematic Parameters Along with the Values of the Kinematic Parameters of the Preceding Strike for Each Monkey (Mean ± s.d. Values of the Kinematic Parameters of the Preceding Strike Are Enclosed Within Parentheses)

Monkey	**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**
Mansinho	– 0.05 ± 0.00	– 0.15 ± 0.11	0.04 ± 0.03	0.29 ± 0.18	– 0.08 ± 0.05	– 0.51 ± 0.30	0.05 ± 0.04	0.44 ± 0.39
	(0.37 ± 0.09)	(3.14 ± 0.48)	(0.34 ± 0.06)	(3.10 ± 0.18)	(0.39 ± 0.08)	(3.25 ± 0.60)	(0.34 ± 0.08)	(2.97 ± 0.49)
Jatobá	– 0.05 ± 0.05	– 0.55 ± 0.46	0.05 ± 0.06	0.61 ± 0.49	– 0.06 ± 0.04	– 0.64 ± 0.24	0.04 ± 0.04	0.49 ± 0.47
	(0.37 ± 0.03)	(3.39 ± 0.37)	(0.31 ± 0.06)	(2.94 ± 0.43)	(0.37 ± 0.06)	(3.31 + 0.66)	(0.33 ± 0.05)	(2.87 ± 0.45)
Teimoso	– 0.05 ± 0.07	– 0.49 ± 0.49	0.06 ± 0.05	0.41 ± 0.29	– 0.10 ± 0.07	– 0.63 ± 0.36	0.05 ± 0.04	0.40 ± 0.39
	(0.43 ± 0.04)	(3.35 ± 0.30)	(0.48 ± 0.03)	(2.88 ± 0.44)	(0.43 ± 0.06)	(3.21 ± 0.40)	(0.37 ± 0.08)	(2.93 ± 0.56)
Tomate	– 0.03 ± 0.02	– 0.33 ± 0.23	0.03 ± 0.03	0.25 ± 0.21	– 0.07 ± 0.04	– 0.73 ± 0.51	0.03 ± 0.02	0.35 ± 0.22
	(0.33 ± 0.03)	(3.07 ± 0.43)	(0.29 ± 0.03)	(2.76 ± 0.34)	(0.31 ± 0.04)	(3.06 ± 0.48)	(0.29 ± 0.04)	(2.80 ± 0.40)
Catu	– 0.05 ± 0.02	– 0.39 ± 0.27	0.09 ± 0.04	0.49 ± 0.32	– 0.09 ± 0.08	– 0.70 ± 0.62	0.06 ± 0.04	0.48 ± 0.38
	(0.38 ± 0.08)	(3.03 ± 0.63)	(0.32 ± 0.07)	(2.61 ± 0.59)	(0.40 ± 0.07)	(3.02 ± 0.55)	(0.35 ± 0.07)	(2.84 ± 0.58)
Coco	– 0.03 ± 0.05	– 0.33 ± 0.21	0.04 ± 0.01	0.28 ± 0.08	– 0.07 ± 0.05	– 0.59 ± 0.39	0.04 ± 0.04	0.38 ± 0.3
	(0.31 ± 0.04)	(2.52 ± 0.31)	(0.33 ± 0.04)	(2.65 ± 0.21)	(0.34 ± 0.07)	(2.67 ± 0.43)	(0.29 ± 0.05)	(2.41 ± 0.34)

Presente	– 0.05 ± 0.01	– 0.38 ± 0.25	0.06 ± 0.08	1.44 ± 0.00	–	–	0.03 ± 0.03	0.32 ± 0.32
	(0.27 ± 0.01)	(2.31 ± 0.25)	(0.21 ± 0.08)	0.88 ± 0.00			(0.25 ± 0.04)	(2.04 ± 0.25)
Cachassa	– 0.01 ± 0.00	–	0.03 ± 0.00	0.83 ± 0.00	– 0.07 ± 0.01	– 0.81 ± 0.30	0.02 ± 0.02	0.29 ± 0.21
	(0.23 ± 0.00)		(0.37 ± 0.00)	2.82 ± 0.00	(0.32 ± 0.12)	(2.79 ± 1.22)	(0.20 ± 0.04)	(1.65 ± 0.42)
Piaçava	– 0.05 ± 0.03	– 0.34 ± 0.24	0.02 ± 0.02	0.11 ± 0.14	– 0.06 ± 0.04	– 0.41 ± 0.15	0.04 ± 0.03	0.31 ± 0.22
	(0.29 ± 0.05)	(2.54 ± 0.30)	(0.28 ± 0.02)	(2.44 ± 0.57)	(0.31 ± 0.06)	(2.74 ± 0.34)	(0.26 ± 0.04)	(2.47 ± 0.28)
Dita	– 0.02 ± 0.02	– 0.42 ± 0.23	0.03 ± 0.02	0.33 ± 0.23	– 0.04 ± 0.03	– 0.55 ± 0.32	0.03 ± 0.02	0.36 ± 0.26
	(0.33 ± 0.04)	(3.30 ± 0.32)	(0.30 ± 0.03)	(2.51 ± 0.33)	(0.30 ± 0.04)	(3.03 ± 0.66)	(0.31 ± 0.04)	(2.96 ± 0.44)
Doree	– 0.02 ± 0.02	– 0.33 ± 0.19	0.04 ± 0.04	0.28 ± 0.19	– 0.05 ± 0.04	– 0.45 ± 0.26	0.03 ± 0.03	0.21 ± 0.15
	(0.31 ± 0.04)	(2.34 ± 0.24)	(0.25 ± 0.05)	(1.99 ± 0.25)	(0.30 ± 0.01)	(2.37 ± 0.23)	(0.28 ± 0.04)	(2.16 ± 0.26)
Chuchu	– 0.02 ± 0.02	– 0.31 ± 0.27	0.03 ± 0.03	0.41 ± 0.29	– 0.09 ± 0.04	– 0.61 ± 0.37	0.03 ± 0.02	0.30 ± 0.27
	(0.31 ± 0.05)	(2.57 ± 0.38)	(0.30 ± 0.04)	(2.29 ± 0.14)	(0.32 ± 0.05)	(2.50 ± 0.31)	(0.27 ± 0.05)	(2.23 ± 0.37)
Pamonha	– 0.01 ± 0.00	– 0.60 ± 0.00	0.03 ± 0.01	0.26 ± 0.15	–	–	0.03 ± 0.03	0.26 ± 0.22
	(0.30 ± 0.00)	(2.87 ± 0.00)	(0.19 ± 0.13)	(1.90 ± 0.91)			(0.18 ± 0.05)	(1.55 ± 0.32)
Pasoca	–	–	–	–	–	–	0.02 ± 0.02	0.26 ± 0.20
							(0.23 ± 0.03)	(2.02 ± 0.18)

‘H:’ Height of the stone from the nut at the zenith point; ‘V:’ Maximum velocity of the stone during the downward phase of the strike

Figure 2.1. 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.

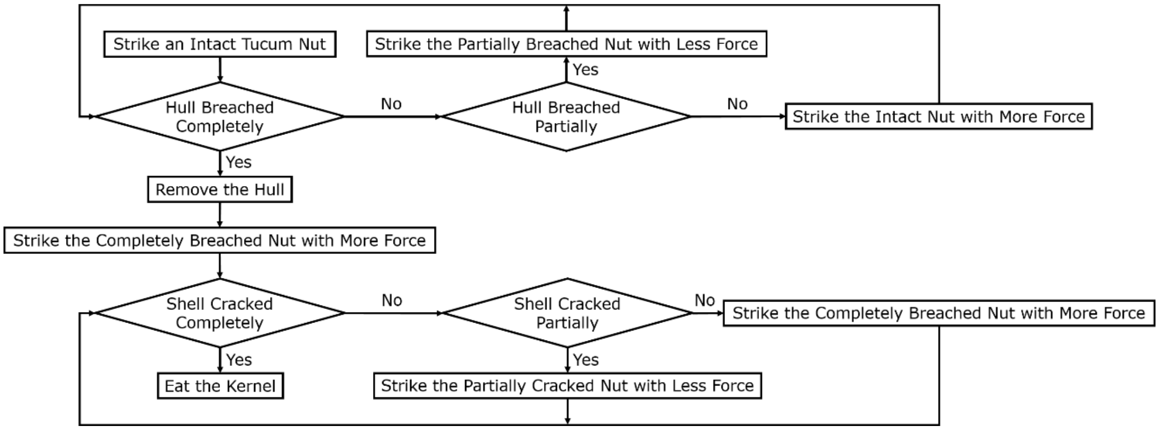

Figure 2.2. The flow chart illustrating the model we hypothesized the monkeys would follow while cracking a single tucum nut to modulate the kinematic parameters of the current strike on the basis of the condition of the nut following the preceding strike.

CHAPTER 3

TASK-SPECIFIC TEMPORAL ORGANIZATION OF PERCUSSIVE MOVEMENTS IN WILD BEARDED CAPUCHIN MONKEYS[2]

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[2] Mangalam, M., Izar, P., Visalberghi, E., and Fragaszy, D. M. Accepted by *Animal Behaviour*.

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Abstract

Tool-assisted percussion is an ancient feature of human technology. Tool-assisted percussion is not uniquely human; chimpanzees, long-tailed macaques and capuchin monkeys 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 nuts of two different species which 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.

Keywords: bearded capuchin monkey; dexterity; nut cracking; *Sapajus libidinosus*; stone knapping; tool use

Introduction

Tool-assisted percussion (here, percussion refers loosely to ‘a forceful, muscle-driven striking of one body against another’ see Marchant and McGrew (2005), p. 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 Myr) (Harmand et al., 2015) and Oldowan Industrial Complexes (2.6–2.5 Myr) (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), long-tailed macaques, *Macaca fascicularis aurea* (Gumert & Malaivijitnond, 2012; Malaivijitnond et al., 2007) and capuchin monkeys, *Sapajus* spp. (Canale, Guidorizzi, Kierulff, & Gatto, 2009; de A. Moura & Lee, 2004; Ferreira, Emidio, & Jerusalinsky, 2010; Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004; Mangalam & Fragaszy, 2015; 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 skillful use of a tool by describing the kinetic, kinematic and spatiotemporal properties of tool-use movements (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, 1986). The physical structure and physiological makeup 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 (Elisabetta 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: (i) the point of percussion, (ii) the angle of percussion, and (iii) the kinetic energy that initiates a fracture (Bril et al., 2012) (Fig. 3.1a). To knap a stone one needs to control the following five functional parameters simultaneously: (i) the exterior platform angle, (ii) the platform depth, (iii) the point of percussion, (iv) the angle of the blow relative to the platform, and (v) the kinetic energy that initiates a fracture (Bril et al., 2012; Dibble & Rezek, 2009; Nonaka, Bril, & Rein, 2010) (Fig. 3.1b). 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 compared to 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).

Skillfully knapping a stone requires different skills and 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). This, however, is not a 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; the former may be less capable of temporal integration of movements than the latter and may not be able to control simultaneously as many physical parameters of the task as knapping demands but, nonetheless, show indicators of these skills (Bril, Parry, & Dietrich, 2015). Empirical results on nonhuman primates support this hypothesis. For example, when cracking a macadamia, *Macadamia integrifolia* or Brazil nut, *Bertholletia excelsa* 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 nuts of two different species which 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: (a) catulé, *Attalea* spp. (mean ± s.d. peak-force-at-failure = 5.15 kN ± 0.26 kN, *n* = 18), (b) tucum, *Astrocaryum* spp. (5.57 kN ± 0.25 kN, *n* = 12), (c) catulí, *Attalea* spp. (8.19 kN ± 0.35 kN; *n* = 20) and (d) piaçava, *Orbignya* spp. nuts (11.50 kN ± 0.48 kN, *n* = 35) (E. 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 to 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 the 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 ± s.d. thickness: 4.12 mm ± 0.14 mm, *n* =

12) encapsulating a relatively soft kernel (the endosperm); the hull can be easily detached from the inner shell manually or using the mouth once it is breached (E. Visalberghi et al., 2008). It follows that (a) breaching the hull should require less force than cracking the shell; (b) 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 (c) when there is no perceptible change in the physical condition of the nut, another more forceful strike should follow (Fig. 3.3a). 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 contrast, a piaçava nut comprises a highly resistant shell (the endocarp) (thickness: 7.66 mm ± 0.30 mm, *n* = 35), and is a composite of several locules encapsulating one kernel (the endosperm) each (mean ± s.d. number of locules = 3.00 ± 0.18, *n* = 35) (Fig. 3.2b) compared to only one kernel for a tucum nut (E. Visalberghi et al., 2008). The piaçava nuts also have an outer hull but the nuts available to the monkeys generally have their hull removed by the cattle (the piaçava nuts also have hulls, but the ones that the monkeys crack have them removed previously by the monkeys themselves or by cattle). We reasoned that (a) completely 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 comprising at least one locule) of a nut should require less force than cracking an intact segment of a nut; (b) cracking a segment of a nut should require equal or (presumably) less force than cracking a partially cracked whole nut; and (c) when there is no perceptible change in the physical condition of the nut, another equally or more forceful strike should follow (Fig. 3.3b). 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 a large number of 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 cracks.

Methods

Ethics Statement

The Institutional Animal Care and Use Committee (IACUC) at the University of Georgia, USA 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 Table 3.1) 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 ca. 1.1 kg (E. 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 ca. 1 kg) (Liu, Fragaszy, & Visalberghi, 2016), 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 CanonTM XF100 camcorder ca. 11.5 m away from and perpendicular to the anvil. We video-recorded 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 video-recorded 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, each strike comprising of the following three phases: (i) a preparatory pre-lift phase (holding and manipulating the stone); (ii) an upward phase (elevating the stone to a zenith point); and (iii) 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: (i) the height of the stone from the surface of the anvil at the zenith point (amplitude) and (ii) the velocity of the stone at the moment it hit the nut (impact velocity. 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 or the nut following the impact. To test our coding for inter-observer 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 ± s.d. absolute difference = 0.007 m ± 0.008 m, dependent samples t-test: $t_{12} = 1.173$, df = 11, $p = 0.266$; impact velocity: 0.133 m/s ± 0.122 m/s, $t_{12} = 0.345$, df = 11, $p = 0.737$) and by the two different observers (amplitude: mean ± s.d. absolute difference = 0.008 m ± 0.006 m, dependent samples t-test: $t_{12} = 0.897$, df = 11, $p = 0.389$; impact velocity: 0.289 m/s ± 0.631 m/s, $t_{12} = 1.100$, df = 11, $p = 0.295$).

Statistical Analysis

We used Fisher's exact tests to compare the proportion of the tucum and piaçava nuts 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 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 all strikes of each sequence. We used Wilcoxon signed-rank 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 did statistical analyses using SPSS 23 and used two-tailed tests at the significance level of $\alpha = 0.05$ (we used nonparametric tests for the data that did not met the assumptions of normality and equality of variance).

Results

Table 3.1 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 a piaçava nut into two or more segments. On the whole, the monkeys took fewer strikes to crack an intact piaçava nut into two or more segments compared to the number of strikes they took to crack a tucum nut completely (Fig. 3.4; Table 3.1).

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 and no perceptible change in the condition of the nut) (Table 2). 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 cracked partially they reduced the amplitude and impact velocity of the subsequent strike (Table 2). They did not modulate their strikes when a whole nut cracked completely or when there was no perceptible change in its physical condition. When a segment of a nut cracked partially, they decreased the amplitude of the subsequent strike but did not alter its impact velocity.

Five monkeys cracked at least three tucum and three piaçava nuts; three of these monkeys raised the heavy stone (1.500 kg) higher in the first strike of each sequence when cracking a piaçava nut compared to a light stone (0.455, 0.439, 1.042 or 1.100 kg) when cracking a tucum nut (Fig. 3.5a; Table 3.3), and two of these monkeys raised the heavy stone higher across all strikes of each sequence compared to a light stone (Fig. 3.5b; Table 3.3). Each monkey lowered both the heavy and light stones with equal velocity in the first strike of each sequence (Fig. 3.5c; Table 3.3), 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. 3.5d; Table 3.3). 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).

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 micro-fractures in its shell; this ultimately causes fatigue failure of the nut. A moderately forceful strike is enough to crack a nut that already has 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 to 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 it might not be feasible to induce and propagate a fracture in a piaçava nut even after striking it less forcefully a large number of 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 produce the maximum force they could to crack a piaçava nut, they did not put positive work into the heavy (1.5 kg) stone when lowering it to increase its impact velocity, but instead they put negative work into it, thus reducing the impact velocity of the stone. The following two hypotheses explain this anomaly: (i) 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 (ii) 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 with a 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., 2016).

Optimizing movements on the basis of the energetic constraints of a task characterizes the skillful 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; de la Torre, Mora, Domínguez-Rodrigo, de Luque, & Alcalá, 2003; Delagnes & Roche, 2005; Roche et al., 1999). 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, long-tailed 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 to induce bonobos and orangutans, *Pongo pygmaeus* to select, transport and save appropriate tools for future use (Mulcahy & Call, 2006). 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 et al., 2010; 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 joint to a comparable degree (Côté, Raymond, Mathieu, Feldman, & Levin). 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 by 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.

Acknowledgements

We thank the Fonseca de Oliveira family for logistical assistance and permission to work at Fazenda Boa Vista and Caroline E. Jones, Hannah Mosley, Michael Haslam and Victoria Tobolsky for help with data collection. We conducted this work under permission from the CNPq (002547/2011-2) and SisBio, Brazil (28689-5). The University of Georgia, USA supported Madhur Mangalam and Dorothy M. Fragaszy.

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Table 3.1

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 a Piaçava Nut into Two or More Segments

Monkey	**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***	n_T	n_P	***p***
Mansinho	M	A	3.44	12/12	9/9	1.000	T = P	27.0	12	9	0.096[‡]
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[†]	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[†]	F	A	2.04	12/13	2/2	1.000	–	–		–	–

‘M:’ Male; ‘F:’ Female. ‘A:’ Adult; ‘SA:’ Subadult; ‘J:’ Juvenile

‘T:’ Tucum; ‘P:’ Piaçava.

[†] Insufficient data.

[‡] After removing an outlier at $p < 0.05$; *$p < 0.05$, **$p < 0.01$

Table 3.2

Number of Strikes in Which the Monkeys Modulated or Did Not Modulate the Kinematic Parameters on the Basis of the Condition of a Tucum Nut Following the Preceding Strike

Monkey	**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
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
Z-test† *Z*	– 2.207		– 2.214		– 0.846		– 2.207		– 2.375		– 2.371		– 2.371		– 2.366	
p	0.027*		0.027*		0.398		0.027*		0.018*		0.018*		0.018*		0.018*	

‘H:’ Height of the stone from the nut at the zenith point; ‘V:’ Maximum velocity of the stone during the downward phase of the strike

‘D:’ Decreased; ‘ND:’ Not decreased; ‘I:’ Increased; ‘NI:’ Not increased

[†] Results of Z-tests comparing the number of strikes in which the monkeys modulate or did not modulate the kinematic parameters

*$p < 0.05$

Table 3.3

Number of Strikes in Which the Monkeys Modulated or Did Not Modulate the Kinematic Parameters on the Basis of the Condition of a Piaçava Nut Following the Preceding Strike

Monkey		**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		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
Z-test†	*Z*	– 2.214		– 2.214		0.378		– 1.294		– 2.271		– 1.190		– 1.709		– 0.966	
	p	0.027*)		0.027*		0.705		0.196		0.023**)		0.234		0.088		0.334	

‘H:’ Height of the stone from the nut at the zenith point; ‘V:’ Maximum velocity of the stone during the downward phase of the strike

‘D:’ Decreased; ‘ND:’ Not decreased; ‘I:’ Increased; ‘NI:’ Not increased

[†] Results of Z-tests comparing the number of strikes in which the monkeys modulate or did not modulate the kinematic parameters

*$p < 0.05$

Table 3.4

Comparison of the Kinematic Parameters of the Strikes That Each Monkey Took to Crack Tucum and Piaçava Nuts

Monkey	**Strike's Amplitude**				**Hammer's Velocity at Impact**		
	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[†]	–	–	–	–	–	–	–
Piaçava	T = P	1.703	13	0.112	T = P	0.519	0.613
Dita[†]	–	–	–	–	–	–	–
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[†]	–	–	–	–	–	–	–
Piaçava	T < P	6.035	150	< 0.001***	T > P	3.398	< 0.001***
Dita[†]	–	–	–	–	–	–	–

'T:' Tucum; 'P:' Piaçava

[†] Insufficient data

*$p < 0.05$, ***$p < 0.001$

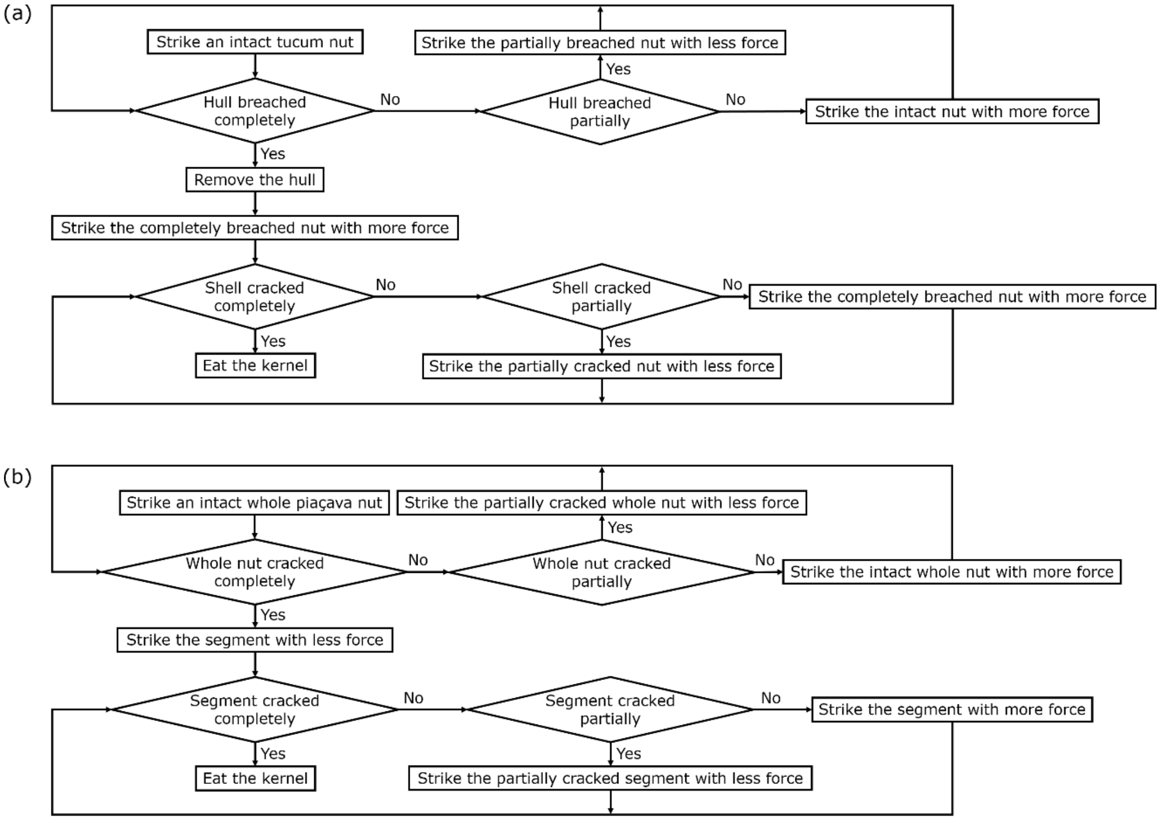

Figure 3.1. Functional parameters of the two percussion tasks. (a) Nut-cracking. (b) Stone-knapping.

Figure 3.2. 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 (exposes multiple locules encapsulating one kernel each); segment cracked partially; segment cracked completely.

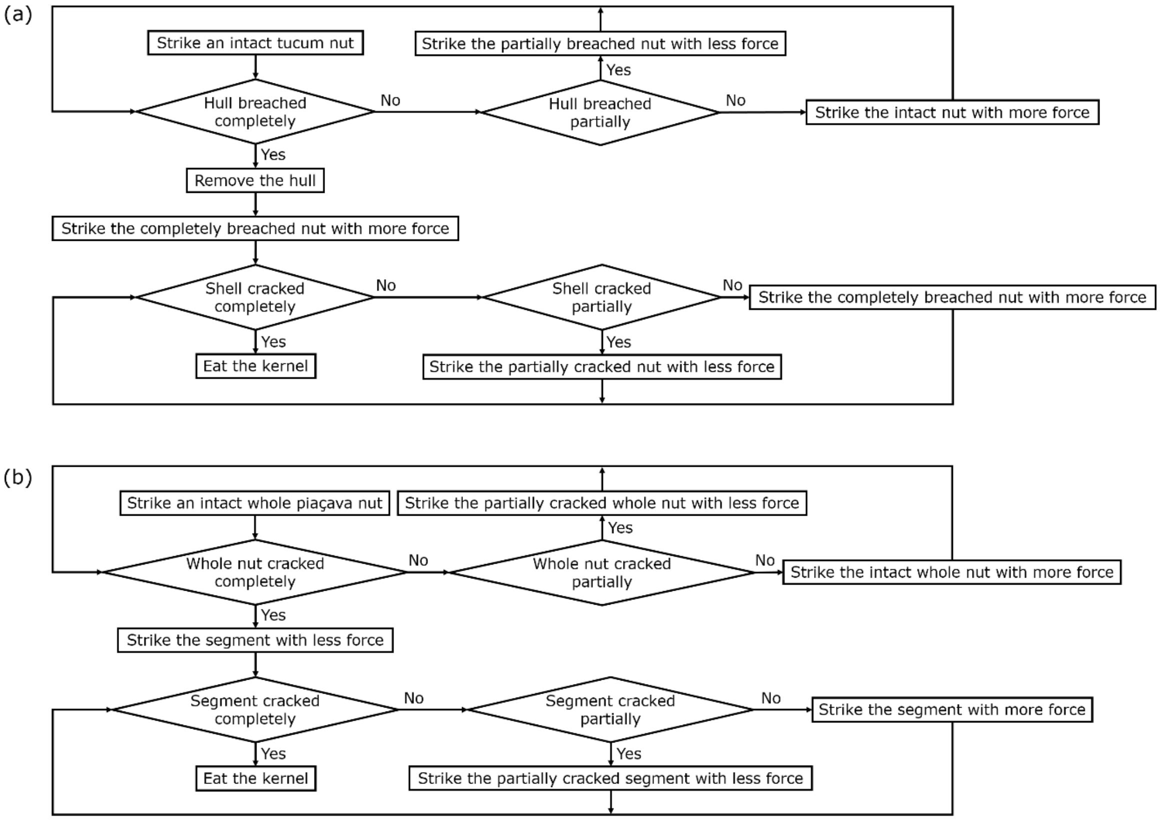

Figure 3.3. Flow charts illustrating the algorithm when cracking a tucum and piaçava nut. (a) A flow chart illustrating the algorithm that we hypothesized that the monkeys would follow when cracking a tucum nut. (b) A similar flowchart illustrating the algorithm that we hypothesized that the monkeys would not follow when cracking a piaçava nut.

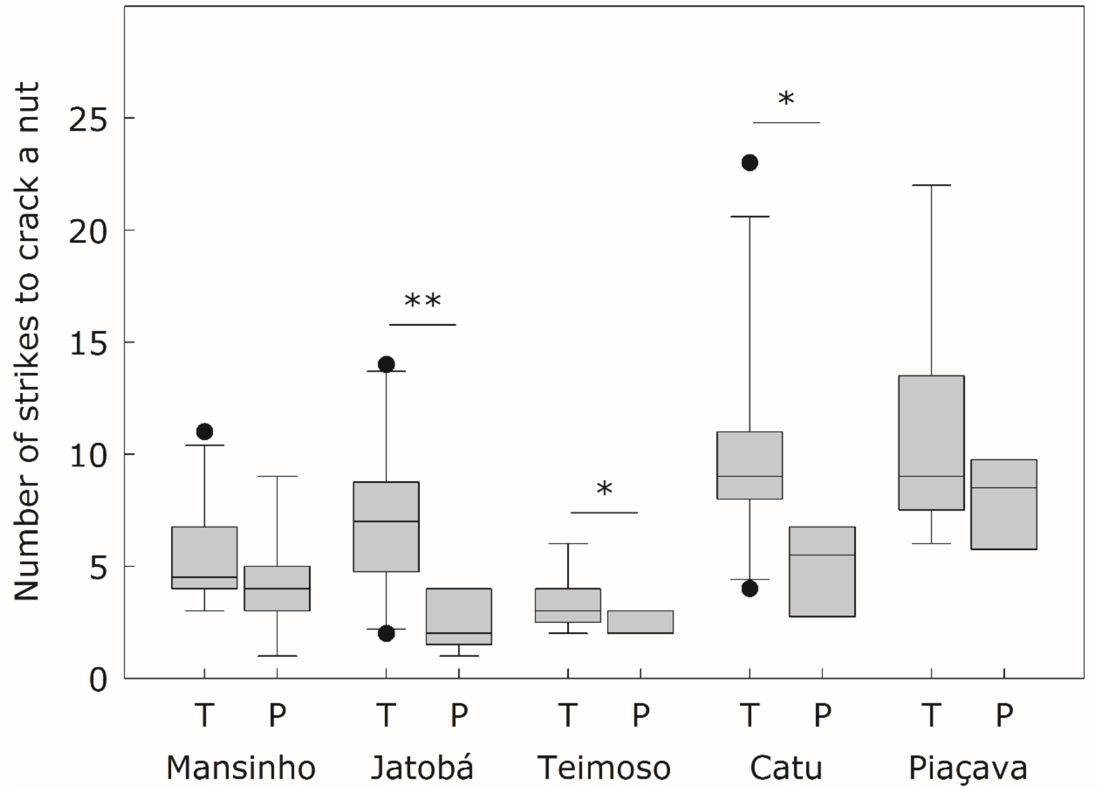

Figure 3.4. Comparison of the number of strikes that each monkey took to crack open a tucum (T) and piaçava (P) nut. The error bars indicate s.e.m. *$p < 0.05$; **$p < 0.005$; ***$p < 0.001$.

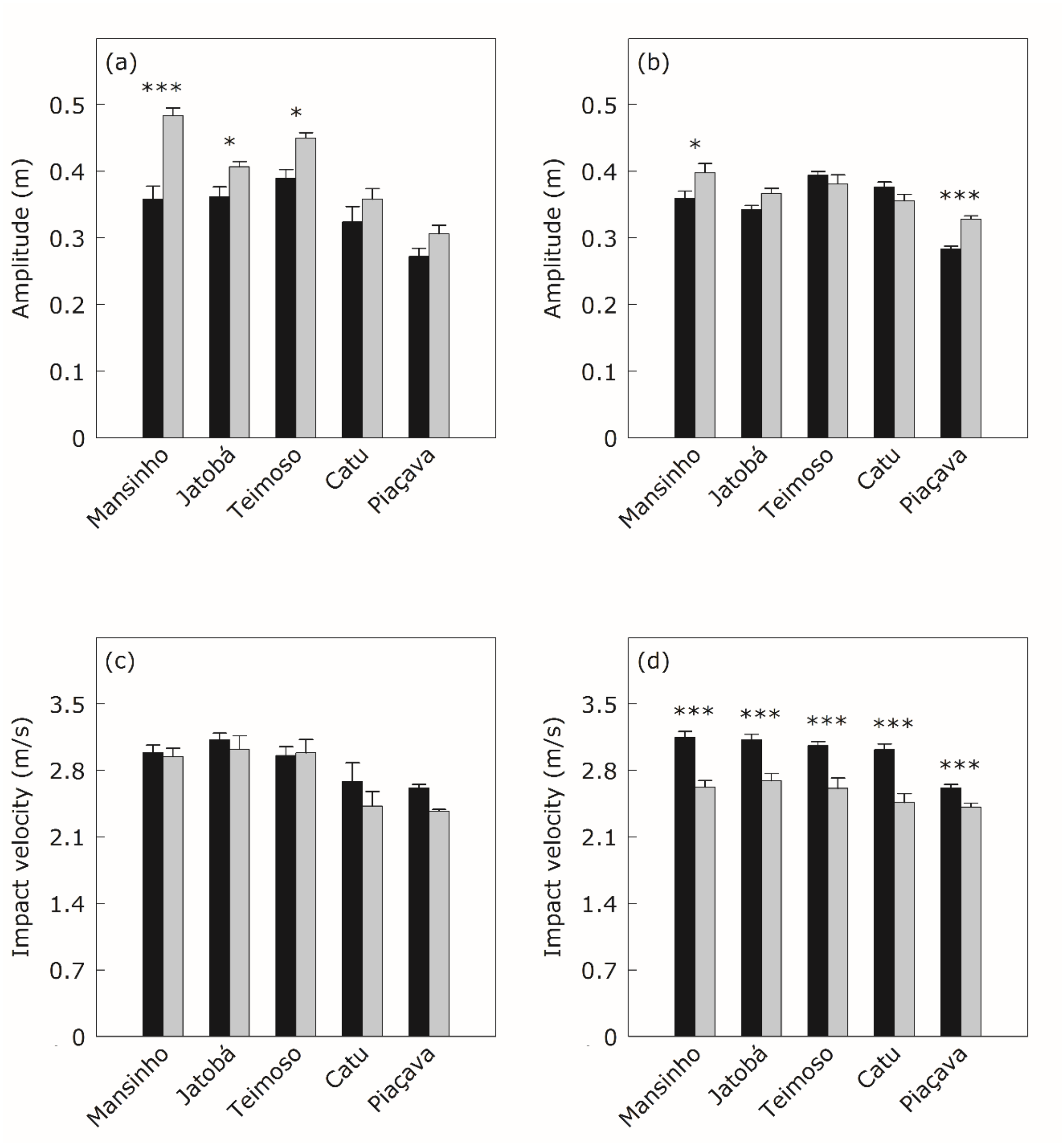

Figure 3.5. Comparison of the kinematic parameters of the strikes that each monkey took to crack a tucum and piaçava nut. The amplitude of (a) the first strike of each sequence and (b) all strikes of each sequence. The impact velocity of (c) the first strike of each sequence and (d) all strikes of each sequence. The error bars indicate s.e.m. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

CHAPTER 4

UNIQUE PERCEPTUOMOTOR CONTROL OF STONE HAMMERS IN WILD MONKEYS[3]

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[3] Mangalam, M., Pacheco, M. M., Izar, P., Visalberghi, E., and Fragaszy, D. M. Accepted by *Biology Letters*.

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Abstract

We analyzed the patterns of coordination of striking movement and perceptuomotor control of stone hammers in wild bearded capuchin monkeys, *Sapajus libidinosus* as they cracked open palm nut using hammers of different mass, a habitual behavior in our study population. We aimed to determine why these monkeys cannot produce conchoidally fractured flakes as do contemporary human knappers or as did prehistoric hominin knappers. We found that the monkeys altered their patterns of coordination of movement to accommodate changes in hammer mass. By altering their patterns of coordination, the monkeys kept the strike's amplitude and the hammer's velocity at impact constant with respect to hammer mass. In doing so, the hammer's kinetic energy at impact—which determines the propagation of a fracture/crack in a nut—varied across hammers of different mass. The monkeys did not control the hammer's kinetic energy at impact, the key parameter a perceiver-actor should control while knapping stones. These findings support the hypothesis that the perceptuomotor control of stone hammers in wild bearded capuchin monkeys is inadequate to produce conchoidally fractured flakes by knapping stones, as do humans.

Keywords: bearded capuchin monkey; movement coordination; nut cracking; *Sapajus libidinosus*; stone knapping, tool use

Introduction

The activity of knapping stones to produce conchoidally fractured flakes— stone-knapping—profoundly altered the relationships between prehistoric hominins and their environment (Ambrose, 2001; Wynn, 2003). Wild bearded capuchin monkeys, *Sapajus libidinosus* smash quartzite stones against rock outcroppings, for no obvious purpose, and in doing so, they occasionally produce flakes similar to those produced by prehistoric hominins (Proffitt et al., 2016). However, no extant non-human primate species is known to produce conchoidally fractured flakes as do contemporary human knappers or as did prehistoric hominin knappers. What might prevent non-human primates from knapping stones? Spatiotemporal coordination of movement determines skill in a motor task (Bernstein, 1967), and we suggest that exploring the coordination of striking movement in non-human primates might help in addressing this question.

Although nut-cracking and stone-knapping differ in specific features (e.g. symmetrical versus asymmetrical bimanual coordination), the propagation of a fracture/crack in a nut and the propagation of a conchoidal fracture in the stone core both depend on specific values of the hammer's kinetic energy at impact (Bril, Parry, & Dietrich, 2015). The ability to control the hammer's kinetic energy at impact is an indicator of expertise in human knappers (Biryukova, Bril, Frolov, & Koulikov, 2015; Bril, Rein, Nonaka, Wenban-Smith, & Dietrich, 2010), and is also evident to a limited degree in captive chimpanzees (Bril, Dietrich, Foucart, Fuwa, & Hirata, 2009). Features of the perceptuomotor control of stone hammers can potentially explain why non-human primates cannot knap stones as do humans.

In the present study, we analyzed the patterns of coordination of striking movements and perceptuomotor control of stone hammers in wild bearded capuchin monkeys proficient in cracking nuts using naturally available unaltered stone hammers (Mangalam & Fragaszy, 2015; Mangalam, Izar, Visalberghi, & Fragaszy, 2016).

Methods

Subjects and Study Site

We analyzed 83 striking movements of five wild adult bearded capuchin monkeys (body mass: 2.1–4.3 kg; Table 3.1) at Fazenda Boa Vista (FBV), Piauí, Brazil (9° 39′ S, 45° 25′ W).

Experimental Procedure

We placed a 1.01, 1.48, or 1.91 kg quartzite stone on a log anvil and provided an intact nut of the piaçava, *Orbignya* spp. palm [resistance to fracture: peak force-at-failure: ~ 11.5 kN (Visalberghi et al., 2008)] to a monkey voluntarily approaching the anvil. Bearded capuchin monkeys may take several strikes to access the kernel(s) of an intact piaçava nut and modulate their strikes in accord with the outcome of the previous strike (i.e., effective vs. ineffective) (Mangalam et al., 2016). Therefore, for each nut each monkey attempted to process, we captured the first striking movement in his/her sagittal plane. We captured mean ± s.d. = 5.2 ± 1.6 striking movements for each monkeys using each of the three hammers (Table 3.1). We used a CanonTM XF100 HD camcorder (29.98 fps, 1920×1080 pi resolution) mounted on a tripod at 10 m from the anvil. Two physical markers attached to the anvil 50 cm apart allowed the calibration of the plane of movement. We measured each monkey's body mass opportunistically when he/she voluntarily stood on a digital scale mounted on a tree.

Data Extraction

We manually coded each striking movement using open-source motion analysis software, Kinovea (https://www.kinovea.org/). We placed digital markers on nine anatomical locations on each monkey (Fig. 4.1a, b; Table 4.2) in the first frame of each striking movement and obtained their *x*-, *y*-coordinates to the nearest pixel. A physical marker attached to the anvil served as the origin of the plane of movement. We advanced the video by a frame, repositioned the digital markers and obtained their new *x*-, *y*- coordinates. We coded each frame of each striking movement by iterating this process.

Data Reduction

We first determined from the Euclidean coordinates: (1) strike's amplitude, (2) hammer's velocity at impact, and (3) hammer's kinetic energy at impact. We then transformed the Euclidean coordinates into joint angles (ankle, knee, hip, lumbar, shoulder, elbow, and wrist angles; Fig. 4.1c) using a custom MATLAB 2017a (MathWorks, Inc.) code, and resampled the joint angle trajectories at 100 Hz and normalized them with respect to the moment the hammer was at the zenith (50% movement duration) using cubic spline function in MATLAB. The lifting phase (mean ± s.d. = 0.50 ± 0.06 s) lasted considerably longer than the lowering phase (mean ± s.d. = 0.25 ± 0.04 s). Therefore, to simplify the analysis, we divided the joint angle trajectories into quartiles (Q1–4); Q1–2 and Q3–4 reflect the lifting and lowering phases, respectively.

Statistical Analysis

We used linear mixed-effects models to examine the influence of body mass and hammer mass on (1) hammer's kinetic energy at impact, (2) strike's amplitude, and (3) hammer's velocity at impact. We also used linear mixed-effects models to examine the influence of body mass and hammer mass on the joint angle trajectories. Changes in the joint angles in each quartile (Q1–4) served as the dependent variable in this analysis. We accounted for individual differences in the joint angle trajectories by introducing random effects in the linear mixed-effects analysis. Given the limited number of subjects ($n = 5$), we allowed only the intercept to vary among individual monkeys. We selected the linear mixed-effects model with the greatest explanatory power using the backward method along with the Bayesian Information Criterion (BIC). To explore the effect of hammer mass on joint angle coordination, we performed cross-correlations among the lumbar, the hip and the knee angles with the other six joint angles. We performed all statistical analyses in MATLAB 2017a and considered the outcomes significant at the alpha level of 0.05.

Results

The hammer's kinetic energy at impact increased with body mass (estimate ± s.e.m. = 1.84 ± 0.21, $t_{11} = 8.80$, $p < 0.001$, CI [1.38, 2.30]) and hammer mass (estimate ± s.e.m. = 3.62 ±

0.54, $t_{11} = 6.73$, $p < 0.001$, CI [2.43, 4.80]; Fig. 4.1d, Table 4.3). The strike's amplitude increased with body mass estimate ± s.e.m. = 0.04 ± 0.01, t11 = 0.009, p < 0.001, CI [0.01, 0.07]), but did not vary with hammer mass (estimate ± s.e.m. = – 0.01 ± 0.02, t11 = – 0.44, p = 0.666, CI [– 0.06, 0.04]; Fig. 4.1e, Table 4.3). The hammer's velocity at impact increased with body mass (estimate ± s.e.m. = 0.24 ± 0.09, t11 = 2.60, p = 0.025, CI [0.04, 0.44]), but did not vary with hammer mass (estimate ± s.e.m. = – 0.33 ± 0.23, t11 = – 1.43, p = 0.182, CI [– 0.85, 0.18]; Fig. 4.1f, Table 4.3).

In Q1—the first mean ± s.d. = 0.25 ± 0.03 s of the lifting phase, the monkeys upwards accelerated the hammer placed on the anvil. They extended their knee, hip and lumbar; the hip followed the lumbar, and the knee followed the hip (Fig. 4.1g–i). The knee extension increased with body mass and hammer mass, and the hip extension increased with body mass (Fig. 4.2a–c; Tables 4.4 and 4.5). These patterns of changes in joint angle trajectories reflect the increase in mechanical constraints on the torso and the hindlimbs in controlling a more massive hammer. Furthermore, the monkeys flexed their elbow and extended their shoulder (Fig. 4.1g–i). The elbow flexion and the shoulder extension increased with hammer mass (Fig. 4.2a–c; Tables 4.4 and 4.5). Apparently, in this way, the monkeys maintained the hammer close to their body to minimize potential changes in their body's center of mass while lifting a massive hammer.

In Q2—the second mean ± s.d. = 0.25 ± 0.03 s of the lifting phase, the pattern of movement was comparable to that in Q1. The monkeys continued to extend their knee, hip and lumbar (Fig. 4.1g–i). The knee extension increased with body mass and decreased with hammer mass, the hip extension increased with body mass and the lumbar extension increased with hammer mass (Fig. 4.2a–c; Tables 4.4 and 4.5). Furthermore, the monkeys flexed their shoulder (Fig. 4.1g–i). The shoulder flexion decreased with body mass and increased with hammer mass (Fig. 4.2a–c; Tables 4.4 and 4.5).

In Q3—the first mean ± s.d. = 0.13 ± 0.02 s of the lowering phase, the monkeys flexed their knee, hip and lumbar; the hip followed the lumbar, and the knee followed the hip (Fig. 4.1g–

i). The knee flexion decreased with body mass, the hip and lumbar flexions increased with hammer mass and the shoulder flexion decreased with body mass (Fig. 4.2a–c; Tables 4.4 and 3.5). Furthermore, the monkeys flexed their shoulder and extended their elbow (Fig. 4.1g–i).

In Q4—the second mean ± s.d. = 0.13 ± 0.02 s of the lowering phase, the pattern of movement was comparable to that in Q3. The monkeys continued to flex their knee, hip and lumbar (Fig. 4.1g–i). The knee, the hip and the lumbar flexions decreased with body mass and increased with hammer mass (Fig. 4.2a–c; Tables 4.4 and 4.5). Furthermore, the monkeys flexed their wrist and extended their shoulder (Fig. 4.1g–i).

The cross-correlation coefficient, *r*, among the lumbar, the hip and the knee angles with the other six joint angles—an indicator of spatiotemporal coordination between two given joints—increased with hammer mass for each monkey (Fig. 4.2 d–f). A larger magnitude of cross-correlation coefficient within a joint angle pair for a given time lag implies a greater coordination of movement.

Discussion

We examined the patterns of coordination of striking movement and perceptuomotor control of stone hammers in wild bearded capuchin monkeys. The monkeys predominantly relied on the movement of their hindlimbs (hip and knee) and their torso (lumbar) to lift and lower a hammer, and to a limited extent, on the movement of their forelimbs (shoulder) to lift a hammer. They altered their patterns of coordination of movement to accommodate changes in hammer mass. By altering their patterns of coordination, the monkeys kept the strike's amplitude and the hammer's velocity at impact constant with respect to hammer mass. In doing so, the hammer's kinetic energy at impact—which determines the propagation of a fracture/crack in a nut—varied across hammers of different masses.

Body mass of wild bearded capuchin monkeys is well under 5.0 kg (Fragaszy et al., 2016), but they can use massive hammers (up to 2.0 kg) constituting up to 100% of their body mass. A more massive hammer poses a more significant challenge in coordinating movement and controlling the hammer’s trajectory. Accordingly, a more massive hammer resulted in more stringent patterns of coordination.

The findings that the strike’s amplitude and the hammer’s velocity at impact did not vary across hammers of different mass suggest that the monkeys actively altered their patterns of coordination of movement to control these parameters. The monkeys did not control the hammer’s kinetic energy at impact, the key parameter a perceiver-actor should control while knapping stones. Perception of the strike’s amplitude and the hammer’s velocity can occur through kinesthesis, from proprioceptive cues generated by the movement of the body and the limbs (Keele, 1968), but perception of the hammer’s kinetic energy cannot. The latter requires the integration of sensory information generated by the movement of the body and the limbs, and by the movement of the grasped hammer (Turvey, Shockley, & Carello, 1999). We hypothesize that the perceptuomotor control of stone hammers in wild bearded capuchin monkeys is inadequate to produce conchoidally fractured flakes by knapping stones, as do humans.

Acknowledgements

The Brazilian National Council for Scientific and Technological Development (CNPq, 002547/2011-2) and Authorization and Information System of Biodiversity (SisBio, 28689-5) permitted us to conduct research in Brazil. We thank Fonseca de Oliveira family for logistical help and permission to conduct research at Fazenda Boa Vista. We thank James Y. Hammers and Ashley Myers for data extraction. We thank Patricia Izar and Elisabetta Visalberghi for shared direction of the EthoCebus project at Fazenda Boa Vista, of which this study is one product.

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Table 4.1

The Number of Striking Movements Analyzed for Each Monkey

Monkey	**Sex**	**Body Mass**	**Number of Striking Movements**		
			1.01 kg Hammer	**1.48 kg Hammer**	**1.91 kg Hammer**
Chuchu	Female	2.1	6	6	N/A
Dita	Female	2.1	5	6	6
Presente	Male	2.2	6	6	6
Teimoso	Male	3.6	6	6	6
Mansinho	Male	4.3	6	6	6

Table 4.2

Anatomical Locations of the Digital Markers Constituting the Kinematic Chain of Striking Movement

Marker	**Anatomical Location**
Finger - INF	Distal phalanx of the index finger
Wrist - WRI	Wrist bar on the thumb side
Elbow - ELB	Lateral epicondyle approximating the elbow joint axis
Shoulder - SHO	Acromioclavicular joint
Anterior superior iliac spine - ASI	Anterior superior iliac spine
Thigh - THI	Lower lateral 1/3 surface of the thigh, just below the swing of the hand
Knee - KNE	Lateral epicondyle of the left knee
Heel - HEE	Calcaneus at the same height above the plantar surface of the foot as the toe marker
Toe - TOE	Second metatarsal head, on the midfoot side of the equinus break between forefoot and midfoot

Table 4.3

Outcomes of Linear Mixed-Effects Models

Variable	**Effect**	**Estimate ± s.e.m.**	t_{11}	p	**CI [Lower, Upper]**
Hammer's kinetic energy at impact	Intercept	– 3.56 ± 0.97	– 3.68	0.004	– 5.68, – 1.43
	Body mass	1.84 ± 0.21	8.80	< 0.001	1.38, 2.30
	Hammer mass	3.62 ± 0.54	6.73	< 0.001	2.43, 4.80
Strike's amplitude	Intercept	0.29 ± 0.05	5.78	< 0.001	0.18, 0.40
	Body mass	0.04 ± 0.01	3.17	0.009	0.01, 0.07
	Hammer mass	– 0.01 ± 0.02	– 0.44	0.666	– 0.06, 0.04
Hammer's velocity at impact	Intercept	2.35 ± 0.42	5.59	< 0.001	1.42, 3.27
	Body mass	0.24 ± 0.09	2.60	0.025	0.04, 0.44
	Hammer mass	– 0.33 ± 0.23	– 1.43	0.182	– 0.85, 0.18

Table 4.4

Mean ± s.d. Changes in Joint Angles (^{O}) Averaged Across All Five Monkeys

Joint	**1.01 kg Hammer**				**1.49 kg Hammer**				**1.98 kg Hammer**			
	QI	**QII**	**QIII**	**QIV**	**QI**	**QII**	**QIII**	**QIV**	**QI**	**QII**	**QIII**	**QIV**
Wrist	16.7 ± 21.4	12.8 ± 18.2	8.6 ± 15.5	– 9.1 ± 21.5	3.3 ± 31.1	10.2 ± 9.2	24.1 ± 12.7	– 15.8 ± 20.5	– 9.6 ± 11.0	20.3 ± 14.8	10.8 ± 12.1	– 30.1 ± 12.5
Elbow	– 17.4 ± 5.3	6.6 ± 8.1	– 2.8 ± 6.2	20.9 ± 11.2	– 20.4 ± 25.8	1.6 ± 8.1	2.2 ± 7.4	28.3 ± 10.7	– 15.5 ± 15.4	0.4 ± 6.2	1.0 ± 10.3	23.2 ± 1.4
Shoulder	23.9 ± 12.1	– 60.4 ± 24.0	– 6.4 ± 10.5	13.1 ± 12.0	26.8 ± 17.5	– 63.4 ± 12.0	– 15.4 ± 10.2	13.6 ± 8.2	35.0 ± 18.6	– 63.9 ± 14.7	– 9.4 ± 13.9	9.1 ± 10.9
Lumbar	17.7 ± 7.2	18.8 ± 9.9	– 13.0 ± 3.8	– 26.0 ± 7.0	26.6 ± 8.2	21.0 ± 9.1	– 10.6 ± 4.3	– 26.2 ± 9.3	29.8 ± 9.0	21.2 ± 4.0	– 12.0 ± 7.2	– 24.5 ± 5.6
Hip	14.9 ± 9.4	12.1 ± 4.8	– 20.4 ± 10.6	– 16.2 ± 14.5	10.6 ± 15.0	3.4 ± 2.9	– 20.6 ± 12.4	– 14.4 ± 17.0	8.0 ± 7.2	4.2 ± 12.9	– 18.6 ± 17.8	– 18.1 ± 12.7
Knee	– 4.1 ± 16.3	4.8 ± 5.3	– 18.7 ± 15.3	– 10.8 ± 10.8	– 0.1 ± 15.0	– 2.9 ± 12.4	– 21.0 ± 19.3	– 10.8 ± 10.7	10.2 ± 12.4	– 10.4 ± 18.3	– 15.9 ± 13.4	– 9.2 ± 12.0
Ankle	– 2.0 ± 10.0	– 3.5 ± 13.8	– 4.7 ± 9.5	0.1 ± 4.2	– 1.8 ± 10.1	– 7.6 ± 8.6	– 4.6 ± 7.6	2.0 ± 8.4	– 1.2 ± 9.1	– 11.3 ± 5.6	0.4 ± 4.6	5.2 ± 12.

Table 4.5

Outcomes of Linear Mixed-Effects Models†

Effect	**Estimate ± s.e.m.**	t_{363}	p	**CI [Lower, Upper]**
Intercept	14.14 ± 2.70	5.23	< 0.001***	8.82. 19.45
Elbow	– 2.17 ± 0.83	– 2.63	0.009**	– 3.79, – 0.55
Knee	– 25.05 ± 7.53	– 3.33	< 0.001***	– 39.86, – 10.25
Ankle	– 11.91 ± 2.18	– 5.46	< 0.001***	– 16.19, – 7.62
Hammer mass × Q4	– 29.56 ± 3.38	– 8.74	< 0.001***	– 36.21, – 22.90
Q2 × Elbow	20.96 ± 4.42	4.74	< 0.001***	12.27, 29.65
Q3 × Elbow	17.99 ± 4.42	4.07	< 0.001***	9.30, 26.69
Q4 × Elbow	63.01 ± 4.80	13.13	< 0.001***	53.58, 72.45
Hammer mass × Shoulder	15.56 ± 1.70	9.14	< 0.001***	12.22, 18.91
Hammer mass × Lumbar	9.62 ± 1.67	5.76	< 0.001***	9.30, 26.69
Hammer mass × Knee	16.15 ± 5.13	3.15	0.002	6.05, 26.24
Q2 × Knee	41.49 ± 14.87	2.79	0.006	12.25, 70.72
Body mass × Hammer mass × Q4	5.11 ± 1.08	4.72	< 0.001***	2.98, 7.24
Hammer mass × Q2 × Shoulder	– 71.02 ± 7.40	– 9.60	< 0.001***	– 85.58, – 56.47
Body mass × Q2 × Shoulder	– 20.33 ± 4.23	– 4.81	< 0.001***	– 28.64, – 12.02
Hammer mass × Q3 × Shoulder	– 50.37 ± 7.39	– 6.82	< 0.001***	– 64.90, – 35.85
Hammer mass × Q3 × Lumbar	– 22.41 ± 2.57	– 8.71	< 0.001***	– 27.46, – 17.35
Hammer mass × Q3 × Hip	– 43.53 ± 7.25	– 6.00	< 0.001***	– 57.79, – 29.27
Hammer mass × Q2 × Knee	– 54.28 ± 12.60	– 4.31	< 0.001***	– 79.06, – 29.50

Hammer mass × Q3 × Knee	– 43.24 ± 7.39	– 5.85	< 0.001***	– 57.77, – 28.71
Hammer mass × Q4 × Ankle	38.29 ± 7.74	4.95	< 0.001***	23.08, 53.50
Body mass × Hammer mass × Q2 × Shoulder	16.35 ± 3.48	4.70	< 0.001***	9.50, 23.19
Body mass × Hammer mass × Q3 × Shoulder	7.66 ± 2.33	3.28	0.001***	3.07, 12.25
Body mass × Hammer mass × Q4 × Lumbar	– 5.48 ± 0.92	– 5.99	< 0.001***	– 7.28, – 3.68
Body mass × Hammer mass × Q3 × Hip	8.63 ± 2.33	3.70	< 0.001***	4.04, 13.22
Body mass × Hammer mass × Q2 × Knee	6.69 ± 2.34	2.86	0.004**	2.09, 11.30
Body mass × Hammer mass × Q3 × Knee	8.92 ± 2.34	3.82	< 0.001***	4.33, 13.52
Body mass × Hammer mass × Q4 × Ankle	– 6.54 ± 2.46	– 2.66	0.008**	– 11.37, – 1.71

[†] The model compares changes in other joint angles with reference to the wrist angle and changes in joint angles in other quartiles with changes in joint angles in Q1.

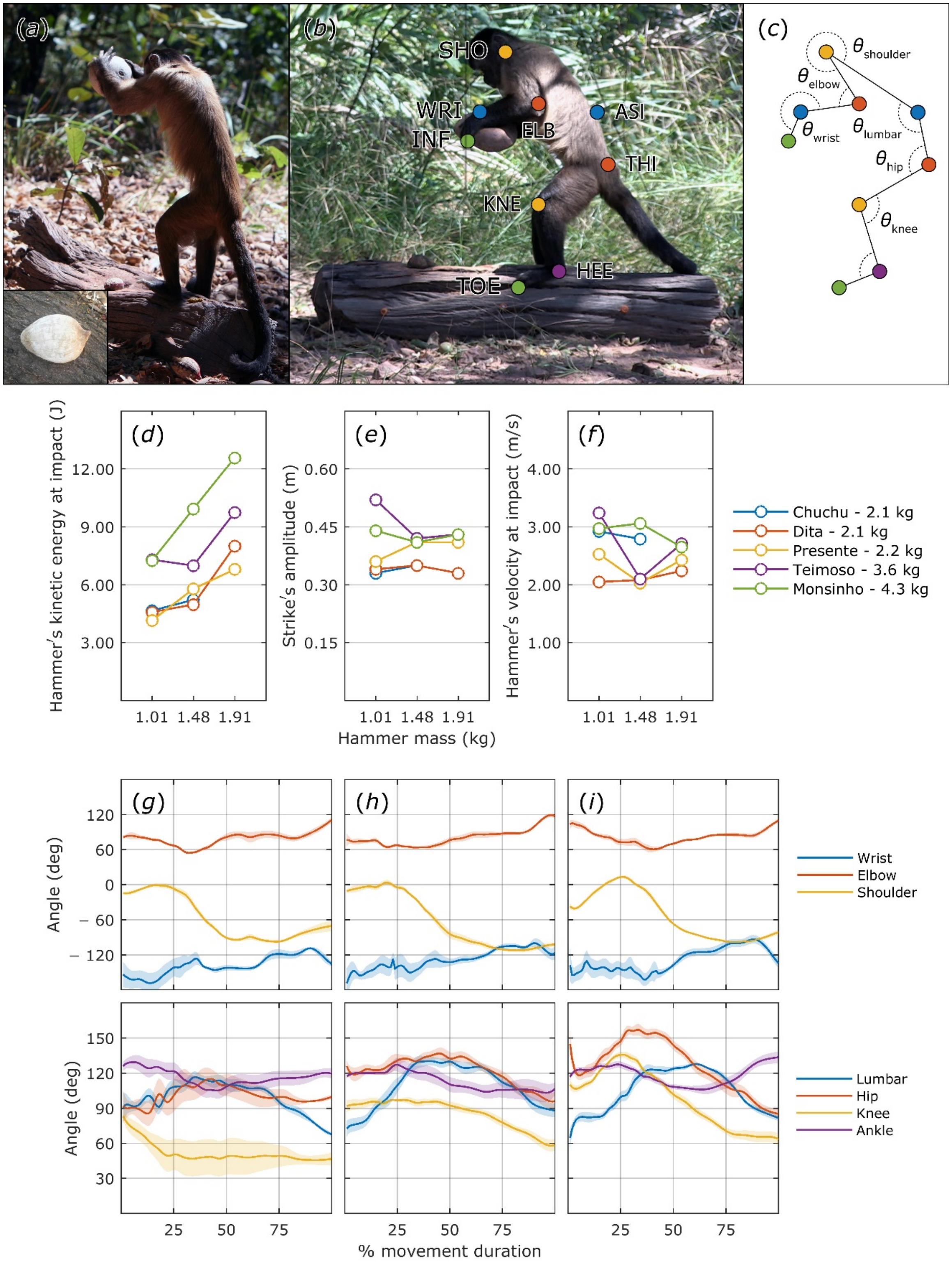

Figure 4.1. Kinematic analysis. (a) A wild bearded capuchin monkey is striking an intact piaçava nut (inset)—placed in a pit on a log anvil—with a quartzite stone hammer (credit: Barth A.

Wright). (b) Anatomical locations of digital markers placed on each monkey. (c) The kinematic chain and the joint angles. (d) Hammer's kinetic energy at impact. (e) Strike's amplitude. (f) Hammer's velocity at impact. Time-series of joint angle trajectories for a representative monkey, Presente (body mass = 2.2 kg) using a (g) 1.01 kg hammer, (h) 1.48 kg hammer and (i) 1.91 kg hammer. Shaded areas represent the s.e.m. ($n = 6$). We normalized the joint angle trajectories with respect to the moment the hammer was at the zenith (50% movement duration).

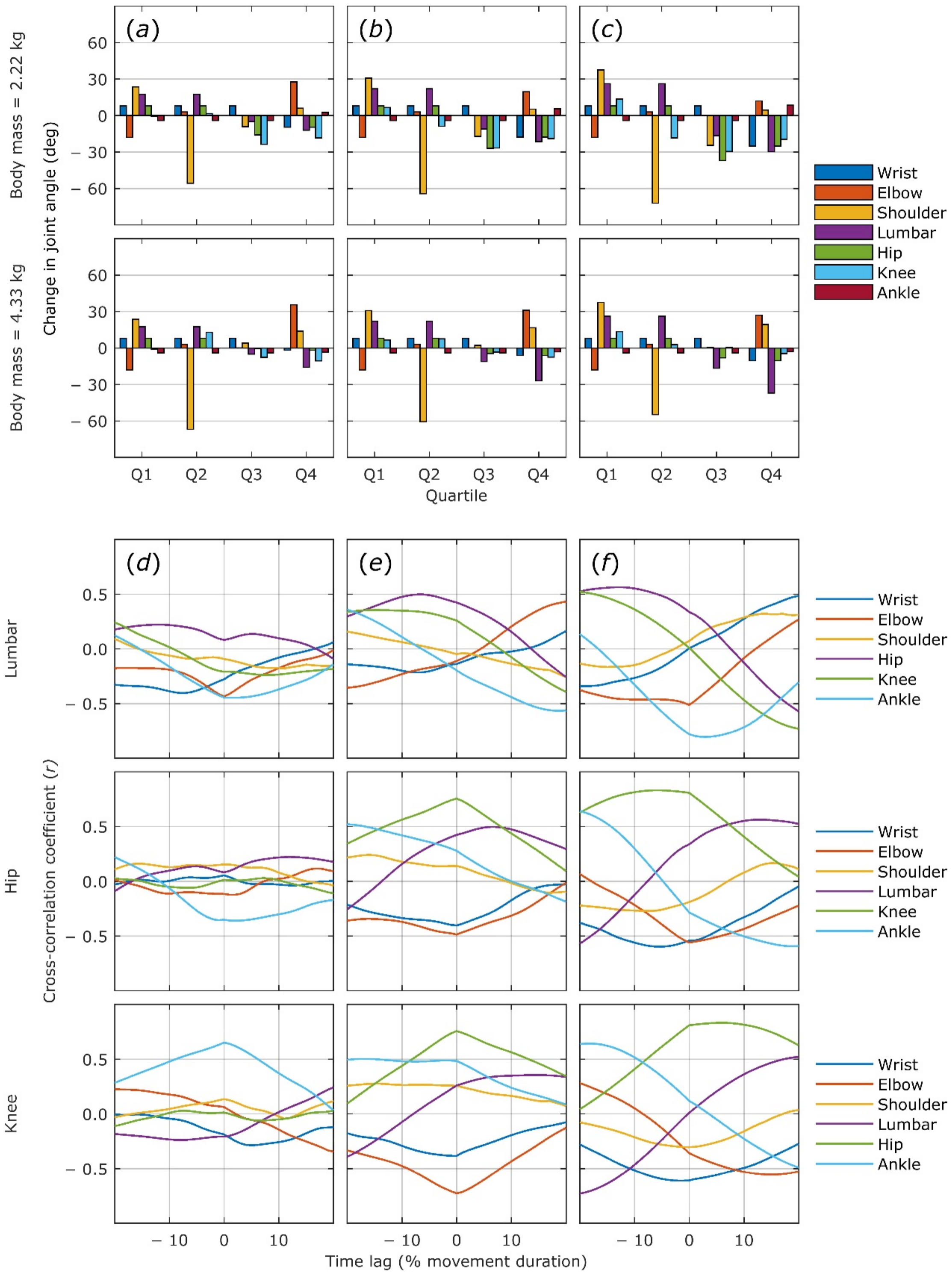

Figure 4.2. Changes in joint angles and cross-correlations. (a–c) Changes in joint angles for two representative monkeys, Presente (body mass = 2.2 kg) and Mansinho (body mass = 4.3 kg). (a) 1.01 kg hammer. (b) 1.48 kg hammer. (c) 1.91 kg hammer. (d–f) Cross-correlations among the

lumbar, the hip and the knee angles with the other six joint angles for a representative monkey, Presente (body mass = 2.2 kg) using a (a) 1.01 kg hammer, (b) 1.48 kg hammer, and (c) 1.91 kg hammer. A larger magnitude of cross-correlation coefficient, r, within a joint angle pair for a given time lag (% movement duration) implies a greater coordination of movement.

CHAPTER 5

BEARDED CAPUCHIN MONKEYS USE JOINT SYNERGIES TO STABILIZE THE HAMMER TRAJECTORY WHILE CRACKING NUTS IN BIPEDAL STANCE[4]

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[4] Mangalam, M., Rein, R., and Fragaszy, D. M. Accepted by *Proceedings of the Royal Society B: Biological Sciences*.

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Abstract

The transition from occasional to obligate bipedalism is a milestone in human evolution. However, because the fossil record is fragmentary and reconstructing behavior from fossils is difficult, changes in the motor control strategies that accompanied this transition remain unknown. Quadrupedal primates that adopt a bipedal stance while using percussive tools provide a unique reference point to clarify one aspect of this transition, which is, maintaining bipedal stance while handling massive objects. We found that while cracking nuts using massive stone hammers, wild bearded capuchin monkeys (*Sapajus libidinosus*) produce hammer trajectories with highly repeatable spatial profiles. Using an uncontrolled manifold analysis, we show that the monkeys used strong joint synergies to stabilize the hammer trajectory while lifting and lowering heavy hammers. The monkeys stringently controlled the motion of the foot. They controlled the motion of the lower arm and hand rather loosely, showing a greater variability across strikes. Overall, our findings indicate that while standing bipedally to lift and lower massive hammers, an arboreal quadrupedal primate must control motion in the joints of the lower body more stringently than motion in the joints of the upper body. Similar changes in the structure of motor variability required to accomplish this goal could have accompanied the evolutionary transition from occasional to obligate bipedalism in ancestral hominins.

Keywords: nut cracking; motor control; movement coordination; *Sapajus libidinosus*; tool use; uncontrolled manifold analysis

Introduction

Comparisons of limb morphology and function among humans, extinct hominins and extant nonhuman primates demonstrate that during the evolutionary transition from occasional to obligate bipedalism, the feet and legs underwent more significant changes than the hands and arms (Harcourt-Smith & Aiello, 2004; Marzke, 1997). However, because of the fragmentary nature of the fossil record and difficulties in reconstructing behavior from fossils, changes in the motor control strategies that accompanied this transition remain unknown. Although supporting evidence is sparse, an accepted proposition is that altered motor control of the feet and legs that resulted in a progressive reduction in the displacement of the body's center of mass (COM) accompanied the evolution of obligate bipedalism in ancestral hominins (Dunbar, Horak, Macpherson, & Rushmer, 1986; Preuschoft, 2004; Schmitt, 2003; Tardieu, Aurengo, & Tardieu, 1993).

Capuchin monkeys (*Cebus* and *Sapajus* spp.), arboreal platyrrhines, spend a significant proportion of time foraging on the ground (Biondi, 2010; Fragaszy, Visalberghi, & Fedigan, 2004). Unusually among primates, they sporadically walk bipedally on the ground (Biondi, 2010). Some wild populations of bearded capuchin monkeys (*Sapajus libidinosus*) crack open nuts and other encased food items using naturally available stone hammers by placing the nuts on stone or log anvils on or near the ground (Fig. 5.1) (Fragaszy, Izar, Visalberghi, Ottoni, & de Oliveira, 2004; Mangalam, Newell, Visalberghi, & Fragaszy, 2017). The monkeys in our study population at Fazenda Boa Vista (FBV) often use massive hammers (> 1 kg; 50% of an adult female's body mass) for processing more resistant nuts (Mangalam, Izar, Visalberghi, & Fragaszy, 2016; Visalberghi et al., 2009). We estimate that other nonhuman primates that use stone hammers typically use proportionally lighter hammers (chimpanzees: < 20% of body mass (Visalberghi, Sirianni, Fragaszy, & Boesch, 2015); long-tailed macaques: < 10% of body mass (Gumert, Kluck, & Malaivijitnond, 2009)). Capuchin monkeys at FBV carry hammers bipedally to anvils (Duarte, Hanna, Sanches, Liu, & Fragaszy, 2012) and stand bipedally while using hammers (Liu et al., 2009). They presumably solve significant biomechanical and postural challenges in lifting and lowering massive hammers while cracking nuts in bipedal stance.

The ancestors of capuchin monkeys diverged from catarrhines, and thus from hominids, long before hominins adopted obligate bipedal locomotion. Studies of locomotion in apes, that occasionally locomote bipedally, have aided our understanding of the origins of bipedal locomotion in hominins (Pontzer, Raichlen, & Rodman, 2014; Pontzer, Raichlen, & Sockol, 2009; Sockol, Raichlen, & Pontzer, 2007) but it is also useful to consider other species and other bipedal activities in extant nonhuman primates for insights into the evolution of obligate bipedalism in ancestral hominins. For example, capuchin monkeys stand bipedally to crack nuts. These monkeys afford an opportunity to study motor strategies that support stable bipedal postures during strenuous action. Thus, although capuchin monkeys do not represent a progressive step in the evolution of bipedalism in ancestral hominins, they offer an independently-evolved comparative reference point that is relevant to hominins' postural control in bipedal stance, as well as to postural control in bipedal locomotion with and without carrying a load in the arms (Demes, 2011; Demes & O’Neill, 2013; Duarte et al., 2012; Hanna et al., 2015).

In the present study, we identified the motor strategies bearded capuchin monkeys use to stabilize the hammer trajectory while cracking nuts in bipedal stance with massive hammers. We hypothesized that if the requirement of maintaining a bipedal stance poses significant biomechanical and postural challenges, then to stabilize the hammer trajectory, capuchin monkeys would more closely control motion in the joints of the lower body compared with the joints of the upper body. To test this hypothesis, we analyzed the kinematics of striking movements performed by five wild adult monkeys. The monkeys struck intact palm nuts on a log anvil with hammers of different masses. We first examined repeatability in the spatial profiles of hammer trajectories and then used an uncontrolled manifold (UCM) analysis to determine whether and how the monkeys control motion differently in the joints of the lower and upper body.

The UCM analysis links trial-to-trial variability in the space of effector-level elemental variables or the degrees of freedom (DoFs) with variability in the task-relevant performance variables (Klishko, Farrell, Beloozerova, Latash, & Prilutsky, 2014; Latash, Scholz, & Schöner, 2007; Scholz & Schöner, 1999; Schöner, 1995). The concept of the UCM analysis is mostly used in the context of muscle synergies: multiple muscles work as functional units such that the central nervous system (CNS) jointly and proportionally activates all muscles in the synergy. When task demands change, the CNS control changes, resulting in changes in muscle synergies. By extending the notion of muscle synergies to ensembles of muscles that span multiple joints, we can understand the coordination of multiple joints. The UCM analysis proceeds by partitioning trial-to-trial variability in the space of effector-level elemental variables into two subspaces: controlled and uncontrolled subspaces. Variability in the controlled subspace influences the performance variable; variability in the uncontrolled subspace leaves the performance variable unchanged. A greater magnitude of variability in the uncontrolled subspace compared to the controlled subspace implies a synergy (Fig. 5.2a, b). The ratio of variability in the uncontrolled subspace to that in the controlled subspace reflects the strength of the synergy: stronger (Fig. 5.2c) or weaker Fig. 5.2d). We examined (i) whether the monkeys structure variability in joint configurations in the two subspaces to minimize variability in the hammer trajectory, and (ii) how the monkeys control the DoFs of the lower and upper limbs while lifting and lowering massive hammers.

Capuchin monkeys use seven body joints (eight including the angle between the feet and the ground) to stabilize the hammer's horizontal and vertical positions (Mangalam, Pacheco, Izar, Visalberghi, & Fragaszy, 2018), rendering the space of effector-level elemental variables a six-dimensional uncontrolled manifold. We anticipated that the monkeys—all proficient nut-crackers

(Mangalam & Fragaszy, 2015; Mangalam et al., 2016)—would use joint synergies to exploit this redundancy in movement space to stabilize the hammer trajectory. We previously found that spatiotemporal coordination between any two joints increases with hammer mass (Mangalam et al., 2018). A higher degree of coordination implies fewer motor solutions and consequently, lesser redundancy in the movement space. We thus expected that the strength of synergy would decrease with hammer mass. Capuchin monkeys predominantly rely on the movement of their hindlimbs (hip and knee) and their torso (lumbar) to lift and lower a hammer, and to a limited extent, on the movement of their forelimbs (shoulder) to lift a hammer (Mangalam et al., 2018). We thus predicted that the monkeys would differently control motion in the joints of the lower and upper body.

Methods

Subjects and Study Site

The subjects were five wild adult bearded capuchin monkeys (body mass: 2.1–4.3 kg) in their natural habitat at Fazenda Boa Vista (FBV) in Piauí, Brazil (9° 39′ S, 45° 25′ W; table 1). The monkeys at FBV crack open palm nuts during routine foraging (Visalberghi et al., 2015). In the present study, the monkeys cracked nuts of the piaçava palm, Orbignya spp., by placing each nut on a log anvil and striking it with a quartzite stone hammer. An intact piaçava nut is extremely resistant to fracture (mean ± s.d. peak-force-at-failure = 11.50 ± 0.48 kN, $n = 35$), has a thick shell (i.e., the endocarp; thickness: 7.66 ± 0.30 mm, $n = 35$), and is a composite of several locules (mean ± s.d. number of locules: 3.00 ± 0.18, $n = 35$), each encapsulating a kernel (i.e., the endosperm) (Visalberghi et al., 2008). A piaçava nut also has an exocarp and an edible mesocarp that the monkeys themselves remove before cracking, or more commonly at our site, grazing cattle remove them. Piaçava palm grows abundantly throughout FBV (Visalberghi et al., 2008). We collected the nuts locally. Their exocarps and mesocarps had already been removed by cattle or other animals. Log anvils and quartzite stones are naturally available at many locations at FBV, particularly near sandstone ridges (Visalberghi et al., 2007). We provided the monkeys with stones of three different masses: 1.01, 1.48 and 1.91 kg.

Experimental Procedure

We collected all data opportunistically. We placed a hammer on a log anvil and waited until a monkey voluntarily approached the anvil. We provided the approaching monkey an intact piaçava nut by rolling the nut on the ground toward the anvil. We used a Canon$^{\text{TM}}$ XF100 HD camcorder (29.98 fps, 1920×1080 pi) mounted on a tripod at approximately 10 m from the anvil to record the monkey's actions. We captured each strike in the monkey's sagittal plane. We attached two physical markers 50 cm apart to the anvil to calibrate the plane of movement. We measured each monkey's body mass when it voluntarily stood on a digital scale mounted on a tree [details in Fragaszy et al. (2016)]

Data Extraction

The monkeys at FBV take several strikes to extract the kernel(s) of an intact piaçava nut and often modulate subsequent strikes according to the outcome of the previous strike (i.e., effective vs. ineffective). Consecutive strikes can thus vary significantly in amplitude or kinetic energy, particularly after the locules of the nut are separated (Mangalam, Izar, Visalberghi, & Fragaszy, 2016). Therefore, to keep the task demands constant across strikes, we coded from video only the first strike for each nut processed by each monkey. We coded six strikes per monkey per hammer (with two exceptions: one monkey provided 5 strikes with the lightest hammer, and one monkey provided no strikes with the heaviest hammer; Table 5.1).

Two lab assistants, A.M. and J.Y.H., manually coded each strike using an open-source motion analysis software, *Kinovea* (https://www.kinovea.org/). A.M. and J.Y.H. placed a digital marker ('+') on each of nine anatomical locations on the monkey's body (Fig. 5.3a; Table 5.2) and obtained the *x*-, *y*-coordinates of each location to the nearest pixel. One of the two physical markers attached to the anvil served as the origin of the plane of movement. The coders then forwarded the video by a frame, repositioned each digital marker and obtained the *x*-, *y*-coordinates of that marker. They iterated this process for the entire strike (i.e., mean ± s.d. = 22.6 ± 2.3 frames). The coding was highly consistent both within and across the two coders. Comparison of the *x*-, *y*- coordinates for three strikes coded twice by each coder over 15 days revealed Cronbach's alphas of 0.99 and 0.99, respectively. Comparison of the *x*-, *y*- coordinates for three strikes across the two coders revealed Cronbach's alpha of 1.00.

Data Reduction

Each strike lasted mean ± s.d. = 0.75 ± 0.08 s. We divided each strike into two parts: the lifting phase up to the zenith and the lowering phase from the zenith to the end, using MATLAB 2017b (MathWorks, Inc., Natick, MA, USA). Since the lifting phase was typically longer than the lowering phase, we re-sampled this time-normalized trajectory to 100 slices (50 slices for lifting and lowering each) through the cubic spline interpolation using *spline* function in MATLAB.

Changes in the *x*-, *y*- coordinates of a digital marker (the distal phalanx of the index finger, marker INF in Fig. 5.3a) constituted the hammer's trajectory. For each monkey, we determined variability in the hammer's trajectory along the horizontal and vertical axes (*x*- and *y*-axes, respectively) across all strikes. We shifted the hammer's *x*-, *y*- coordinates at the onset of each strike (i.e., $t = 0$) to the origin (i.e., $x, y = 0$). We then determined the standard deviation of the hammer's *x*-, *y*- positions in each of the 100 slices.

To perform the UCM analysis, we determined the eight joint elevation angles of each monkey constituting the kinematic chain of movement: foot (θ_{foot}), shank (θ_{shank}), thigh (θ_{thigh}), pelvis (θ_{pelvis}), trunk (θ_{trunk}), upper arm ($\theta_{\text{upper arm}}$), lower arm ($\theta_{\text{lower arm}}$) and hand ($\theta_{\text{hand}}$) (Fig. 5.3b). Each elevation angle increased with counterclockwise rotation of the respective segment about the preceding segment in the kinematic chain. In the UCM analysis, the elevation angles of the foot, shank and thigh constituted the DoFs of the lower body, and the elevation angles of the pelvis, trunk, upper arm, lower arm and hand constituted the DoFs of the upper body.

Uncontrolled Manifold (UCM) Analysis

To begin the UCM analysis, we constructed a forward kinematic model—a set of equations—that allowed computing the hammer's *x*-, *y*-positions from the specified values of a monkey's joint configurations (figure 3*b*):

,

$$
\begin{aligned}
x_{m,hammer} = {} & x_{m,toe} \\
& + l_{m,foot} cos(\theta_{foot}) \\
& + l_{m,shank} cos(\theta_{foot} + \theta_{shank}) \\
& + l_{m,thigh} cos(\theta_{foot} + \theta_{shank} + \theta_{thigh}) \\
& + l_{m,pelvis} cos(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis}) \\
& + l_{m,trunk} cos(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis} + \theta_{torso}) \\
& + l_{m,upperarm} cos(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis} + \theta_{torso} + \theta_{upperarm}) \\
& + l_{m,lowerarm} cos(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis} + \theta_{torso} + \theta_{upperarm} + \theta_{lowerarm}) \\
& + l_{m,hand} cos(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis} + \theta_{torso} + \theta_{upperarm} + \theta_{lowerarm} + \theta_{hand})
\end{aligned}
$$

,

$$
\begin{aligned}
y_{m,hammer} = {} & y_{m,toe} \\
& + l_{m,foot} sin(\theta_{foot}) \\
& + l_{m,shank} sin(\theta_{foot} + \theta_{shank}) \\
& + l_{m,thigh} sin(\theta_{foot} + \theta_{shank} + \theta_{thigh}) \\
& + l_{m,pelvis} sin(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis}) \\
& + l_{m,trunk} sin(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis} + \theta_{torso}) \\
& + l_{m,upperarm} sin(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis} + \theta_{torso} + \theta_{upperarm}) \\
& + l_{m,lowerarm} sin(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis} + \theta_{torso} + \theta_{upperarm} + \theta_{lowerarm}) \\
& + l_{m,hand} sin(\theta_{foot} + \theta_{shank} + \theta_{thigh} + \theta_{pelvis} + \theta_{torso} + \theta_{upperarm} + \theta_{lowerarm} + \theta_{hand})
\end{aligned}
$$

where $x_{\mathrm{m,hammer}}$, $y_{\mathrm{m,hammer}}$ denote the hammer's *x*-, *y*-positions for m^{th} monkey (1 through 5), $x_{\mathrm{m,toe}}$, $y_{\mathrm{m,toe}}$ denote the *x*-, *y*-positions of m^{th} monkey's toe, l_{s} denotes the average length of m^{th} monkey's s^{th} segment (1 through 8), and θ_{foot}, θ_{shank}, θ_{thigh}, θ_{pelvis}, θ_{trunk}, $\theta_{\mathrm{upper\ arm}}$, $\theta_{\mathrm{lower\ arm}}$ and θ_{hand} denote the DoFs constituting a strike.

We calculated the average joint vector, $\theta_{\mathrm{m,t}}$, for m^{th} monkey at t^{th} time slice (n = 24) averaged across all six strikes per hammer. Second, we calculated the difference between the average joint vector and the joint vector in i^{th} strike, that is, the deviation joint vector, $\partial\theta_{\mathrm{m,t,i}} = \theta_{\mathrm{m,t}} - \theta_{\mathrm{m,t,i}}$. Finally, based on the forward kinematic model, we calculated the Jacobian, $J_{\mathrm{m,t}}$, for m^{th} monkey in t^{th} time slice:

$$J_{m,t} = \begin{pmatrix} \frac{\partial x_{hammer}}{\partial\theta_{foot}} & \frac{\partial x_{hammer}}{\partial\theta_{ankle}} \cdots & \frac{\partial x_{hammer}}{\partial\theta_{wrist}} \\ \frac{\partial y_{hammer}}{\partial\theta_{foot}} & \frac{\partial y_{hammer}}{\partial\theta_{ankle}} \cdots & \frac{\partial y_{hammer}}{\partial\theta_{wrist}} \end{pmatrix}.$$

This Jacobian is a linearized representation mapping infinitesimal changes across the DoFs onto the hammer's *x*-, *y*-positions. By calculating the null space of the Jacobian, $J_{\mathrm{m,t}}\theta_{\mathrm{j}}$, we estimated the uncontrolled manifold (UCM) that contained V_{UCM}. All joint configurations specifying the same *x*-, *y*-positions of the hammer lay in this subspace. The subspace perpendicular to V_{UCM} represented the controlled subspace (ORT) and contained V_{ORT}. All joint configurations specifying different *x*-, *y*-positions of the hammer lay in this subspace. We then obtained a projection vector, $V_{\mathrm{UCM-m,t,i}}$, for V_{UCM} for m^{th} monkey in t^{th} time slice during i^{th} movement by projecting the deviations vectors, $\partial\theta_{\mathrm{m,t,i}}$, onto the subspace of V_{UCM}. We obtained a similar projection vector for V_{ORT} by subtracting $V_{\mathrm{UCM-m,t,i}}$ from $\partial\theta_{\mathrm{m,t,i}}$. The Jacobian is described by an $n \times d = 2\times 8$ matrix, where N represents the two dimensions of the task variable or the hammer's x-, y-positions and d represents the eight dimensions of the space of effector-level elemental variables, that is, corresponding to the eight DoFs. Accordingly, UCM had $d - N = 8 - 2 = 6$ dimensions and ORT had $N = 2$ dimensions. We calculated V_{UCM} and V_{ORT} for m^{th} monkey at t^{th} time slice averaged across all six strikes. Finally, to facilitate comparison between V_{UCM} and V_{ORT}, we normalized the magnitudes of the two projection vectors by the dimension of the respective subspaces:

$$V_{UCM-m,t} = \frac{\Sigma\left|V_{UCM-m,t,i}\right|^2}{(d-n)N},$$

$$V_{ORT-m,t} = \frac{\sum \left| V_{ORT-m,t,i} \right|^2}{nN}.$$

In addition to estimating V_{UCM} and V_{ORT} across all eight DoFs (i.e., the whole kinematic chain), we were interested in the geometrical properties of the UCM. We thus estimated the projections of individual DoFs onto the UCM. Thus, in contrast to the standard UCM procedure in which the projected deviations from the average vector are squared and summed across all elemental variables (Scholz & Schöner, 1999), we retained the squared, individual joint deviations, each of which represented the accumulated variability for the respective DoF in either V_{UCM} or V_{ORT}. We then calculated (i) V_{UCM} per DoF, V_{ORT} per DoF and $R_{\mathrm{V}} = V_{\mathrm{UCM}}/V_{\mathrm{ORT}}$ across the whole body, and (ii) V_{UCM} and V_{ORT} for each DoF in the lifting and lowering phases by averaging the values over time slices 1–12 and 13–24, respectively.

Statistical Analysis

We used linear mixed-effects models and constructed separate models for each response variable (Table 5.3). We considered the fixed effects of body mass, hammer mass, strike phase, subspace, body part and DoF, whenever we incorporated these variables in the model; we dummy coded for strike phase, subspace, and DoF. We accounted for inter-individual differences in each response variable by introducing a random effect of subject identity. Given the relatively small number of subjects ($n = 5$), we allowed only the intercept of this random effect to vary among individual monkeys. We performed all statistical analysis using MATLAB and considered all statistical outcomes significant at the alpha level of 0.05.

Results

The monkeys produced hammer trajectories with highly repeatable spatial profiles across strikes (Fig. 5.4). Strike-to-strike variability in the hammer trajectory along the horizontal axis increased with hammer mass ($t_{11} = 2.474$, $p = 0.031$, 95% CI [0.002, 0.036]; Fig. 5.4; Table 5.3), and variability along the vertical axis increased with body mass ($t_{11} = 2.353$, $p = 0.038$, 95% CI [0.001, 0.022]; Fig. 5.4; Table 5.3). Thus, although using a heavier hammer was relatively more challenging, a heavier monkey could more flexibly alter the strike's amplitude [and, consequently, the kinetic energy at impact] independent of the hammer movement along the horizontal axis.

Next, we examined the structure of motor variability. The monkeys employed strong joint synergies while lifting and lowering hammers, as V_{UCM} per DoF was considerably greater than V_{ORT} per DoF ($t_{51} = -8.159$, $p < 0.001$, 95% CI [– 0.297, – 0.179]; Fig. 5.5a; Table 5.3). The strengths of the synergies reduced with hammer mass ($t_{24} = -3.724$, $p < 0.001$, 95% CI [– 3.465, – 0.994]; Fig. 5.5b; Table 5.3), confirming that the task became increasingly challenging for the monkeys while using a heavier hammer.

We examined the patterning of V_{UCM} and V_{ORT} across the eight DoFs. Given the direct relationship between foot stiffness and bipedal load-carrying capacity in humans (Cheung, Zhang, & An, 2004), and the load-bearing role of the trunk while carrying loads bipedally in bearded capuchin monkeys (Duarte et al., 2012; Hanna et al., 2015), we anticipated that the monkeys would control movement more stringently in the feet and legs, and the torso (pelvis and trunk), compared to the hands and arms. Variability (V_{UCM} and V_{ORT}) decreased with hammer mass ($t_{11} = -2.226$, $p = 0.027$, 95% CI [– 0.064, – 0.004]; Fig. 5.6; Table 5.3). Although V_{UCM} was greater than V_{ORT} across all DoFs, the difference between V_{UCM} and V_{ORT} was significantly greater in θ_{thigh} ($t_{429} = -2.771$, $p = 0.006$, 95% CI [– 0.207, – 0.035, 0.01]), $\theta_{\mathrm{lower\ arm}}$ ($t_{429} = -2.808$, $p = 0.005$, 95% CI [– 0.208, – 0.037]) and θ_{hand} ($t_{429} = -11.761$, $p < 0.001$, 95% CI [– 0.599, – 0.428]) than in θ_{foot} (Fig. 5.6; Table 5.3). These results demonstrate that the monkeys stringently controlled the motion of the foot. They controlled the motion of the lower arm and hand rather loosely, showing a greater variability across strikes, although producing strikes with highly repeatable spatial profiles. Overall, monkeys use strong joint synergies to stabilize the hammer trajectory while maintaining bipedal stance.

Discussion

In the present study, we identified the motor strategies bearded capuchin monkeys use to stabilize the hammer trajectory while cracking nuts with massive hammers. We hypothesized that if the requirement of maintaining a bipedal stance poses significant biomechanical and postural challenges, then to stabilize the hammer trajectory, capuchin monkeys would control motion in the joints of the lower body joints more stringently than motion in the upper body joints. To test this hypothesis, we analysed the kinematics of striking movements performed by five wild adult monkeys. We found that the monkeys produce hammer trajectories with highly repeatable spatial profiles. Using an uncontrolled manifold analysis, we show that the monkeys used strong joint synergies to stabilize the hammer trajectory while lifting and lowering heavy hammers. The monkeys stringently controlled the motion of the foot. They controlled the motion of the elbow and hand rather loosely, showing a greater variability across strikes.

Although it appears to the casual observer that lifting and lowering a massive hammer is challenging to the coordination of the upper limbs, variability in the upper body joints was not crucial in controlling the hammer trajectory. Instead, the challenge of maintaining a stable bipedal stance dictates the structure of motor variability in capuchin monkeys cracking nuts. Variability in the controlled subspace [which did not influence the hammer trajectory] was predominantly concentrated in the DoFs of the upper body, whereas variability in the controlled subspace [which influences the hammer trajectory] was predominantly concentrated in the DoFs of the lower body. In other words, the hammer trajectory was highly sensitive to variability in the motion of the foot, and only to a limited extent, to variability in the motion of the arms and the hand. No such distinction was apparent in the trunk and the pelvis, as comparable magnitudes of variabilities in both controlled and uncontrolled subspaces characterized the motion of both these joints.

Here, our interpretation of the projections of individual DoFs onto the UCM surpasses the traditional interpretation that V_{UCM} and V_{ORT} for individual DoFs in the model reflect the geometry of the UCM (Latash et al., 2007; Scholz & Schöner, 1999; Schöner, 1995). Given that the UCM analysis is an analysis of covariation among elemental variables, the geometry of the UCM for the hammer trajectory defines the magnitudes of V_{UCM} and V_{ORT} for individual DoFs. For a multi-joint action such as that performed by the monkeys while cracking nuts, the angles between the UCM and individual axes corresponding to each DoF likely differ for different DOFs. This is because the geometry of the UCM is likely influenced by the distinct anatomical and physiological constraints on movements about each DoF. Accordingly, the magnitudes of the projections of individual DoFs onto the UCM reflect the underlying patterns of joint coordination. This possibility opens a new direction for the UCM analysis.

The challenges of balancing a massive hammer while standing bipedally generalize to other dynamic bipedal activities, including walking bipedally with or without a load, as accomplishing each task benefits from minimizing changes in the body's COM. Change in motor control of the lower limbs that resulted in a progressive reduction in the displacement of the body's COM are posited to have accompanied the evolution of obligate bipedalism (Dunbar et al., 1986; Preuschoft, 2004; Schmitt, 2003; Tardieu et al., 1993). Humans show strong joint synergies while walking that reduce variability in the body's COM (Monaco, Tropea, Rinaldi, & Micera, 2018), but Japanese macaques (*Macaca fuscata*) trained to walk bipedally show weaker joint synergies (Kaichida, Hashizume, Ogihara, & Nishii, 2011). This discrepancy indicates that evolutionary changes in the structure of motor variability that served the postural demands of moving objects, such as lifting and lowering stones or other heavy objects could also have supported occasional bipedalism. Thus, while capuchin monkeys do not represent a progressive step in the evolution of bipedalism in ancestral hominins, they highlight the potential involvement of varied activities, such as using percussive tools in bipedal stance, in the evolutionary transition from occasional to obligate bipedalism.

The present findings highlight that a specific structure of motor variability is required for members of a quadrupedal species such as the bearded capuchin monkey to lift and lower massive hammers. Capuchin monkeys must control motion in the joints of the lower body joints more stringently than motion in the upper body joints. Similar task demands likely demand similar motor strategies. Given the role of constraints in the development of coordination (Newell, 1986; Newell & Jordan, 2007), phylogenetically distant species might show biomechanically comparable behavior under identical constraints. We thus anticipate that other nonhuman primates that use stone hammers in bipedal stance will show similar motor strategies to lift and lower stone hammers.

Young capuchin monkeys practice striking nuts with stone hammers for three or more years before becoming proficient at cracking nuts (Fragaszy et al., 2013, 2017). Assuming that a key outcome of their motor learning is the stabilization of the hammer trajectory, (i) a larger reduction in V_{ORT} compared to V_{UCM} can occur, resulting in the emergence or strengthening of a synergy. (ii) Comparable reductions in both V_{UCM} and V_{ORT} can occur, resulting in an invariant strength of the synergy, R_{V}. (iii) Finally, a larger reduction in V_{UCM} compared to V_{ORT} can occur, resulting in a reduction in the strength of the synergy (Latash et al., 2007). Given that each of the three scenarios is possible at different stages of motor learning (Domkin, Laczko, Djupsjöbacka, Jaric, & Latash, 2005; Latash, Yarrow, & Rothwell, 2003), developmental changes in motor variability in young monkeys practicing cracking nuts with stone hammers can reveal whether these monkeys discover joint synergies specific to this behavior, or as we predict, refine existing joint synergies engaged in quadrupedal locomotion. Analogously, human infants might refine existing joint synergies engaged in quadrupedal locomotion (crawling) while mastering walking bipedally and carrying a load bipedally (Garciaguirre, Adolph, & Shrout, 2007).

Acknowledgements

We thank Fonseca de Oliveira family for logistical help and permission to conduct research at Fazenda Boa Vista, Piauí, Brazil. We thank James Y. Hammers and Ashley Myers for data extraction. We thank Patricia Izar and Elisabetta Visalberghi for shared direction of the EthoCebus project at Fazenda Boa Vista, of which this study is one product.

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Table 5.1

The Number of Striking Movements Analyzed for Each Monkey

Monkey	**Sex**	**Body Mass**	**Number of Striking Movements**		
			1.01 kg Hammer	**1.48 kg Hammer**	**1.91 kg Hammer**
Chuchu	Female	2.1	6	6	N/A
Dita	Female	2.1	5	6	6
Presente	Male	2.2	6	6	6
Teimoso	Male	3.6	6	6	6
Mansinho	Male	4.3	6	6	6

Table 5.2

Anatomical Locations of the Digital Markers Constituting the Kinematic Chain of Striking Movement

Marker	**Anatomical Location**
Finger - INF	Distal phalanx of the index finger
Wrist - WRI	Wrist bar on the thumb side
Elbow - ELB	Lateral epicondyle approximating the elbow joint axis
Shoulder - SHO	Acromioclavicular joint
Anterior superior iliac spine - ASI	Anterior superior iliac spine
Thigh - THI	Lower lateral 1/3 surface of the thigh, just below the swing of the hand
Knee - KNE	Lateral epicondyle of the left knee
Heel - HEE	Calcaneus at the same height above the plantar surface of the foot as the toe marker
Toe - TOE	Second metatarsal head, on the midfoot side of the equinus break between forefoot and midfoot

Table 5.3

Outcomes of Linear Mixed-Effects Models

Response variable	**Effect**	**Estimate ± s.e.m.**	***t***	**df**	***p***	**95% CI [Lower, Upper]**
s.d. of hammer’s *x*-position	body mass	0.006 ± 0.004	1.432	11	0.180	– 0.003, 0.016
	hammer mass	0.019 ± 0.008	2.474	11	0.031*	0.002, 0.036
s.d. of hammer’s y-position	body mass	0.011 ± 0.005	2.353	11	0.038*	0.001, 0.022
	hammer mass	– 0.005 ± 0.005	– 0.935	11	0.370	– 0.016, 0.007
variability per DoF (whole body)	body mass	– 0.006 ± 0.016	0.392	51	0.697	– 0.026, 0.038
	hammer mass	– 0.061 ± 0.041	– 1.513	51	0.136	– 0.143, 0.020
	strike phase (lowering – lifting)	0.024 ± 0.029	0.772	51	0.444	– 0.036, 0.081
	subspace (ORT – UCM)	– 0.238 ± 0.029	– 8.159	51	< 0.001***	– 0.297, – 0.180
strength of synergy (whole body)	body mass	0.000 ± 0.233	– 0.001	51	1.000	– 0.480, 0.480
	hammer mass	– 2.229 ± 0.599	– 3.724	51	0.001**	– 3.465, – 0.994
	strike phase (lowering – lifting)	– 0.117 ± 0.430	– 0.273	51	0.788	– 1.004, 0.770
Variability in individual DoFs	body mass	– 0.003 ± 0.006	– 0.515	429	0.606	– 0.015, 0.009
	hammer mass	– 0.034 ± 0.015	– 2.226	429	0.027	– 0.064, – 0.004
	strike phase (lowering – lifting)	0.012 ± 0.011	1.133	429	0.258	– 0.009, 0.034
	subspace (ORT – UCM) × DoF ($\theta_{\text{shank}} - \theta_{\text{foot}}$)	– 0.058 ± 0.044	– 1.319	429	0.188	– 0.143, 0.028
	subspace (ORT – UCM) × DoF ($\theta_{\text{thigh}} - \theta_{\text{foot}}$)	– 0.121 ± 0.044	– 2.771	429	0.006**	– 0.207, – 0.035
	subspace (ORT – UCM) × DoF ($\theta_{\text{pelvis}} - \theta_{\text{foot}}$)	– 0.030 ± 0.044	– 0.687	429	0.493	– 0.116, 0.056

subspace (ORT – UCM) × DoF ($\theta_{\text{trunk}} - \theta_{\text{foot}}$)	0.027 ± 0.044	0.623	429	0.534	– 0.059, 0.113
subspace (ORT – UCM) × DoF ($\theta_{\text{upper arm}} - \theta_{\text{foot}}$)	– 0.017 ± 0.044	– 0.394	429	0.694	– 0.103, 0.069
subspace (ORT – UCM) × DoF ($\theta_{\text{lower arm}} - \theta_{\text{foot}}$)	– 0.123 ± 0.044	– 2.808	429	0.005**	– 0.208, – 0.037
subspace (ORT – UCM) × DoF ($\theta_{\text{hand}} - \theta_{\text{foot}}$)	– 0.514 ± 0.044	– 11.761	429	< 0.001***	– 0.599, – 0.428

*$p < 0.05$, **$p < 0.005$, ***$p < 0.001$

Figure 5.1. A wild bearded capuchin monkey is striking an intact piaçava nut with a quartzite stone hammer. (*Source:* Photo by Noemi Spagnoletti.)

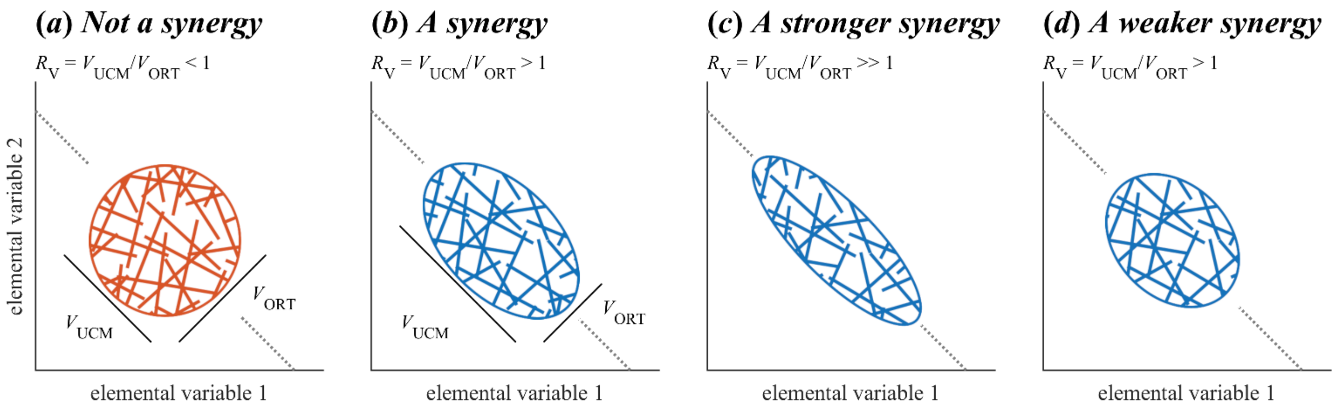


Figure 5.2. Schematic illustration of the uncontrolled manifold (UCM) concept/analysis. (a) Not a synergy. Variability in the elemental variables in the controlled subspace, V_{UCM}, is smaller than variability in the uncontrolled subspace, V_{ORT}, that is, $R_{\mathrm{V}} = V_{\mathrm{UCM}}/V_{\mathrm{ORT}} < 1$. (b) A synergy. V_{UCM} is greater than V_{ORT}, that is, $R_{\mathrm{V}} = V_{\mathrm{UCM}}/V_{\mathrm{ORT}} > 1$. The magnitude of R_{V} reflects the strength of the synergy. (c) A stronger synergy. (d) A weaker synergy.

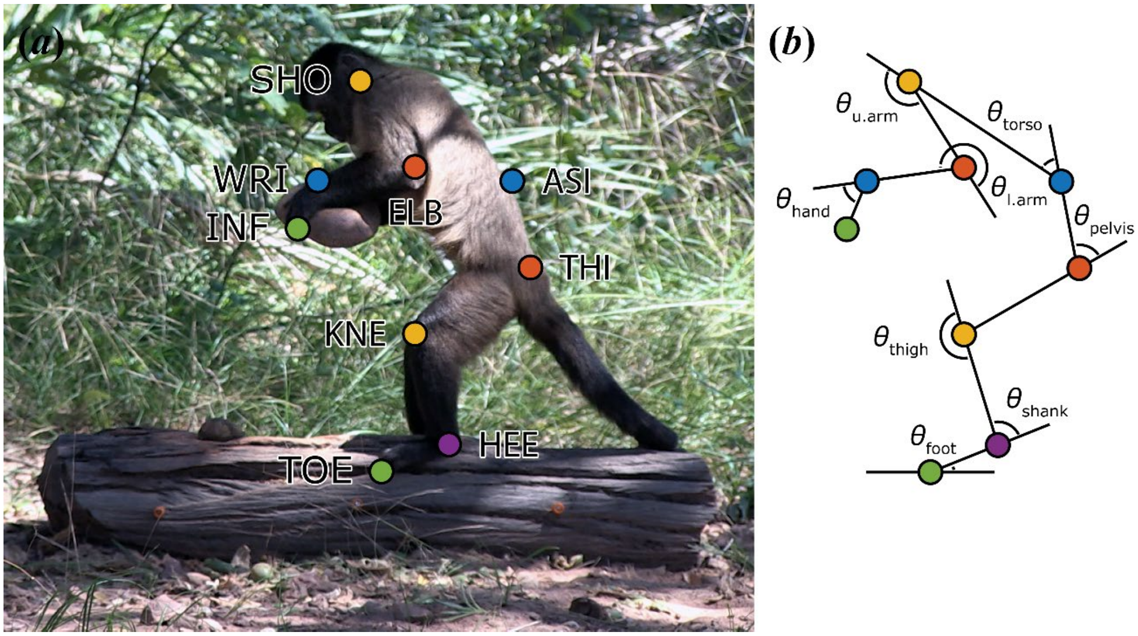
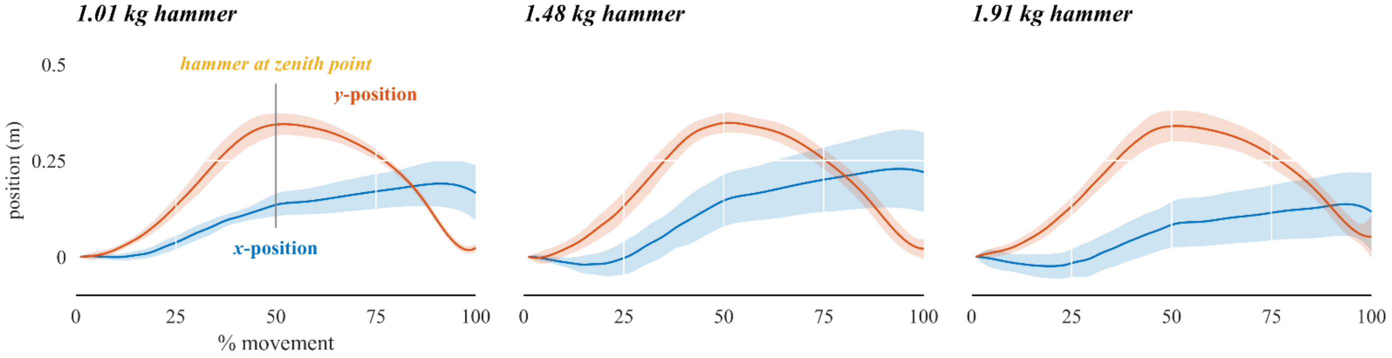


Figure 5.3. UCM analysis. (a) The anatomical locations of the digital markers constituting the kinematic chain of striking movement. (b) The DoFs of the forward kinematic model linking the hammer's *x*-, *y*-positions to the monkey's joint configurations.

(a) *Hammer trajectory for Presente* *(body mass: 2.2 kg)*



(b) *Hammer trajectory for Mansinho* *(body mass: 4.3 kg)*

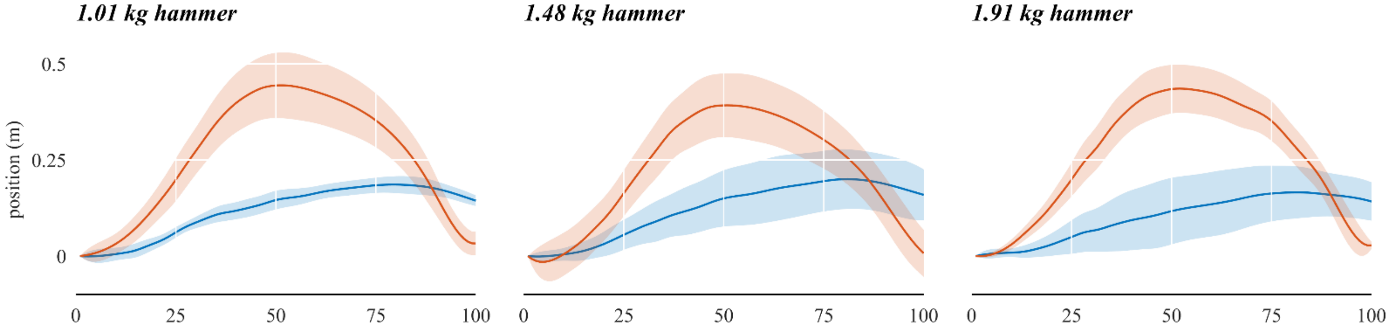
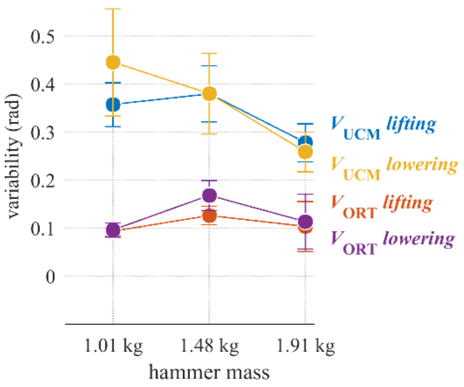


Figure 5.4. The monkeys produced hammer trajectories that were highly repeatable across hammers of different masses. (a) Hammer trajectory for Presente (body mass: 2.2 kg). (b) Hammer trajectory for Mansinho (body mass: 4.3 kg). The hammer was at the zenith at 50% movement. Shadings represent s.d.

(a) V_{UCM} and V_{ORT} per DoF



(b) Strength of the synergy

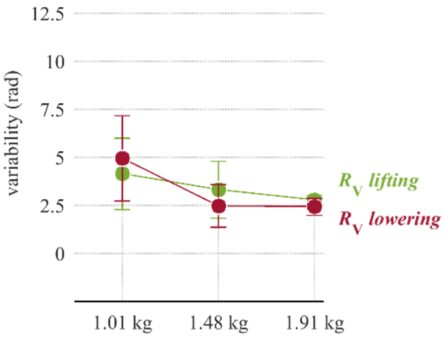


Figure 5.5. The monkeys employed strong joint synergies. (a) V_{UCM} and V_{ORT} per DoF. (b) The strengths of the synergies. Error bars indicate the s.e.m ($n = 5$).

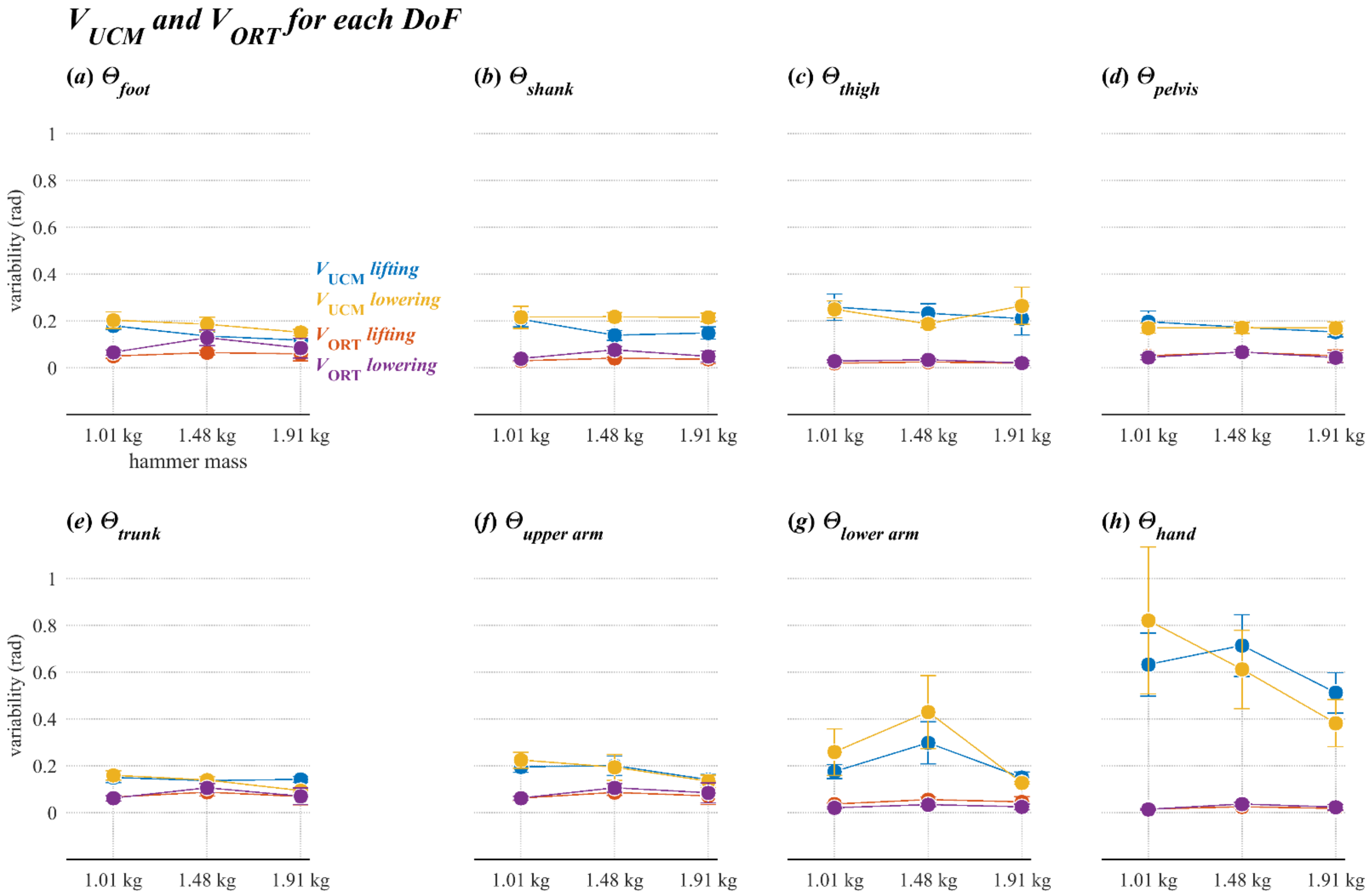


Figure 5.6. V_{UCM} and V_{ORT} for each DoF. (a) θ_{foot}. (b) θ_{shank}. (c) θ_{thigh}. (d) θ_{pelvis}. (e) θ_{trunk}. (f) $\theta_{\mathrm{upper\ arm}}$. (g) $\theta_{\mathrm{lower\ arm}}$. (h) θ_{hand}. Error bars indicate the s.e.m ($n = 5$).

CHAPTER 6

GENERAL DISCUSSION

The overall objective of my dissertation research was to clarify specific aspects of the evolution of bipedal striking, such as how an occasional bipedal species can solve the biomechanical challenges of posture and movement control while using massive hammers. To this end, I first investigated how wild bearded capuchin monkeys control stone hammers to meet the energetic demands of the nut-cracking task, and then identified the motor control strategies they use to solve the challenges associated with standing bipedally while using massive hammers. I captured the striking movements of monkeys in their natural habitat at Fazenda Boa Vista (FBV), Piauí, Brazil, as they cracked nuts using stone hammers. I conducted the biomechanical analysis of multi-joint posture and movement control to examine how constraints from different sources influence patterns of coordination. I manipulated several putative sources of constraints on the monkeys' striking movements. First, I included both juvenile and adult monkeys to examine the influence of body mass (a source of organismic constraint) on the coordination of movement. Second, I manipulated the environmental constraints by providing the monkeys with hammers of different masses. Third, I manipulated the task constraints by providing the monkeys with the tucum and piaçava nuts, which, in addition to lying at the extremes of the spectrum of resistance to fracture, also differ structurally. I analyzed the resulting changes in patterns of coordination to elucidate how these constraints shape the monkeys' striking movements. I found that (1) the monkeys crack nuts dexterously, (2) have a unique way of controlling the hammers, and (3) skillfully structure motor variability across different joints to stand bipedally while lifting and lowering massive hammers.

Evidence for Dexterity in Nut-Cracking

The findings of the first study (Chapter 2) show that wild bearded capuchin monkeys modulate the kinematic parameters of individual percussive movements as driven by the changing requirements of the task. Their behavior is similar to that in contemporary hunter-gatherers cracking nuts with stone hammers. For example, 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) (Bock, 2005), and Nigerian farmers crack the oil palm nuts (Luedtke, 1992, p. 471) by placing the nuts between two stones and varying the applied force over consecutive strikes. The findings of the second study (Chapter 3) show that in addition to modulating the kinematic parameters of individual strikes, these monkeys also modulate the organization of successive strikes according to the type of the nut. When cracking a nut with a more resistant shell encapsulating a soft kernel, an optimal strike should be forceful enough 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, which ultimately causes fatigue failure of the nut. A moderately forceful strike is enough to crack a nut that already has 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; Manuwa (2007) repeatedly, less forcefully reduces the rate of damage to the kernel of the nut. However, the locules of the piaçava nut 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. Accordingly, the monkeys cracked each piaçava nut by striking it repeatedly with the maximum force they could generate (i.e., without compromising on the angle and point of percussion) until that nut cracked.

Evidence for Unique Perceptuomotor Control of Hammers in Bearded Capuchin Monkeys

In the third study (Chapter 4), I examined the patterns of coordination of striking movement and perceptuomotor control of stone hammers in wild bearded capuchin monkeys. The monkeys predominantly relied on the movement of their hindlimbs (hip and knee) and their torso (lumbar) to lift and lower a hammer, and to a limited extent, on the movement of their forelimbs (shoulder) to lift a hammer. They altered their patterns of coordination of movement to accommodate changes in hammer mass. By altering their patterns of coordination, the monkeys kept the strike's amplitude and the hammer's velocity at impact constant with respect to hammer mass. In doing so, the hammer's kinetic energy at impact—which determines the propagation of a fracture/crack in a nut—varied across hammers of different masses. Body mass of wild bearded capuchin monkeys is well under 5.0 kg (Fragaszy et al., 2016), but they can use massive hammers (up to 2.0 kg) constituting up to 100% of their body mass. A more massive hammer poses a more significant challenge in coordinating movement and controlling the hammer's trajectory. Accordingly, a more massive hammer resulted in more stringent patterns of coordination. These findings show that while bearded capuchin monkeys alter patterns of coordination of movement to control the hammer' trajectory, the monkeys use a different perceptuomotor strategy of controlling the hammer's velocity at impact instead of the hammer's kinetic energy at impact. Perception of the strike's amplitude and the hammer's velocity can occur through kinesthesis, from proprioceptive cues generated by the movement of the body and the limbs (Keele, 1968), but the perception of the hammer's kinetic energy cannot. The latter requires the integration of sensory information generated by the movement of the body and the limbs, and by the movement of the grasped hammer (Turvey, Shockley, & Carello, 1999). Accordingly, I hypothesize that the perceptuomotor control of hammers in bearded capuchin monkeys—that relies predominantly on the modulation of kinematic variables of strikes—is inadequate to produce conchoidally fractured flakes by knapping stones that requires modulating the hammer's kinetic energy at impact, as do humans.

Evidence for Skilled Movements while Lifting and Lowering Massive Hammers

In the fourth study (Chapter 5), I investigated motor strategies bearded capuchin monkeys use to control the hammer trajectory while cracking nuts with massive hammers. Although it appears that lifting and lowering a massive hammer is challenging to the coordination of the upper limbs, I found that variability in the upper body is inconsequential to controlling the hammer's trajectory. Instead, challenges of maintaining a stable bipedal stance dictates the structure of motor variability in capuchin monkeys cracking nuts. While the uncontrolled variability [which did not influence the hammer's trajectory and, therefore, is referred to as "uncontrolled"] was predominantly concentrated in the upper body, the controlled variability [which influences the hammer's trajectory and, therefore, referred to as "controlled"] was predominantly concentrated in the lower body. In other words, the hammer's trajectory was highly sensitive to variability in the motion of the lower body joints, and only to a limited extent, to variability in the motion of the upper body joints. No such distinction was apparent in the trunk and the pelvis, as comparable magnitudes of controlled and uncontrolled variabilities characterized the motion of both these joints. These findings highlight that a specific structure of motor variability is required for a quadrupedal species such as bearded capuchin monkey to lift and lower massive hammers. Capuchin monkey must control the movement of the lower limbs more stringently than the movement of the upper limbs. They highlight that the movements of the monkeys are embedded within the posture they need to attain while lifting and lowering massive hammers and this postural demand dictates how bearded capuchin monkeys structure motor variability across different joints. Given the role of constraints in the development of coordination (Newell, 1986; Newell & Jordan, 2007), phylogenetically distant species might show biomechanically comparable behavior under identical constraints. Accordingly, other nonhuman primates that use stone hammers would show similar motor strategies to lift and lower stone hammers. For example, humans lifting and lowering comparable weights (e.g., weightlifters) may structure motor variability across joints akin to the monkeys, although because of different task demands, they may not control the weights' trajectory but instead focus solely on minimizing changes in the body's COM.

Future Directions

Young capuchin monkeys practice striking nuts with stone hammers for three or more years before becoming reaching adult's proficiency at cracking nuts (Fragaszy et al., 2013, 2017). Assuming that a key outcome of their motor learning is the stabilization of the hammer's trajectory, (i) a larger reduction in V_{ORT} compared to V_{UCM} can occur, resulting in the emergence or strengthening of a synergy. (ii) Comparable reductions in both V_{UCM} and V_{ORT} can occur, resulting in an invariant strength of the synergy, R_V. (iii) Finally, a larger reduction in V_{UCM} compared to V_{ORT} can occur, resulting in a reduction in the strength of the synergy (Latash, Scholz, & Schöner, 2007). Each of the three scenarios is possible at different stages of motor learning (Domkin, Laczko, Djupsjöbacka, Jaric, & Latash, 2005; Latash, Yarrow, & Rothwell, 2003). In an ongoing study, by performing the UCM analysis on movements of both young and adult monkeys, I plan to investigate the developmental changes in motor variability in young monkeys attempting to crack nuts with stone hammers, as well as walking quadrupedally. This research will reveal how young monkeys discover joint synergies engaged in bipedal hammering and walking.

Human infants have to solve comparable postural challenges while learning to walk bipedally. It is believed that the magnitude, distributed nature, and variability of infants' walking experience might underlie such developmental change. Thousands of steps, each slightly different from the last because of variations in the continuously varying biomechanical constraints may help infants to identify the relevant combinations of parameters for strength and balance. These continually changing constraints may also allow infants to acquire more efficient recruitment of their leg and hip muscles, better exploit passive forces and differentiate the perceptual information required for maintaining balance (Adolph et al., 2012; Adolph, Vereijken, & Shrout, 2003). I hope to collaborate with developmental psychologists to investigate how human infants discover joint synergies while mastering walking bipedally and carrying load bipedally (Garciaguirre, Adolph, & Shrout, 2007).

I hope to investigate the role of postural control in the context of the broader problem of tooling. Research on human tooling has mostly focused on the coordination and control of manual actions and the distalization of the end-effector (Arbib, Bonaiuto, Jacobs, & Frey, 2009; Bongers, Smitsman, & Michaels, 2003; Smitsman, 1997; Smitsman, Cox, & Bongers, 2005; Umiltà et al., 2008; van der Steen & Bongers, 2011; Vernooij, Mouton, & Bongers, 2012). However, the postural demands of tooling have received almost no attention. This omission is no surprise given that actions with tools are mostly executed against a rigid body (e.g., loosening the nuts of the wheel of a car), or involve a substrate (e.g., the table serves as a substrate while cutting bread). A few studies that have touched upon this topic highlight the importance of posture in tooling. Among human knappers, posture preparation is learned before the stroke execution, as indicated by the finding that the level of functionality of posture preparation in the high-level learners is similar to that in the high-level experts, even when the functionality of stroke execution is not yet mastered (Biryukova, Bril, Frolov, & Koulikov, 2015). A postural synergy comprising legs and trunk provides a stable platform for the displacement while displacing distant objects using a rod (Bongers, Michaels, & Smitsman, 2004). By artificially imposing constraints on the posture of the actor, I plan to investigate how actions with tools are embedded within the posture of the actor and how the task demands dictate the level of such embeddedness.

Conclusions

To date, most research on nonhuman primate tooling has focused on the species-specificity of tooling behaviors. In stark contrast with the existing approaches, the findings of the present biomechanical analysis of tooling movements in wild bearded capuchin monkeys highlight the importance of studying the evolution of bipedal striking, and more generally, research on tooling in nonhuman animals, using method of biomechanics and human movement science (Biryukova & Bril, 2012). Determining the changing energetic constraints of the task and dynamically optimizing movements using those as criteria are dexterous accomplishments. The capability to solve the biomechanical challenges of posture and motor control reflects skilled behavior. Thus, first, I measured the dexterity of monkeys in terms of the spatiotemporal organization of tooling movements that optimize at least one composite performance outcome variable. I then explained the development of coordination for striking movements in terms of constraints imposed by different features of the body, environment, and task. Finally, I measured the complexity in the use of stone hammers in terms of the control of the biomechanical DoFs of the body-plus-hammer system. This kind of embodied analysis of tooling is applicable across species, tasks, and environments and I hope that it will provide useful directions for future research.

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