Chapter 20
Evolution, Constraint, and Optimality in Primate Feeding Systems

Callum F. Ross and Jose Iriarte-Diaz

Evolutionary biomechanical studies of primate feeding systems have benefited from deployment of techniques for measurement of food material properties, digital collections of morphological and experimental data, comparative analyses of the effects of phylogeny, size, and shape, and computational modeling of bone function. Techniques for quantification of three-dimensional jaw and hyoid kinematics across large numbers of cycles have shifted the focus of primate feeding biomechanics from mechanistic studies of small numbers of gape cycles to studies of variation within and between individuals and species. These large-scale studies reveal that the majority of variation in jaw kinematics, in relative timing of jaw muscle activity, and in bone strain patterns is found across gape cycle types and behaviors, not across chews on different foods. This suggests that performance of different kinds of feeding behaviors might be an important determinant of skull design: specifically, external measures of skull morphology might more strongly reflect variation in the ability of the feeding system to *generate* bite force and transmit it to the bite point, rather than in its ability to *resist* internal forces (stresses). Variation in feeding system design is structured by three fundamental constraints imposing trade-offs between bite force and gape: the sarcomere structure of skeletal muscle imposes a trade-off between muscle fiber length and muscle force; the primate mandible functions as a third-class lever, so that in combination with the length–tension properties of skeletal muscle, jaw depression and elevation are associated with trade-offs between bite force and gape; and to avoid putting the temporomandibular joint in tension the jaw elevator muscle resultant must pass through the triangle of support defined by the two jaw joints and the bite point. Several decades of in vivo bone strain, morphometric, and modeling studies also suggest that primate crania are impacted by trade-offs with

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V. Bels and I. Q. Whishaw (eds.), *Feeding in Vertebrates*,
Fascinating Life Sciences, https://doi.org/10.1007/978-3-030-13739-7_20

non-feeding functions, including protecting and positioning sense organs. For example, primate gape distances are driven by jaw length and canine overlap, and brow ridge morphology is likely adapted for visual signaling or to protect the brain and eyes during agonistic interactions with conspecifics, revealing the impact of social interactions on feeding system morphology. Scaling analyses reveal that primate feeding systems are heavily damped, reflecting the importance of displacement and force control in primate feeding systems, rather than speed and energetic efficiency. Primates do recruit their jaw muscles according to the triplet motor pattern, but this is by no means the only pattern observed and we still have much to learn about the determinants of variation in muscle motor patterns in the primate feeding system. Large proportions of variance in muscle mechanical advantage, muscle firing patterns, mandibular corpus bone strain magnitudes, and mandibular morphology are nested at high taxonomic levels. We hypothesize that this reflects ancient selection for divergent feeding behaviors at the base of major primate clades: what those behaviors might have been is an important avenue for future research.

20.1 Introduction

Evolutionary biomechanical studies of primate feeding are poised to take advantage of a well-grounded primate phylogeny, rich fossil record, and vibrant, skilled communities of primate ecologists, and experimental biologists. The last two decades have witnessed development and deployment of techniques for measurement of material properties of primate foods in the wild and the laboratory (Williams et al. 2005; Darvell et al. 1996; Coiner-Collier et al. 2016), creation of digital collections of morphological and experimental data (Wall et al. 2011; Copes et al. 2016), analyses of morphological form that precisely separate the effects of size and shape (Cooke and Terhune 2015), comparative analyses that explicitly take phylogeny into account (Vinyard et al. 2011), computational modeling of bone function (Smith et al. 2012, 2015a, b; Strait et al. 2007, 2009a, b; Panagiotopoulou et al. 2017), three-dimensional (3D) quantification of primate jaw and hyoid kinematics during feeding (Orsbon et al. 2018; Nakamura et al. 2017; Iriarte-Diaz et al. 2011, 2012, 2017; Iriarte-Diaz and Ross 2010), techniques for measurement of muscle architecture dynamics (Orsbon et al. 2018; Camp et al. 2016); quantification of metabolic costs of primate feeding (Wall et al. 2013), and recording of spiking activity and local field potentials from populations of neurons in orofacial sensorimotor cortex (Arce et al. 2011a, b, 2013).

One important innovation in primate evolutionary biomechanics is a recent shift in emphasis from mechanistic studies based on limited numbers of gape cycles to studies of variation within and between individuals and species. This shift has facilitated large-scale studies that have yielded important insights into patterns of evolution of primate feeding systems (Vinyard et al. 2008; Williams et al. 2011). However, there is still much to learn about primate feeding mechanisms, how feeding system morphology and function contribute to feeding performance, and even, from the perspective of feeding system design, what the important performance variables are. One measure of feeding performance is particle reduction effectiveness, whether overall or on a per-chew basis. Other measures might include feeding time, feeding efficiency (energy expended/energy acquired), avoidance of dental wear and breakage, and maintenance of safe bone strain magnitudes.

This review emphasizes experimental and modeling approaches to these questions that were not included in previous papers (Ross 2016; Ross and Iriarte-Diaz 2014; Vinyard et al. 2007). It discusses issues regarding the terminology used in studies of primate feeding raised by application of high-resolution motion capture (Reed and Ross 2010; Iriarte-Diaz et al. 2011, 2012) and biplanar videoradiography (Orsbon et al. 2018) techniques to the quantification of primate jaw, hyoid, and tongue kinematics. We then present three fundamental biomechanical constraints on the ability of the primate feeding system to generate bite force at different gapes and bite points, reviewing recent data on the dynamics of the mandibular rotational axis. Results of recent scaling analyses are summarized to address questions regarding the determinants of chewing frequency and short-term food intake rate in primates. The determinants of variation in primate jaw kinematics are discussed, followed by a critical evaluation of the Triplet motor pattern hypothesis explaining primate jaw muscle activity. Particular attention is paid to important future research directions in the study of primate feeding system biomechanics.

20.2 Primate Feeding Behavior: Definitions

In wild and laboratory primates, feeding processes occur in bouts, comprising one or more *feeding sequences* (Fig. 20.1). Each feeding sequence consists of a series of jaw and tongue movement cycles during which a number of processes are performed: *ingestion*, in which food passes through the oral fissure into the oral vestibule or oral cavity; food transport (*stage 1 transport*, from the ingestion point to the molars for mastication; food fracture; bolus manipulation; and *stage 2 transport* from the oral cavity into the oropharynx). Multiple processes can co-occur in individual gape cycles: for example, stage 2 transport can occur during mastication cycles, accumulating food in the valleculae, or it can occur during the oral phase of swallow cycles (Hiiemäe and Crompton 1985).

To understand these processes, experimental studies collect data on several physiological variables that can be categorized according to their [fundamental dimensionalities].

- Kinematic variables [space and time] include translation and rotation of the mandible with varying rotational components of: depression and elevation—pitch—about a horizontal axis; yaw about a vertical axis, producing transverse movements of the lower teeth during occlusion; axial rotation or roll about an anteroposterior axis (possible only with unfused mandibular symphyses), associated with asymmetrical movements of the condyles, and/or rotation of the hemimandibles. Of equal importance are hyoid and tongue movements and movements

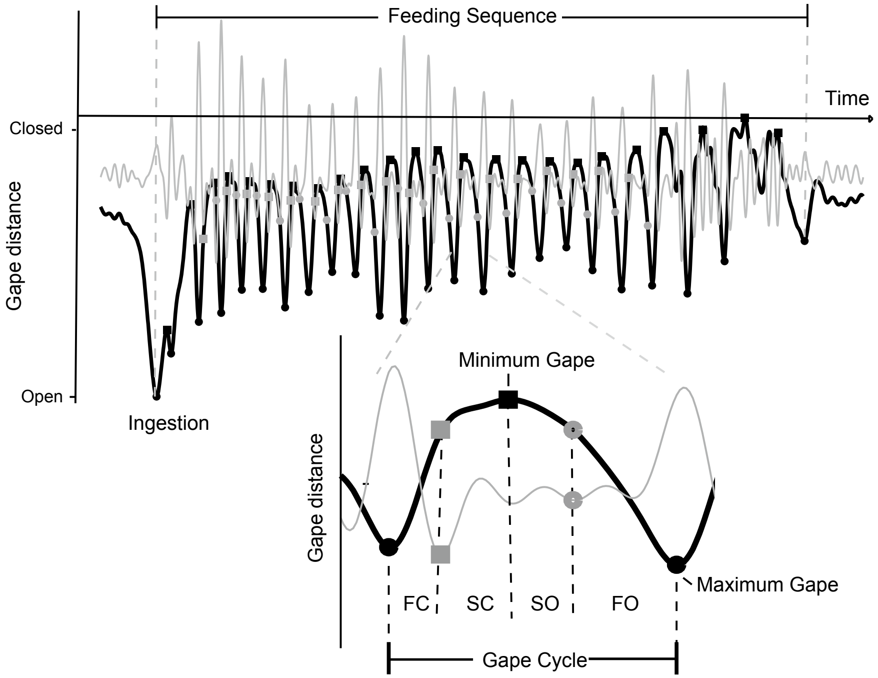

Fig. 20.1 Definitions of feeding sequence, gape cycle, and gape cycle phases. The upper graph plots (black line) the open–close displacements (gape) of the lower jaw during a complete feeding sequence from ingestion to final swallow. The second derivative of the displacement, the gray line, is used to define the four vertical kinematic (VK) phases: FC begins at maximum gape and ends at the start of SC (slow-close); SC starts when the teeth contact the food and mandibular closing movements slow; SC ends and SO begins when the mandible stops moving upward and begins moving downward (minimum gape); SO ends when the mandible starts depressing quickly (SO–FO) (slow-open–fast-open) transition, in theory when tongue has captured the food item ready for transport); and FO ends when the mandible changes from depression to elevation (maximum gape). Modified from Reed and Ross (2010)

of lips and cheeks that manipulate and position the food bolus. Relative movements of the teeth during occlusion are important for the processes involved in food fracture.

- Kinetic variables [force and time] include: *muscle forces*, transmitted by the mandible to the teeth, where they result in *bite forces*; *joint reaction forces* associated with the class three lever arrangement of the jaw and jaw elevator muscles; and internal and external forces acting on the food bolus through the tongue, palate, and oropharynx.
- Stress [force, area], strain [dimensionless local shape change], and deformation [shape and size change] regimes (sensu Ross et al. 2011) caused by external forces acting on the mandible and cranium.

- Neural and muscular activity [changes in electrical potential] recorded from the periphery or central nervous system, reflecting neural control of feeding behavior.

20.2.1 The Kinematics of the Gape Cycle

As the name suggests, *gape cycles* are defined by cyclic elevation and depression of the mandible. Gape cycles involving food fracture between the teeth have been categorized into *puncture crushing cycles*, in which the mandible moves more vertically, and the teeth do not contact each other, and *mastication cycles*, in which more transversely oriented jaw and tooth movements occur with the teeth in occlusion (Hiiemäe and Kay 1973). The gape cycle can be delineated by minimum gape or maximum gape, depending on the focus of the study. Studies of hyolingual kinematics benefit from using gape cycles defined using minimum gape because both hyoid and mandible change movement direction at or around minimum gape (Oron and Crompton 1985); studies of food breakdown are best performed using gape cycles defined using maximum gape so that the food breakdown events (slow-close and early slow-open) are not split between adjacent cycles (Reed and Ross 2010).

Division of the gape cycle into phases is useful because, although jaw movements are usually continuous, the concept of gape cycle phases has historical momentum and empirical utility. We adopt the subdivision of the gape cycle into four phases as defined by Bramble, Wake, Hiiemäe, and Crompton (Bramble and Wake 1985; Hiiemäe and Crompton 1985), a subdivision that might be best called the vertical kinematic (VK) phases because they are defined and named with reference to jaw vertical position and its temporal derivatives (velocity, acceleration) (Fig. 20.1): *fast-close* begins at maximum gape and ends at the time of the most rapid decrease in jaw elevation velocity (largest negative peak in the second derivative of displacement between maximum and minimum gape); *slow-close* begins at the end of fast-close and ends at minimum gape; *slow-open* begins at minimum gape and ends at the time when jaw depression velocity increases most rapidly (the largest negative peak in the second derivative of displacement between the times of minimum and maximum gape); *fast-open* ends at maximum gape.

Vertical kinematics are useful for gape cycle phase definitions because they are associated with the largest rotation components during feeding (opening and closing of the mouth, depression and elevation of the jaw), and hence can be identified with the greatest accuracy and replicability, facilitating the automated data processing and analysis necessary for collection of large sample sizes. Moreover, the events defining the four VK gape cycle phases are associated with changes in sensory afferent input that are likely to be important in sensorimotor control (Lund 1991). Of course, primate jaw movements are not limited to vertical displacements and pitch rotations and this is especially true during the time when the food is broken down between the teeth. All primates for which there are data resemble *Didelphis, Tupaia, Tenrec*, and many other mammals in moving their working-side mandibles and teeth *upward, medially, and anteriorly* during slow-close and early slow-open:

Otolemur, *Saimiri, Ateles* (Hiiemäe and Kay 1972, 1973; Kay and Hiiemae 1974b), *Cebus/Sapajus* (Iriarte-Diaz et al. 2017; Reed and Ross 2010), *Homo* (Ahlgren 1976; Buschang et al. 2000), *Papio* (Wall et al. 2002; Iriarte-Diaz et al. 2017), and *Macaca* (Hiiemäe 1978; Hylander et al. 1987; Iriarte-Diaz et al. 2017; Luschei and Goodwin 1974) (Fig. 20.1). This period of the gape cycle—roughly slow-close through early slow-open, but see below—is when food breakdown between the teeth occurs, and hence has been termed the *power stroke* (Hiiemäe 1967).

20.2.2 What Is the Power Stroke?

The term *power stroke* refers to the time during the gape cycle when work is done on the food by the teeth but, as the early definitions of the term reveal, the *power stroke* sensu stricto is very difficult to quantify and study in vivo. The term was first defined as one of the gape cycle subdivisions by Hiiemäe and colleagues in descriptions of feeding by rats (Hiiemäe 1967), opossums (Crompton and Hiiemae 1970; Hiiemäe and Crompton 1971), and primates (Hiiemäe and Kay 1972, 1973; Kay and Hiiemae 1974a, b) using not only *measurable* kinematic events, such as time of maximum gape, but also events (in **bold** below) that are so difficult/impossible to measure that their timing had to (and mostly still has to) be inferred indirectly. The *preparatory stroke* (later called the *closing stroke,* Hiiemäe 1976, 1978) was defined as beginning at maximum gape and ending with **tooth–food–tooth contact** (in puncture crushing cycles), or **tooth–tooth contact** (in chewing cycles). The *power stroke* was divided into two phases: Phase I beginning with **tooth–food–tooth** or **tooth–tooth contact** between laterally placed lower molars and continuing with their upward and anteromedial movement into **centric occlusion** (i.e., the protocone is in the talonid basin); and Phase II beginning at **centric occlusion** and "continuing until the downward and anteromedial movement of the lower molars carries them out of **occlusal contact** on the active side" (Kay and Hiiemäe 1974a, b: 228). By definition, the *recovery stroke* (later called the *opening stroke* (Hiiemäe 1976, 1978)) begins when **occlusal** or **tooth–food–tooth contact** is lost and ends at maximum gape (Hiiemäe and Kay 1973).

It was necessary to define Phase I and II of the power stroke using these inferential variables because the cineradiographic images used to study feeding were (and are) obscured by the overlapping densities of enamel during occlusion (Crompton and Hiiemäe 1970; Hiiemäe and Crompton 1971), and because the spatial precision of jaw movement measurements was too low to make precise statements about relative tooth movements during occlusion. In practice, Phase I and II kinematics were estimated from 2D data by combining cineradiographic measures of jaw movement (upward, medial, and anterior during Phase I; down, medial, and anterior during Phase II) with occlusal analysis of dental morphology. Occlusal analysis develops the assumption, axiomatic in orthodontics and prosthodontics (Rilo et al. 2009; Wang and Mehta 2013; Woda et al. 1979; Mills 1966), that "[o]nce the teeth have come into occlusion, their form determines the path of movement of the lower molars across the uppers, and therefore, to a considerable extent, although not entirely, the movement of the mandible on the active side" (Crompton and Hiiemäe 1970).

The first detailed studies of primate jaw kinematics by Hiiemäe and Kay used this combination of occlusal analysis and lateral, frontal, and dorsal plane cineradiography (at 60 frames per second [fps]) to quantify feeding kinematics in one individual each of *Tupaia, Galago, Ateles*, and *Saimiri*. To address the difficulty of identifying occlusal events from cineradiographic data, Hiiemäe and Kay introduced the concept of "clear freeway" to identify the start and end of the power stroke. The clear freeway is the space, visible in lateral cineradiographic or videoradiographic images, between the cusps of the upper and lower teeth that disappears as the teeth approach each other during jaw elevation and appears as the teeth move apart during jaw depression. Because of the complex morphology of the teeth, which varies interspecifically and ontogenetically, upper and lower tooth cusps can overlap in this view prior to and after **tooth–tooth contact**, making it an imprecise criterion for delimiting the time of **tooth–tooth contact** within and between both individuals and species. Hiiemäe and Kay used the appearance of freeway to identify the start of a power stroke, but equivocated about its utility for identifying its end (Kay and Hiiemäe 1974a, b: 502–3; Hiiemäe and Kay 1973: 44). Shaded areas in their gape—time plots are sometimes used to indicate the times when clear freeway is not visible (Hiiemäe and Kay 1973; Fig. 20.5), and at others "the range of gapes, defined as 'wide freeway space', 'narrow freeway space' and into **occlusion** (i.e., equivalent to 5, 2.5, and 0 degrees of gape)" (Kay and Hiiemäe 1974a, b; Fig. 20.4). Similar shaded areas appear in reviews by Hiiemäe (1978) and Vinyard et al. (2006).

The difficulty of applying the concept of the power stroke to studies of primate feeding has made us leery of the term power stroke sensu stricto. While it has utility as an informal term to describe the time during chewing and puncture crushing cycles when food is broken down, its actual application to in vivo studies of primate feeding is fraught with problems. Recognizing the value of defining a phase before and after which the molars cannot be in contact and during which any molar occlusal contact must occur, we instead advocate the use of an *intercuspal phase*.

20.2.3 Intercuspal Phase

The kinematics and kinetics of occlusion are fundamental for understanding the processes of food breakdown during chewing. Hiiemäe and Kay employed Simpson's (1933) terminology to hypothesize links between orientation of individual wear facets and specific actions by the teeth on the food: food shearing, when force is applied to the food in a plane parallel to the plane of contact between the teeth; crushing, when force is applied normal to the contact surface; and grinding, when movement of the occlusal surfaces across each other is accompanied by large components of force *both* orthogonal *and* parallel to the surfaces (Simpson 1933; Hiiemäe and Kay 1972, 1973; Kay and Hiiemae 1974a, b). These terms—shearing, crushing, and grinding—continue to be used in discussions of occlusal function in primates and other mammals. For example, microwear data from *Australopithecus africanus, Paranthropus robustus, Pan troglodytes, Piliocolobus badius, Cebus apella, C. nigrivittatus, C. capucinus,* and *Hapalemur griseus* (Daegling and Grine 1999) are said to reveal that "crushing and grinding" facets have a greater proportion of pits, whereas "shearing" facets have a greater number of striations (Gordon 1982, 1984; Grine 1986; Krueger et al. 2008; Teaford 1985, 1986; Teaford and Walker 1984). Importantly, these differences are not absolute: striations are found on "crushing" facets and pits are found on "shearing" facets, albeit in smaller numbers, suggesting that either microwear features are not simple readouts of jaw movements, or there is a wider range of jaw movement during occlusion than commonly assumed. Clearly, ascribing shearing, crushing, and grinding functions to specific tooth facets requires data on the direction of relative tooth movement during occlusion, along with methods for measuring, inferring or modeling the orientation of the bite force.

In in vivo studies, the time during the gape cycle when these occlusal interactions occur is the *intercuspal phase*. Hiiemäe et al. (1995: 232–233) defined an intercuspal period (IP) as the time between "End close (EC): the first most closed position for the lower jaw in each cycle" and "[f]irst open (IO): the frame marking the start of consistent downward (opening) jaw movement." However, noting that "[l]ow-amplitude opening and closing may occur within IP" (Hiiemäe et al. 1995), and that "[t]he time at which the teeth actually reached and left **centric occlusion** is difficult to determine from lateral projection cinefluorographs," they arbitrarily designated "marker positions within 0.5 mm of maximum closure/**centric occlusion**" as within intercuspal range and the intercuspal period (p. 231) (**bold** font added to indicate inferred variables). Eschewing arbitrary definitions of the start and end of intercuspal phase, Orsbon et al. (2018) defined the *intercuspal phase* as the time when the planes through the cusp tips of the upper and lower molars intersect, making the definition independent of the VK phases. Hence, the intercuspal phase is not interposed *between* slow-close and slow-open, but overlaps the end of (slow) close and start of (slow-open), which are separated by minimum gape.

Application of this definition focuses inference of occlusal kinematics to the spatial resolution (microns) needed to test hypotheses about relative movements of tooth cusps. The recent development of occlusal fingerprinting analysis (OFA), which uses high-resolution imaging to visualize and quantify the interactions between the geometries of the occlusal surfaces of upper and lower teeth (Kullmer et al. 2009), promises significant advances in occlusal analysis. OFA methods have been shown to accurately predict the position of wear facets produced by jaw movements in an ex vivo experimental environment (Kullmer et al. 2012), and have been applied to the fossil record (von Koenigswald et al. 2013; Schultz and Martin 2014). As yet, however, the accuracy and precision with which OFA can predict jaw movements have not been tested in vivo.

20.2.4 The Functional Significance of Phase II of the Power Stroke

Phase II of the power stroke is the period after minimum gape and prior to the loss of tooth–tooth or tooth–food–tooth contact when the jaw is moving down, medially, and slightly anteriorly. The functional significance of Phase II has been debated. Crompton and Hiiemäe (1970) noted that upward components of bite force cannot be applied between the teeth when the teeth and jaws are moving downward during Phase II of the power stroke, although they hypothesized that it might be possible, but inefficient, through complex recruitment of jaw elevator and depressor muscles. Kay and Hiiemäe (1973) later suggested that a grinding effect could "result from simple 'drag' between two surfaces held rather than forced together" (p. 54), presumably through some combination of friction and wet adhesion. Hiiemäe and Crompton (1985) later suggested that, although EMG activity in macaques ceases prior to centric occlusion, it takes 50–75 ms for the force to decline so there may be residual muscle force being generated after centric occlusion [see also (Byrd and Garthwaite 1981; Luschei and Goodwin 1974)]. Wall et al. (2002) later used the relative timing of EMG and jaw kinematics to suggest that bite forces are also very low after minimum gape in *Papio.*

Some indication of the timing of bite force generation can be obtained from bone strain data from the mandibular corpus. Hylander (1986) showed that the timing and magnitude of mandibular corpus (especially compressive) bone strain is highly correlated with vertical components of bite force during isometric transducer biting. However, he pointed out that this relationship between corpus bone strain and bite force could not simply be extrapolated to mastication, during which the mandible is subject to multiple and changing loading and deformation regimes (Hylander 1986).

Hylander et al. (1987) presented simultaneous data on corpus bone strain and jaw kinematics (lateral projection cineradiography at 90 fps) to argue that, in *Macaca,* because peak principal compressive strain in the mandibular corpus precedes minimum jaw gape by an average of 15–50 ms, bite force must drop to very low levels before jaw opening, and by inference, before Phase II of the power stroke (Hylander et al. 1987). Importantly, however, Hylander et al.'s (1987) data included some gape cycles with strain profiles indicative of residual mandibular loading after the first appearance of maximum intercuspation of the teeth, along with strain orientation data suggestive of the increased importance of lateral transverse bending of the corpus after peak corpus strain. Together with EMG data suggesting that the balancing-side deep masseter might be generating transversely oriented components of bite force after minimum gape, Hylander et al.'s strain and kinematic data suggest that in some cycles there may be laterally directed components of bite reaction force acting on the teeth during Phase II.

Our own data for capuchins are presented in Fig. 20.2 and Table 20.1, along with data for one macaque, the results from which closely resemble those presented by Hylander et al. (1987). Figure 20.2a shows the average profile of maximum principal strain in the lateral aspect of the mandibular corpus during chewing of two or three different foods aligned relative to minimum gape. As reported by Hylander et al., the average timing of maximum principal strain precedes minimum gape by 13–41 ms, depending on the foods. However, it is noteworthy that, as noted by Hylander et al. for macaques, there is still significant bone strain in the lateral aspects of the corpus after minimum gape, suggesting that even as the jaw moves down and medial, bite force may still be generated. Hylander et al. (1987) also identified some chews in which peak strains occur after minimum gape: our data on this in capuchins are shown in Fig. 20.2b. Instead of averaging strain profiles across all chews, Fig. 20.2b presents the proportion of cycles that show peak strain in the corpus at different times relative to minimum gape. Not only does the average strain profile reveal the persistence of principal strain after minimum gape (Fig. 20.2a), but there are a significant number of cycles that show peak strain after minimum gape (Fig. 20.2b).

Together with the microwear data summarized above, our data and those of Hylander et al. (1987) suggest that bite force may well be generated after minimum gape, at the end of the intercuspal phase. Experimental data combining high-resolution jaw kinematics, EMG, OFA, with mandibular bone strain or, better, more direct measures of occlusal bite force, are needed to better address the question of the functional significance of Phase II of the power stroke.

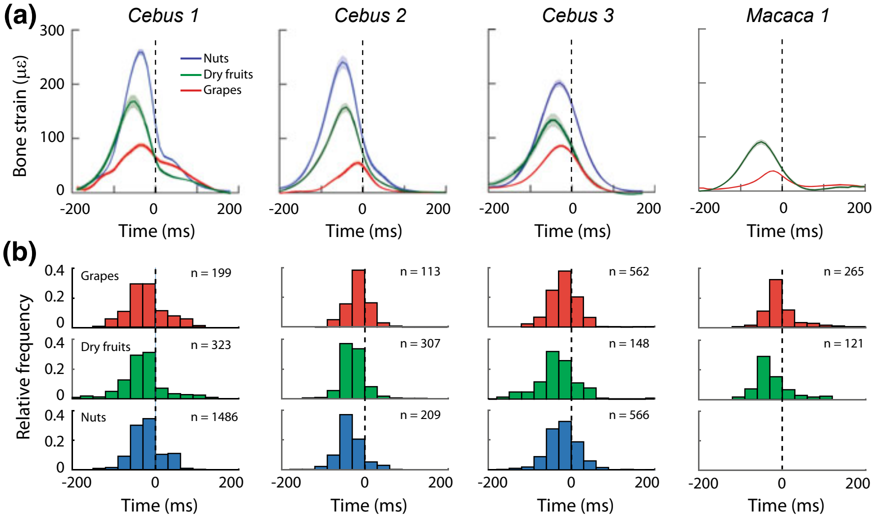

Fig. 20.2 Timing of maximum principal strain in the lateral aspect of the mandibular corpus relative to minimum gape for three *Cebus* and one *Macaca*. Data collected by the authors. Vertical dashed lines at 0 ms represent the time of minimum gape. **a** Plots of the mean ± SE of maximum principal strain during gape cycles of chewing of grapes, dry fruits, and nuts. **b** Histograms of the timing of peak bone strain with respect to the timing of minimum gape for each of the types of foods. The portions of the distributions to the left of the vertical dashed line represent cycles when peak bone strains occurred before minimum gape; those to the right represent cycles when peak bone strain occurred after minimum gape. If minimum gape is taken to be centric occlusion, corpus strains after minimum gape must occur during opening

Table 20.1 Timing of peak strain with respect to minimum gape in milliseconds (ms). Data are presented as mean ±SD. Sample sizes are in parenthesis

Individual	Time of peak strain with respect to minimum gape (in ms)		
	Grapes	Dry fruits	Nuts
Cebus 1	−26.0 ± 45.4 (199)	−37.1 ± 59.2 (323)	−26.7 ± 38.9 (1486)
Cebus 2	−19.8 ± 38.9 (113)	−31.3 ± 33.6 (307)	−40.1 ± 34.2 (209)
Cebus 3	−23.7 ± 41.6 (562)	−41.1 ± 52.1 (148)	−24.4 ± 49.4 (566)
Macaca 1	−13.1 ± 52.3 (265)	−31.0 ± 41.8 (121)	

20.3 The Fundamental Constraints

There are three fundamental constraints on the ability of primate feeding systems to generate and transmit forces to the bite point, constraints which impose pervasive trade-offs between bite force and gape (Hylander 2013, 2017; Spencer 1995): the sarcomere structure of skeletal muscle imposes a trade-off between muscle fiber length and muscle force, represented by the length–tension curve for sarcomeres and muscle fibers (Gordon et al. 1966) (Fig. 20.3); the primate mandible functions as a third-class lever—the jaw elevator muscle resultant lies between the axis of rotation and the bite point in lateral view—so that, in combination with the length–tension properties of skeletal muscle, jaw depression and elevation are associated with trade-offs between bite force and gape (Hylander 2013, 2017) (Fig. 20.4); the jaw elevator muscle resultant must pass through the triangle of support defined by the two jaw joints and the bite point to avoid putting the TMJ (temporomandibular joint) in tension (Greaves 1978; Spencer 1998, 1999).

20.3.1 The Sarcomere Structure of Skeletal Muscle

The amount of force that a sarcomere produces varies as a function of its length, as described by the length–tension, or length–force curve described for frog muscle by Gordon et al. (1966) (Fig. 20.2). In parallel fibered muscles, consisting of many sarcomeres in series, the length–tension curve of the sarcomere describes the length–tension curve of the whole muscle fairly accurately. The same relationship holds in pennate muscles, like the jaw elevator muscles of primates, except that the ascending and descending limbs of the length–tension curve are steeper; i.e., the muscle is much stiffer (McMahon 1984; Ross et al. 2009b). Hence, in pennate muscles, increases and decreases in length are accompanied by faster increases and decreases in the active force generating capacity of the muscle, and increases in length result in rapid increases in the passive tension developed by the sarcomeres.

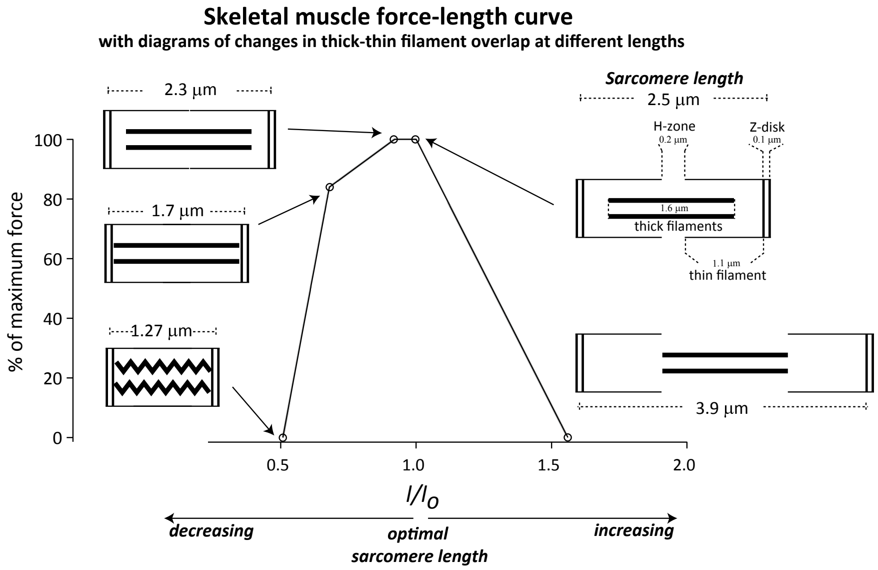

Fig. 20.3 Diagram illustrating relationships between length-related changes in overlap of thick and thin filaments in the sarcomeres of skeletal muscles and the associated length-related changes in force generation potential (redrawn from Porro et al. (2011), based on Herzog (2007)). Force is expressed as a % of maximum. l/l_o = sarcomere length as a proportion of optimal. There is an optimal length for muscle force generation capability: stretching or shortening jaw muscles away from this optimal part of the length–force curve decreases their force generation potential. Because of these length–force properties of the sarcomeres, jaw gape affects the amount of force that the jaw muscles can produce (see Fig. 20.4)

20.3.2 The Mandible Is a Third-Class Lever

The way in which the length–tension relationship of skeletal muscle impacts primate feeding performance is impacted by the location of the jaw elevator muscle force resultant between the jaw joints and axis of rotation posteriorly and the bite point anteriorly. The functional consequence of this for the primate feeding system is that, because the muscles are near the peak of their length–tension curve at only a few degrees or millimeters of gape (Anapol and Herring 1989), increases in gape decrease the amount of force that the muscles can generate. Hence, there is a force–gape trade-off in primate jaw elevator muscles (Hylander 2013, 2017): primates attempting to generate bite forces at large gapes—eating large food objects—cannot generate as much bite force as they can at smaller gapes. One way to alleviate the length–tension trade-off inherent in skeletal muscle is to increase the mechanical advantage of the muscle, the ratio of its lever arm to the load arm of the bite point. However, when mechanical advantage is improved through rostral displacement of the jaw elevator muscles, the maximum possible gape distance is decreased (Fig. 20.4). Thus, selec-

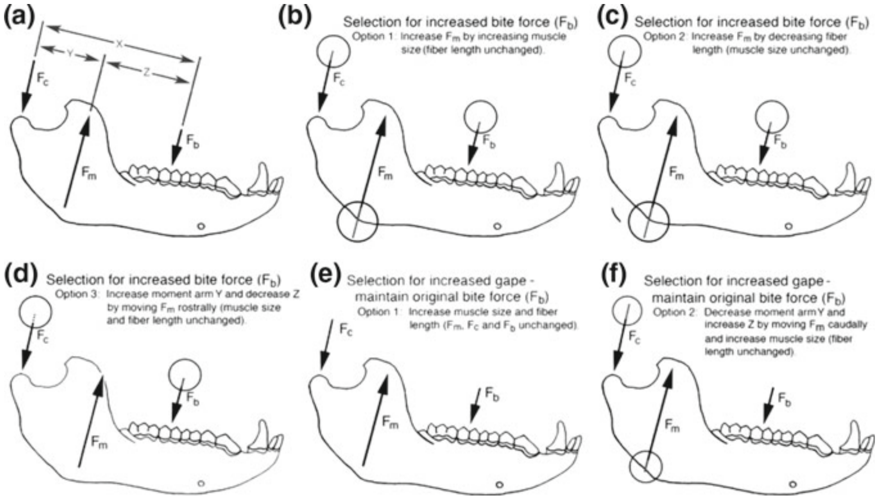

Fig. 20.4 Diagram illustrating the consequences of the fundamental properties of primate feeding systems that constrain feeding performance: the jaw elevator muscles and mandible form a third-class lever, and vertebrate skeletal muscle manifests a length–tension curve. From Hylander (2017) (with permission)

tion for improved mechanical advantage has to trade off with large gape requirements imposed by feeding behaviors, such as gouging, and social behaviors such as threat displays.

20.3.3 *The Jaw Elevator Muscle Resultant Must Lie Within the "Triangle of Support"*

In a third-class lever model of the primate jaw, all other things being equal, the mechanical advantage of the jaw muscles is increased by moving the bite point closer to, and the muscle resultant further from, the jaw joints. This should encourage selection to move the distal end of the tooth row back toward the jaw joints and the jaw elevator muscles rostrally. However, there is evidence that primate jaw elevator muscles are recruited so that the TMJs are not subjected to tensile (distractive) forces (Greaves 1978). In order to achieve this, the resultant of the jaw elevator muscle forces must lie within a "triangle of support", with vertices at the two TMJs and the bite point, in order to keep both jaw joints in compression. In order to maintain the jaw elevator muscle resultant within the "triangle of support", the balancing-side muscle force amplitudes must be reduced during biting at the most distal (posterior) extremes of the tooth row. Reduction in balancing-side muscle activity moves the muscle resultant toward the working side and into the "triangle of support" but reduces the maximum bite force that can be generated at non-midline—most—bite points. Morphological and experimental evidence corroborates this hypothesis in primates (Spencer 1998, 1999), suggesting that the need to keep the TMJs in compression constrains bite force magnitudes in primates during biting and chewing (Ledogar et al. 2016; Smith et al. 2015b).

20.4 The Force–Gape Trade-off, the Axis of Jaw Rotation, and Muscle Architecture During Feeding

The precise impact of the first two fundamental constraints—the length–force relationship of skeletal muscle and the third-class lever arrangement of primate jaw elevator muscles—on the force–gape trade-off in primate feeding performance is dependent on two important factors: the location of the axis of rotation of the mandible (Carlson 1977; Hylander 1978; Smith 1985) and the static and dynamic muscle architecture of the jaw elevators (Taylor et al. 2018).

20.4.1 The Axis of Rotation

During chewing in primates the axis of rotation of the mandible (AoR) lies inferior to the temporomandibular joint (TMJ) so that jaw depression and elevation are accompanied by anterior and posterior translation of the mandibular condyles (Bennett 1908; Gallo et al. 1997, 2000; Iriarte-Diaz et al. 2017; Wall 1999). Moreover, during chewing the AoR is neither static nor orthogonal to the sagittal planes, reflecting the changing magnitudes of lateral jaw movement during the chewing cycle (Fig. 20.5). It has been argued that locating the axis of rotation of the mandible below rather than at the TMJ ameliorates the detrimental effects of jaw depression on the force generating capacity of the masseter, in part because this decreases the amount of muscle strain in the masseter and in part because it improves muscle moment arms during chewing (Carlson 1977; Hylander 2006; Weijs et al. 1989). To test this idea, Carlson (1977) calculated the relationships between “functional gape angle” and masseter length and moment arm both in a theoretical location through the TMJ as well as with the AoR in its actual location—inferior and posterior to the TMJ. He showed that, compared with an axis located at the TMJ, the actual location of the AoR does ameliorate the decreases in masseter moment arm during jaw opening. It also reduces the amount of masseter muscle sarcomere stretch associated with jaw depression, which, if masseter muscle sarcomeres are at their optimal length at centric occlusion, would ameliorate the reductions in masseter muscle force associated with jaw opening. In other words, the positioning of the AoR means that jaw opening is associated with smaller decreases in the torque-generating capacity of the masseter, with the benefits due to reduced sarcomere stretch being greater than those due to reduced decreases in moment arms.

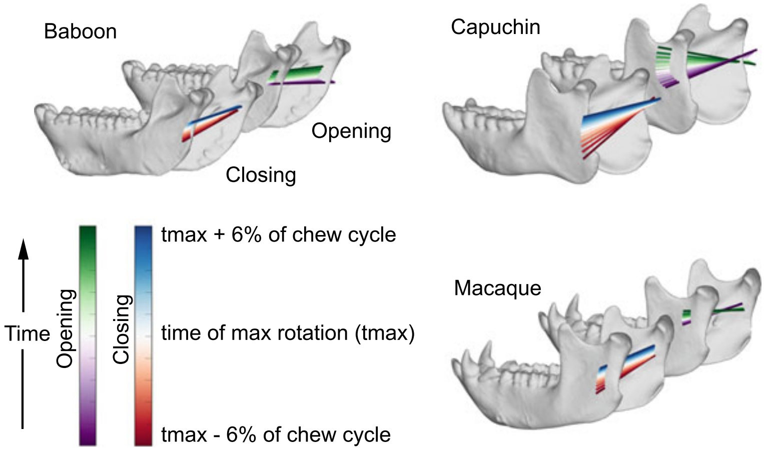

Fig. 20.5 Changes in the mean position and orientation of the helical axis (HA) during the opening and closing phases of chewing cycles in three species of primates. Orientations of HA from left chews were inverted around the sagittal plane, so all chews are represented as right chews. The different locations of the HA during the opening and closing phases of the gape cycle are represented by different colored lines: purple to green during the opening phase and red to blue during the closing phase. The timing of maximum rotation in both opening and closing phases is indicated by the white lines. Modified from Iriarte-Diaz et al. (2017)

In a study of rabbits, Weijs et al. (1989) modeled the effects of AoR location on jaw elevator muscle forces, measured the magnitude of passive elastic forces resisting jaw depression with the AoR in its normal position, and compared them with those at a range of positions further from and closer to the TMJ. They concluded that the location of the AoR "is as low as necessary to minimize the passive forces in the jaw-closing muscles" while simultaneously allowing "maximal active forces to be generated over a large range of gapes" (Weijs et al. 1989, p. 145). The benefits of AoR location for energetics and motor control remain to be understood.

Modeling of masseter function during symmetrical jaw opening raises important questions about the impact of AoR location on the lever arms and muscle stretch of the jaw elevator muscles in the static and dynamic situations in vivo. How do these effects differ across the three jaw elevator muscles (temporalis, masseter, and medial pterygoid) during mastication? To address these questions Iriarte-Diaz et al. (2017) used 3D jaw kinematic data to estimate the location of the instantaneous helical axis (IHA) in 7,320 gape cycles by eight individuals from three species of primates (*Macaca mulatta* [n = 3], *Papio anubis* [2], and *Cebus/Sapajus apella* [3]) and to quantify the impact of IHA location on whole muscle–tendon strain and muscle lever arms of three segments each in the temporalis, masseter, and medial pterygoid muscles. Lever arms were calculated both about the TMJ, the traditional point for calculation of moment arms in static analyses of the jaw, and the IHA, about which the muscles generate their dynamic torques during jaw movement.

Muscle strain during chewing varied between muscles, with medial pterygoid showing the least strain, masseter showing the most, and temporalis in macaques experiencing muscle strains similar to or larger than those in the masseter (Fig. 20.6). In vivo muscle strains in the masseter and medial pterygoid were similar to or lower than those calculated with a theoretical AoR location through the TMJ, but those in the temporalis were higher—actual AoR locations do decrease strain in the masseter and medial pterygoid muscles compared to a hinge-joint condition (Carlson 1977; Hylander 1978), but they increase strain in the temporalis, the largest of the jaw elevator muscles in primates.

Lever arm lengths during chewing vary within muscles. Anterior segments of masseter, medial pterygoid, and temporalis experience fairly constant or increased moment arms during chewing, while the posterior and intermediate muscle segments experience decreased moment arms about the TMJ. In contrast, if jaw elevation and depression occurred about an axis through the TMJ, almost all muscle regions would experience *decreases* in moment arms. The largest difference between actual and theoretical moment arms is seen in anterior temporalis, in which the *actual* location of the helical axis (HA) *increases* the moment arm of the jaw elevator muscles. Together these results suggest that the location of the AoR can improve muscle torques, especially those of the temporalis, in static biting conditions.

When muscle moment arms are calculated about the HA—providing insight into their contribution to jaw elevation movements—moment arms tend to decrease during jaw opening then increase during closing. Comparisons with a theoretical axis through the TMJ suggest that the largest effects of AoR location are seen in the posterior temporalis: the *actual* location of the AoR improves the dynamic moment arms of the posterior temporalis about the AoR, improving its ability to rotate the mandible during jaw elevation. As predicted by Carlson, Iriarte-Diaz et al. found AoR location has its largest effects on moment arms at the largest gapes.

The importance of mechanical advantage for primate feeding performance suggested by these experimental approaches is supported by a number of studies showing associations between diet or feeding behavior and mechanical advantage. Mechanical advantage of the masseter and the attachment areas for masseter and medial pterygoid muscles are larger in the more folivorous colobines than in the less folivorous cercopithecines (Ravosa 1996a, 1990). Compared to other macaques, *Macaca fuscata* exhibits a more anteriorly placed masseter muscle and a tougher, harder diet (Antón 1996). Seed eating Asian colobines (*Presbytis rubicunda* and *Trachypithecus phayrei*) have better jaw muscle mechanical advantage than species that rarely exploit seeds (*Presbytis comata, Trachypithecus obscurus*, and *Semnopithecus vetulus*) (Koyabu and Endo 2010). Tufted capuchins have larger jaw muscles with better mechanical advantage than other capuchins, facilitating feeding on large, hard objects (Taylor and Vinyard 2009; Wright 2005). Among hominins, Inuit generate relatively high bite forces and have enlarged muscle attachment areas and better jaw mechanical advantage than other native Americans (Hylander 1972). Moreover, the ability to generate and transmit force to the bite point is impacted by gape, and gape is also related to diet and feeding behavior. Anteroposteriorly long TMJs are linked to wide gape tree gouging in callitrichids and *Phaner* (Vinyard et al. 2003), to wide gape

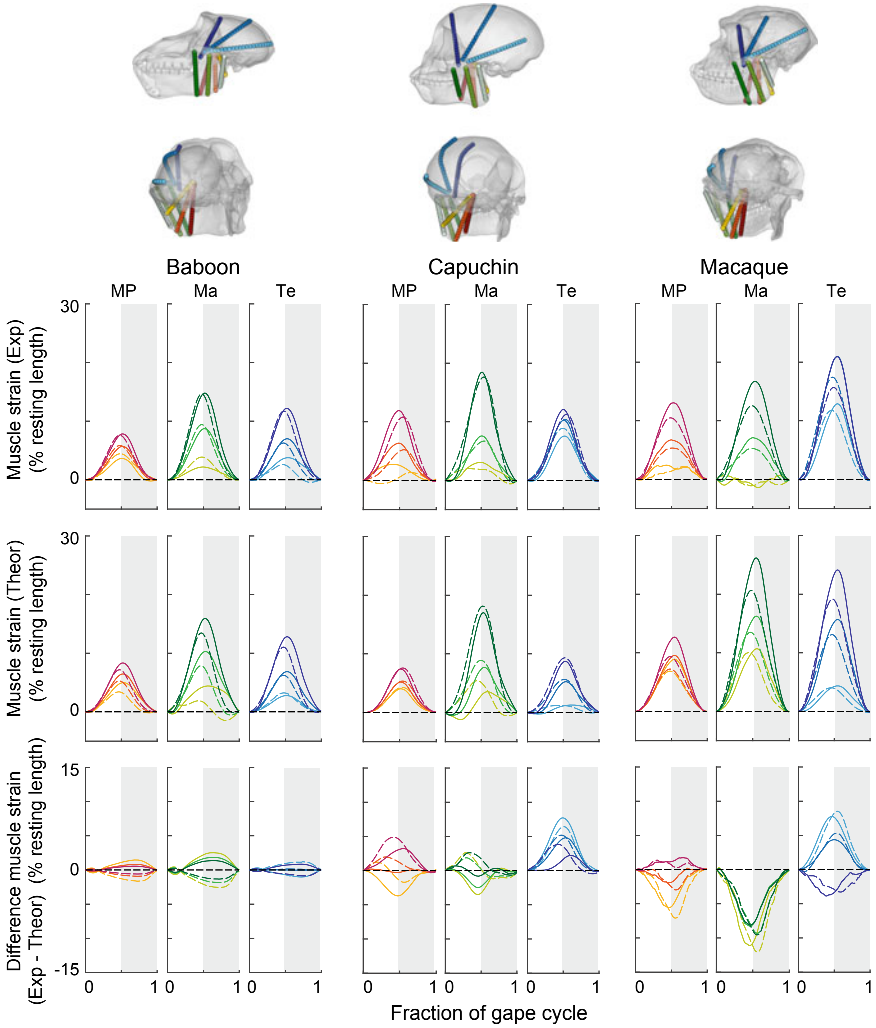

Fig. 20.6 Muscle strains (changes in total muscle length as a percentage of resting length) of the major masticatory muscles throughout a standardized gape cycle for a baboon, a capuchin, and a macaque. The colors of the traces match the segments of the muscles indicated in the diagrams at the top. Segments of the medial pterygoid (MP) are identified by shades of red; segments of the masseter (Ma) by shades of green; and segments of the temporalis (Te) by shades of blue. For each muscle, the anterior, middle, and posterior segments are identified by dark, intermediate, and lighter colors, respectively. Muscles of the balancing and working side are indicated by solid and dashed lines, respectively. The plotted data are the experimentally observed data (Exp), the theoretical, hinge-joint condition data (Theor), and the difference between them (Exp−Theor). Gray bars indicate the jaw-closing phase of the gape cycle. Modified from Iriarte-Diaz et al. (2017)

vocalization in *Alouatta*, to wide gape seed predation in pitheciines (Terhune 2011), and to other adaptations for gape in great apes (Terhune 2011). Callitrichid mandible shapes also facilitate large gapes and their jaw muscles are designed for the extensive excursion required for gouging at large gapes (Hogg et al. 2011; Vinyard and Ryan 2006; Vinyard et al. 2003).

Together these data support the hypothesis that external measures of skull morphology might more strongly reflect variation in the ability of the feeding system to *generate* force and transmit it to the bite point, rather than in its ability to *resist* internal forces (stresses) (Iriarte-Diaz et al. 2011, 2012; Ross 2016; Ross and Iriarte-Diaz 2014). In capuchins, strain regimes in the corpus vary most across different behaviors (incisor bites, canine bites, premolar bites, chews) and strain magnitudes associated with premolar, molar, and incisor biting are larger than those recorded during mastication, suggesting that performance of these behaviors might be an important determinant of skull design (Ross et al. 2016). Better data are needed on relationships between biting performance and feeding system morphology in primates.

20.4.2 Muscle Architecture: Statics and Dynamics

The precise impact of whole muscle–tendon strain on force generation is also dependent on muscle architecture dynamics, the changes in muscle fiber orientation at different gapes (Azizi et al. 2008). Static measures of muscle architecture are accumulating for a wide range of primates (Taylor and Vinyard 2004, 2008, 2009; Taylor et al. 2008, 2015), but the complexities and subtleties of muscle architecture dynamics and their effects on muscle force and shortening velocity are just now being investigated in primates (Orsbon et al. 2018; Laird et al. 2019). XROMM-based measurements of muscle architecture dynamics during primate feeding promise to significantly improve our understanding of the ways that the fundamental constraints on primate feeding systems affect feeding performance.

20.5 Primate Feeding Systems Are Not Built for Speed

In the 1970s several workers advanced the argument that aspects of feeding behavior related to short-term food intake rate (a timescale of seconds and hours) are driven by the requirements of overall metabolic rate. These arguments developed in the context of attempts to link scaling of tooth surface area to scaling of metabolic rate via estimates of the volume of food processed per chew (V_c). Pilbeam and Gould argued that if V_c scales with dental occlusal area (A_m) as $V_c \; \alpha \; A_m^{1.0}$, and A_m scales relative to body mass as $A_m \; \alpha \; M_b^{\approx 0.75}$, then V_c would increase isometrically with basal metabolic rate ($V_c \; \alpha \; M_b^{\approx 0.75}$), and metabolic requirements would be satisfied by scaling of per-chew food processing rate, $R_c = V_c / T_c$ (Gould 1975; Pilbeam and Gould 1974). Kay noted that if primate molar areas scale isometrically with body mass as $A_m \alpha M_b^{\approx 0.67}$ (Gingerich et al. 1982; Kay 1975, 1985; Vinyard and Hanna 2005) and $V_c \alpha A_m^{1.0}$, then V_c would not keep up with basal metabolic rate and larger primates would run into a metabolic crisis (Fortelius 1985; Kay 1975). He suggested that this problem could be alleviated and larger animals meet their size-related energy requirements if either T_f increased and/or T_c decreased (Kay 1985). In fact, his limited data set suggested that T_c actually *increases* with body size, so feeding time must increase accordingly to compensate. In contrast to Kay's hypothesis, Fortelius (1985) argued that the food bolus is three-, and not two-dimensional, so that V_c increases isometrically with body *mass*—$V_c \alpha M_b^{1.0}$—so mammals can meet their food intake requirements on a per-chew basis if chew cycle time scales as $T_c \alpha M_b^{0.25}$.

Over the last decade, experimental, scaling, and modeling studies reviewed here suggest that chewing speed is not driven by metabolic needs, but by the requirements of efficient and controlled bite force production (Ross et al. 2017, 2009a). Excluding foraging and extraoral processing—i.e., once the feeding system is recruited—short-term food intake rate is proportional to the volume of food ingested into the oral cavity (V_b), and inversely proportional to ingestion time (T_i) and $N_{chew} * T_c$, i.e., gape cycle time (T_c) multiplied by the number of chewing cycles (N_{chew}) prior to final swallow. For a given food item, $N_{chew} * T_c$ yields chewing sequence duration (T_{seq}), and $T_i + T_{seq}$ multiplied by the number of food items (N_s) over a day determines overall feeding time (T_f). Hence, assuming constant energetic concentration in the food, short-term energy acquisition rate (*E/T*) is as follows:

$$\frac{E}{T} = \frac{V_b}{(T_i + (T_c * N_{chew})) * N_s} = \frac{V_b}{T_f} \tag{20.1}$$

Among anthropoids and folivorous strepsirrhines, maximum ingested bite volume (an estimate of V_b) scales with negative allometry (Perry et al. 2015), and in catarrhines (at least) maximum gape distance (L_g) scales with negative allometry against jaw length (L_j) ($L_g \alpha L_j^{.79}$, 95% CI exclude 1.0) (data from Hylander 2013). This suggests that larger anthropoids and folivorous strepsirrhines emphasize higher bite forces and more efficient bite force production more than the larger gapes that would facilitate larger V_b (Hylander 2013, 2017; Perry et al. 2015). The negative allometry of V_b raises the specter of an energetic crisis in larger primates and, indeed, female adult mountain gorillas eating low quality forage can spend nearly 80% of the day feeding (Watts 1988).

But is there really an energetic crisis in large bodied primates, and does it demand faster chewing speeds? Here, we address these questions by examining scaling of the terms in the denominator of Eq. (20.1) for which data are available— N_{chew}, T_f, and T_c. One way to compensate for negative allometry of ingested bite size is to decrease chewing investment (N_{chew}), i.e., chew food less. The problem with this solution is that food has to be chewed enough to cross the oropharynx safely, to fit into the esophagus, and to facilitate efficient digestion (Alexander 1999; Prinz and Lucas 1997; Virot et al. 2017). Common sense and experimental data from humans suggest that avoiding choking is the most important of these factors: chewing investment is proximally (sensorily) constrained by the number of chews needed to produce a swallow-safe bolus (Prinz and Lucas 1997), and not by the need to feed quickly. In captive primates across a wide range of body sizes the number of chewing cycles per feeding sequence has a modal value of ten and an average value of around 15 chews (Ross et al. 2009a; Virot et al. 2017) suggesting that chewing investment is constrained by the requirements of processing the food bolus for swallowing, not by some size-related crisis in metabolic needs. That said, mathematical models of the ideal number of chews yield higher estimates than these empirical estimates (Alexander 1999), suggesting a disconnect between theory and data that deserves attention.

Negative allometry of V_b could also be compensated for by increasing daily feeding time (T_f), presumably at the expense of other activities, such as predator avoidance and social interactions. Phylogenetically informed linear estimates of T_f scaling in primates include $T_f \ \alpha \ M_b^{0.24}$ (Organ et al. 2011) and $T_f \ \alpha \ M_b^{0.18\pm0.1}$ (mean ± 95% CI) (Ross et al. 2012b). Of course, some of the increase in daily feeding time is driven by increases in T_c, which increases with body mass $\alpha \ M_b^{0.12\pm0.06}$ (mean ± 95% CI). The scaling exponents of T_{c} and T_f overlap significantly and the exponent of T_f lies at the upper end of the CI for T_c. This suggests that T_f scaling in primates is not just a function of slower chewing, but of greater numbers of food items and/or longer ingestion times (Ross et al. 2009a, 2012b), but it also suggests that any size-related changes in metabolic needs are not driving feeding times up much faster than dictated by chew cycle times. Indeed, curvilinear regression of T_f on body mass, arguably more appropriate (Packard 2017; Ross et al. 2009a), reveals that increases in body size from 0.1 to 20 kg are associated with increases in feeding time from 10 to around 50% of daily activity budget, but that increases in T_f at body masses above 20 kg are much less substantial. If larger anthropoids are confronting a pervasive energetic crisis it is not reflected in increases in feeding times as rapid as those seen in smaller primates and the drivers of daily feeding time are more likely to be related to overall dietary and digestion strategies (Clauss et al. 2007, 2008).

If overall metabolic rate is not responsible, what does drive T_c scaling in primates? Ross et al. (2009b) attempted to predict the scaling of primate T_c using a mathematical model of primate feeding system function, named the *Spring Model* because it modeled the skeletal muscles that drive jaw oscillations using spring constants and scaling coefficients of jaw elevator muscle physiological cross-sectional areas (PCSAs). The *Spring Model* predicted scaling of T_c relative to L_j fairly well (Ross et al. 2009b) until accurate rotational inertia values derived from CT scans of primate mandibles were included (Ross et al. 2017). With these new data the model actually performed worse, suggesting that scaling of mandible morphology has little effect on the scaling of chew cycle period. Inaccurate jaw elevator PCSAs might explain the poor performance of the model: jaw elevator PCSA scales isometrically across prosimians and anthropoids, but with negative allometry across platyrrhines and positive allometry across hominoids (Perry and Wall 2008; Taylor et al. 2015; Taylor and Vinyard 2013). However, substitution of any of the published scaling coefficients into the *Spring Model* makes little difference: the model predicts much greater increases in T_c with decreasing L_j than actually observed: larger primates chew more quickly and/or smaller primates more slowly than predicted by the *Spring Model*.

One explanation for the slower chewing speeds of smaller primates than predicted by the *Spring Model* is that the jaw system is heavily damped by the properties of the muscles that drive it. This effect is accentuated at the smallest sizes, where inertial properties of oscillating musculoskeletal systems become less important than the muscular properties (Hooper 2012; Turvey et al. 1988). This would also explain why chew cycle periods are longer than step cycle periods at equivalent jaw/limb lengths: the jaws in feeding systems oscillate more slowly than limbs of similar lengths in locomotor systems because they are heavily damped by the properties of the chewing muscles (Fig. 20.7) (Ross et al. 2017). This reflects the negligible importance of mass-related momentum effects and the greater importance of force and displacement control in the primate feeding system, in contrast with the importance of speed in primate locomotion systems. Thus, we conclude that whole organism metabolic rates are not important drivers of chewing frequency or chew investment (number of chews per gram of food) in primates. More proximate metabolic constraints preventing jaw muscle fatigue may well play an important role (Wall et al. 2013), but these operate at spatial and temporal scales well below those of the organism overall.

Recently, Virot et al. (2017) have pointed out that T_c scaling[1] may best be explained not with reference to a “single functional relation”, but by multiple factors determining “range of frequencies where animals can chew their food” (p. 2). Based on the Spring Model, they propose that muscle mechanics constrain T_c to scale to M_b with a slope below 1/3—$T_c \; \alpha \; M_b^{<0.33}$—with a lower limit to cycle duration of 1/8 s, as predicted by maximum sarcomere shortening velocity. Data on jaw kinematics and muscle architecture dynamics in small primates are needed to address this hypothesis, but this could explain why smaller primates have longer chew cycle periods than predicted by the Spring Model. They also propose that the lower limit of chew cycle period scaling is driven by the rate at which saliva fills the oral cavity. They hypothesize that saliva fills the oral cavity during chewing at a rate that scales with body mass $\alpha \; M_b^{5/6}$, and that the food bolus has to be broken down to small enough fragments to pass through the esophageal sphincter before saliva fills the oral cavity. Given isometric scaling of both the oral cavity (V_{oral}) and ingested bolus volume (V_b), and a constant number of chews, chew cycle period would need to scale to M_b with a slope greater than 1/6 (>0.167) in order for mammals to break the food down before the saliva+food bolus filled the oral cavity.

In contrast with the exponent range of $0.17 < b < 0.33$ predicted by Virot et al., the primate data suggest that $0.06 < b < 0.18$ (Ross et al. 2012a, b). Primate chew cycle periods certainly increase slower than the 0.33 limit imposed by muscle mechanics, but they also increase more slowly than predicted by the saliva limit hypothesis. We suspect that this is because primates sort saliva and swallow-ready particles from the rest of the bolus and swallow them—intercalated swallows—during chewing sequences (Inokuchi et al. 2014; Hylander et al. 1987), so that they are not as con-

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[1] Virot et al. discuss chew frequency, $1/T_c$. We invert their models to match the conventions in this paper, which discusses T_c.

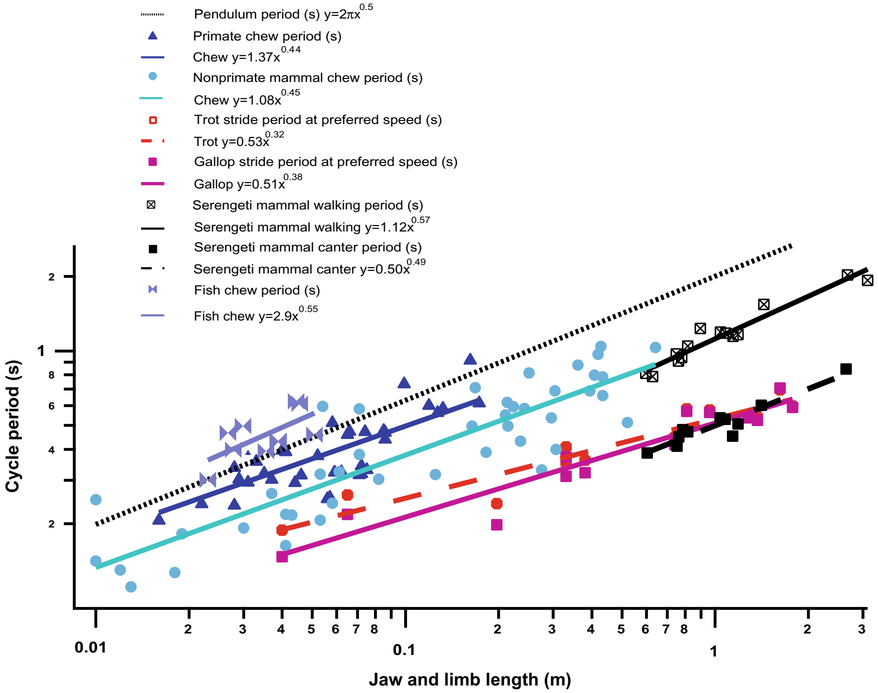

Fig. 20.7 Bivariate plot of chew cycle period in mammals and fish, and of locomotion step cycle period in mammals. ▬ pendulum period y = $2\pi x^2$; ☒ Serengeti mammal walking, ▬ y = $1.12x^{0.57}$; ■ Serengeti mammal canter, - - - $0.50x^{0.49}$; ▲ primates; dark blue line, primate chew cycle period scaling; light blue circles, non-primate mammal chew cycles; ▬ non-primate chew cycle period scaling; ⧓, fish chewing; ▬ fish chew cycle scaling $0.29x^{0.55}$; ■ gallop stride period at preferred speed, ▬ $0.51x^{0.38}$; □ trot stride period at preferred speed; ▪▪▪▪ $0.53x^{0.32}$. From Ross et al. (2017)

strained by saliva flow rate as Virot et al. propose. Data on flow rates and frequency of intercalated swallows in primates are needed to confirm this hypothesis.

Hence, we conclude that primates are not time-constrained during feeding, and that maximizing short-term food intake rate is not an important design criterion of their feeding systems. Primate chew cycle periods are longer than step cycle periods of limbs with similar lengths, suggesting that feeding systems are more heavily damped, reflecting the importance of displacement and force control in primate feeding systems rather than speed and energetic efficiency. Primate gape distances are driven by jaw length and canine overlap, reflecting the impact of social interactions on feeding system morphology. Together these data suggest that chewing rate need not be closely yoked to metabolic rate in order to meet the overall metabolic demands of the body.

20.6 Jaw Kinematics

Mandible kinematics are related to most feeding system performance variables. Relative tooth movements interact with tooth morphology to facilitate food breakdown during occlusion. Condylar movements relative to the mandibular fossa interact with muscle activity to drive patterns of stress in the joint during feeding. Movements of the mandibular attachments of the jaw and hyolingual muscles alter their orientations, lengths, and lever arms throughout the gape cycle, interacting with muscle activity patterns to drive bite force and TMJ reaction forces. And jaw kinematics impact the orientations of the muscle, bite, and joint reaction forces acting on the mandible, and hence internal forces (stresses) in the mandible during feeding. Data on jaw kinematics are therefore central to testing many hypotheses regarding the design of the primate feeding system.

20.6.1 Jaw Kinematics and the Temporal Structure of the Gape Cycle

Using jaw kinematic variables to study the temporal structure of the gape cycle provides insight into the control mechanisms in primate chewing and their likely optimality criteria. The vast majority of variation in feeding sequence duration (T_{seq}) is driven by variation in n_{chew} (Ross et al. 2009a, b; Reed and Ross 2010) because variation in T_c is low in mammals, including primates; i.e., mammals chew very rhythmically (Ross et al. 2007b). Relatively high rhythmicity is also found in the locomotor systems of mammals and birds, suggesting a relationship between high rhythmicity and high metabolic rates (Ross et al. 2012a). High rhythmicity might be more energetically efficient, lowering overall energetic costs during locomotion, and postponing fatigue in the feeding systems of highly active animals (Ross et al. 2012).[2]

Rhythmicity also has advantages for motor control, increasing predictability and stability in the face of changing external conditions, which in the feeding system may lower rates of tooth wear and breakage (Ross et al. 2007b, 2012a). The distribution of variance in T_c within and between species and individuals provides insight into the mechanisms underlying high rhythmicity in primate chewing. After size-related variation in T_c nested at the species level (Fig. 20.8), the largest proportion of T_c variance (20%) is distributed between cycles within individual sequences (Iriarte-Diaz et al. 2011; Ross et al. 2012b). This is approximately twice the amount of variance found either between individuals of the same species, or between different chewing sequences, which includes variation elicited by different ingested FMPs (Fig. 20.8). Low levels of variation in T_c associated with variation in ingested FMPs

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[2] Gintof et al. (2010) showed that fish chew with low levels of variation in T_c, similar to those in mammals, possibly because chewing in an aquatic environment imposes constraints on jaw velocity profiles related to intraoral prey manipulation in the absence of a tongue.

seem to contradict the literature documenting effects of variation in food material properties on durations of the chew cycle and its phases, however, detailed studies reveal that FMP effects are mostly concentrated at the beginning of the chewing sequence (Reed and Ross 2010). In capuchins, effects of FMPs on overall chew cycle durations and durations of the constituent phases are minimal by the 15th chew cycle. Average differences in slow-close duration (T_{sc}) between chews on these different food types were significant in only seven out of the first 12 chews, and not significant in later chews (Reed and Ross 2010). One behavioral mechanism contributing to low variance in T_{sc} is rate modulation of bite force: during slow-close, mandibular corpus strain magnitudes—and presumably bite force—are correlated primarily with the rate of loading, rather than with the duration of loading (Ross et al. 2007a; Ravosa et al. 2010). Hence, in capuchins variance in T_{sc} explains the greatest amount of variance in overall cycle duration only for the first 4–6 chews, after which variation in slow-open duration (T_{so}) becomes more important.

A second behavioral mechanism contributing to high rhythmicity appears to be differences in jaw movement velocities. Although Reed and Ross found that effects of FMPs on T_c and phase durations decreased through the feeding sequence, FMP effects on maximum vertical and lateral displacements remained consistent and often significant throughout. These findings confirm the results of studies on humans that food material properties have stronger effects on spatial aspects of jaw kinematics than do geometrical properties of the foods (Foster et al. 2006). In the capuchin study it was concluded that the differences in jaw kinematics during non-SC phases likely reflects differences in patterns of jaw and tongue movement associated with bolus management.

A third behavioral mechanism facilitating high rhythmicity appears to be trade-offs in durations of SO, FO, and FC gape cycle phases. Hiiemäe and Kay (1973) found that T_c did not differ significantly between puncture crush cycles (usually early in a sequence) and chew cycles (later in the sequence) because of trade-offs in durations of the gape cycle phases: in puncture crush cycles the FC phase was relatively longer than in the chews, but the opening phases were relatively shorter. Similar trade-offs in durations of gape cycle phases are also seen in *Eulemur*, *Cebus/Sapajus*, *Chlorocebus,* and *Macaca* (Ross et al. 2010; Ravosa et al. 2010). This is not say that there is no variation in T_c and its constituent phases in primates, but whereas in lepidosaurs increases in T_c are associated with increases in the relative proportion of the cycle made up by SO, in primates variation in T_c is driven more evenly by variation in durations of all the phases of the gape cycle. It seems that low levels of variation in T_c in primates are associated with maintenance of a relatively constant temporal shape of the gape cycle. If trade-offs in phase durations do indeed function to maintain high rhythmicity, it implies that primates have internal models of gape cycle duration to which ongoing progress in the gape cycle phases can be compared and then adjusted. Internal models are a common component of neural models of motor control (Kawato and Wolpert 1998) but they have yet to be applied to control of the primate feeding system.

Hiiemäe and Kay (1973: 50) interpreted the similarity of jaw kinematic profiles in primates to suggest that: “changes in the morphology of the masticatory apparatus in

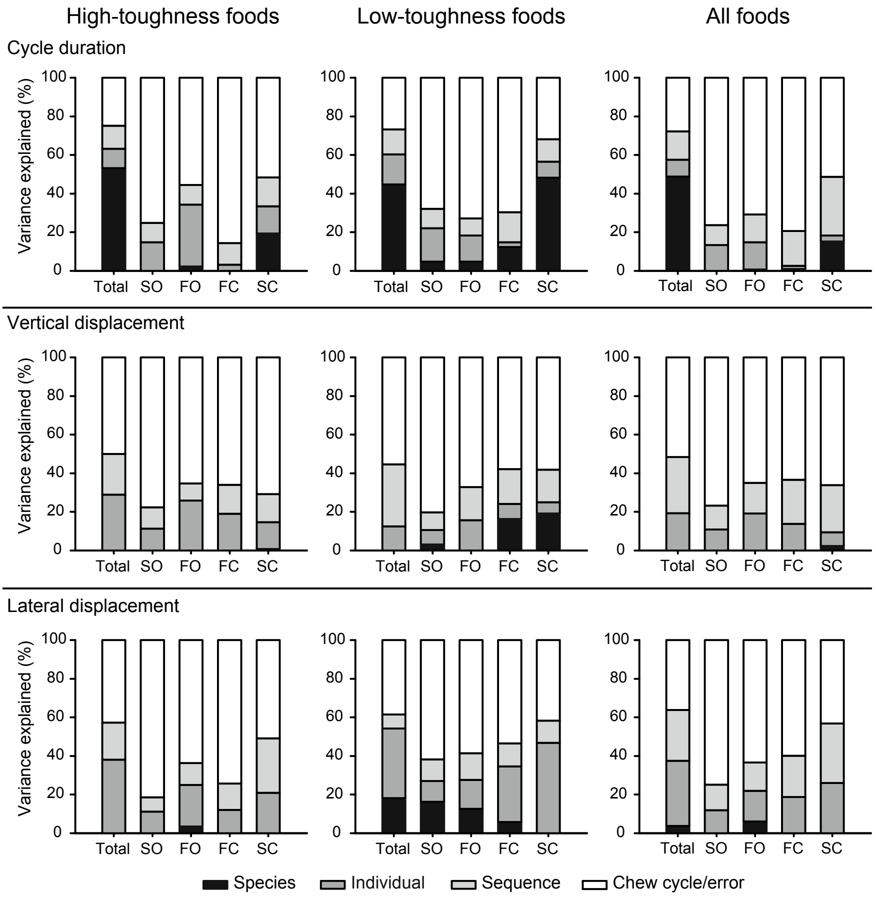


Fig. 20.8 Percentage of variance in temporal and spatial variables of jaw kinematics in primates explained by each hierarchical factor in a nested ANOVA. Factors assessed were species (*Cebus, Macaca, Papio*), individual (3 *Cebus*, 2 *Macaca, 2 Papio*), feeding sequence (n = 817) (where food material properties are nested), and chewing cycles (n = 7436) (where variance in bolus properties is nested). Data included were the first 10 chewing cycles (*Cebus*, n = 2,036 cycles; *Macaca*, n = 1,767; *Papio*, n = 3,633). To control differences in body size, spatial variables were standardized by the individual's jaw length. Displacement and temporal variables were calculated for the whole chew cycle (Total), and the slow-open (SO), fast-open (FO), fast-close (FC), and slow-close (SC) phases of the chewing cycle. The phases of the gape cycle were expressed as a percentage of total cycle duration

general, and of the cheek teeth in particular, have not involved any significant change in the pattern of mastication as expressed by absolute cycle times or the percentage duration of each of the strokes [gape cycle phases]." However, our studies suggest that there are species-specific differences in the ways that FMPs impact jaw kinematics during feeding. Agrawal et al. found that humans eating high-toughness foods chew with larger lateral jaw displacements than when eating less tough foods, whereas the opposite is true of macaques and capuchins (Agrawal et al. 2000; Iriarte-Diaz et al. 2011; Reed and Ross 2010). We also found interspecific effects on variance in jaw kinematics that might be linked to variation in feeding system morphology. The largest interspecific effects on variance in jaw displacements are seen during feeding on low-toughness foods, with species effects on vertical displacements during the closing phases and on lateral displacements during the opening phases (Fig. 20.9). Species effects on jaw kinematics during SC, evident for hard, brittle foods (such as nuts), may be due to species-specific variation in muscle forces, or in morphology of occlusal surfaces, TMJs, and/or craniomandibular ligaments (Hylander 1979a, 1988; Osborn 1989, 1993, 1995; Terhune et al. 2011) with occlusal morphology probably an important determinant of jaw movement during SC (Kullmer et al. 2012) (p. 50). Whether there are morphological correlates of species effects on jaw kinematics during opening phases remains to be evaluated.

The complexity of interspecific effects on jaw kinematic responses to variation in FMPs emerges when jaw kinematic profiles of *Macaca* and *Cebus/Sapajus* are compared (Fig. 20.5). In *Macaca* variation in FMPs elicits little variation in the temporal profile of the chewing cycle, but they require more chews to consume low-toughness foods than capuchins. In contrast, capuchins exhibit more variable temporal profiles but consume low-toughness foods in fewer cycles than macaques (Iriarte-Diaz et al. 2011). "The relative importance of interspecific differences in tongue morphology, tongue–jaw coordination, and composition of saliva (for example) in explaining these differences remains to be explored" (Iriarte-Diaz et al. 2011: 11).

20.7 Jaw Elevator Muscle Activity

EMG estimates of jaw muscle activity provide important insights into the determinants not only of kinematics of primate jaws but also stress, strain, and loading regimes in the mandible and cranium. The 3D movements of the primate mandible described by the dynamics of the AoR are produced by subtle differences in relative timing of activity of the subdivisions and sides (left vs. right) of the jaw elevator muscles (Weijs 1994). The relative timing of jaw elevator muscle activity in primates has been investigated using Weijs' concept of the triplet motor pattern (Weijs 1994), adapted to primates by Hylander and colleagues (Hylander et al. 2005, 2000b; Vinyard et al. 2005, 2006). The concept of the triplet motor pattern has its origins in the observation that in many mammals jaw-closing is accompanied by asymmetry in timing (and amplitude) of activity in masseters, temporales, and medial pterygoids (Herring and Scapino 1974; Herring 1976; Gorniak 1977, 1985; Weijs and Dantuma

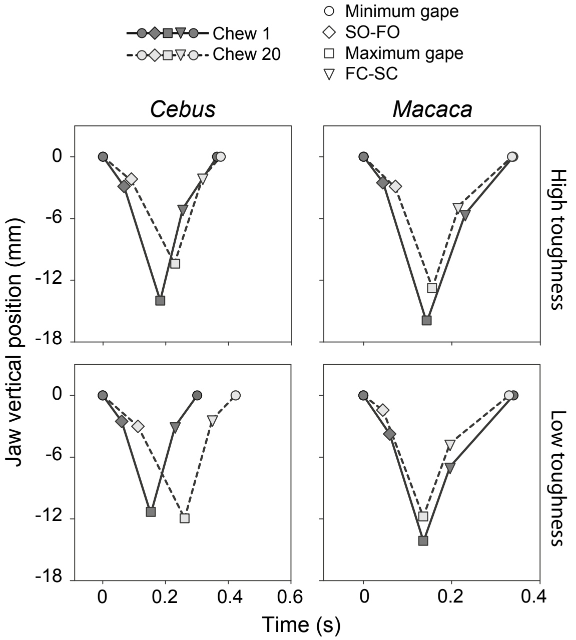


Fig. 20.9 Effects of food material properties on jaw kinematics are species-specific. Comparison of profiles of the average vertical position of the jaw in the gape cycle between the first chew and chew 20, for *Cebus* and *Macaca* feeding on high- and low-toughness foods. Symbols represent the average position of all individuals at transitions between phases (minimum gape, SO–FO transition, maximum gape, FC–SC transition, and minimum gape, respectively). Closed symbols and solid lines represent the vertical position during chew 1, and open symbols and dashed lines represent the jaw vertical position during chew 20. Gray lines represent the profile of vertical position of the jaw for each individual of each species to show the amount of interindividual variability. Modified from Iriarte-Diaz et al. (2011)

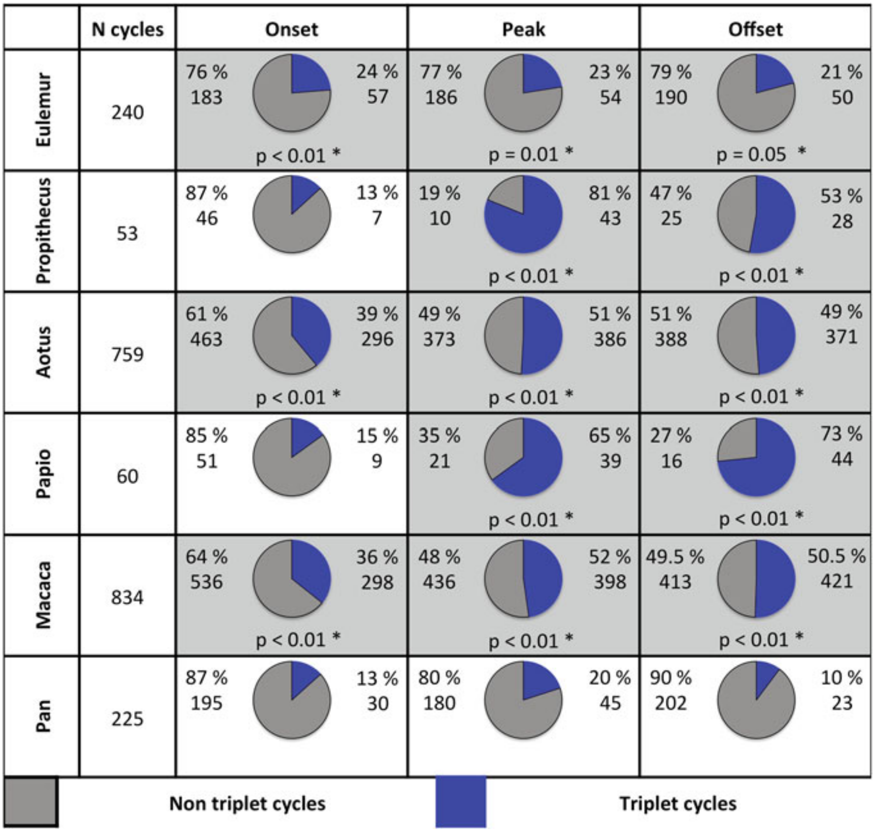
1981). According to the triplet hypothesis, primates achieve transverse movements of the tooth row during closing by sequential activity of two muscle triplets. Triplet I, consisting of the working-side temporalis and the balancing-side superficial masseter and medial pterygoid, is recruited first during FC and its activity continues into SC. Triplet II consisting of the balancing-side temporalis and the working-side superficial masseter and medial pterygoid muscles is then active during SC, with extensive overlap with Triplet I (Hylander et al. 2005).

In anthropoid primates, the triplet motor pattern of peak muscle activity has been identified in *Sapajus*/*Cebus* (Williams et al. 2011), *Homo* (Møller 1966; Langenbach and Hannam 1999), *Papio* and *Macaca*, but not in *Aotus* and *Callithrix* (Hylander and Johnson 1994; Hylander et al. 2000a, 2005). The triplet motor pattern has been identified in the strepsirrhines *Otolemur*, *Hapalemur*, *Lemur*, *Propithecus* (Hylander et al. 2011) and *Eulemur,* as well as in *Pan* (Ram and Ross 2018). The presence of this firing pattern in *Tupaia* and *Oryctalagus* suggests that the earliest primates may have employed a triplet motor pattern as well (Williams et al. 2011). Whether the triplet motor pattern is so widespread among primates because its presence is in some way inherited and/or because it represents the motor pattern that is biomechanically preferable remains to be determined. Ontogenetic studies of the emergence of chewing motor patterns in primates would help to answer these questions.

Of course, the sequence of muscle recruitment can—and needs to—vary between chewing cycles as the demands of jaw kinematics and kinetics change during a sequence. This results in variation in motor patterns between chewing cycles, even in species in which the triplet pattern is observed during rhythmic chewing. Moreover, while the studies above identify the triplet motor pattern using the average relative timing of *peak* activity in the jaw elevator muscles, there is also variation in the timing of muscle firing within chewing cycles; e.g., a triplet pattern at peak muscle activity, but not at muscle activity onset. Ram and Ross (2018) investigated this variation in *Eulemur fulvus, Propithecus verreauxi, Papio anubis, Macaca fuscata*, and *Pan troglodytes* by quantifying the prevalence (proportion of cycles) of the triplet motor pattern at onset, peak, and offset, as well as whether the average relative timing of muscle activity indicated the presence of a triplet motor pattern at these times (Fig. 20.10). The average relative timing of the jaw elevator muscles confirmed the triplet motor pattern at peak in all five species, at offset in *Propithecus, Macaca*, and *Papio,* and at onset in *Eulemur*. The proportion of cycles displaying the triplet motor pattern was significantly greater than expected at random at these times in the same species, and also at onset in *Macaca* and *Pan*. However, neither the average relative timing nor the prevalence of triplet cycles support the hypothesis that the triplet motor pattern occurs at onset in *Propithecus* and *Papio*, or at offset in *Eulemur* or *Pan*. Moreover, the percentages of cycles that show the triplet motor pattern at peak are *Eulemur* 24%, *Propithecus* 81%, *Macaca* 48%, *Papio* 65%, and *Pan* 28%, and the triplet motor pattern was only seen at *all* three times in the chewing cycle in the following percentages—*Eulemur*, 8%; *Propithecus*, 9%; *Macaca* 22%; *Papio* 5%; and *Pan* 2%. Thus, while the triplet motor pattern is more commonly found than expected at random in the primates said to possess it, it is by no means the only pattern observed. This study did not evaluate the relationship between variation in muscle motor patterns and jaw kinematics, FMPs, or relative timing in the feeding sequence, all of which would be interest. Moreover, common non-triplet motor patterns were observed, suggesting that we still have much to learn about the determinants of variation in muscle motor patterns in the primate feeding system and the role they play in the functioning and evolution of the feeding system.

20.7.1 Muscle Activity and Jaw Morphology

Interspecific variation in the details of primate jaw elevator motor patterns has long been hypothesized to be related to variation in jaw morphology. Weijs (1994) associated the primitive mammalian motor pattern with the unfused mandibular symphyses seen in most strepsirrhines, and the fused mandibular symphysis of anthro-



	N cycles	Onset	Peak	Offset
Eulemur	240	76 % 183 24 % 57 p < 0.01 *	77 % 186 23 % 54 p = 0.01 *	79 % 190 21 % 50 p = 0.05 *
Propithecus	53	87 % 46 13 % 7	19 % 10 81 % 43 p < 0.01 *	47 % 25 53 % 28 p < 0.01 *
Aotus	759	61 % 463 39 % 296 p < 0.01 *	49 % 373 51 % 386 p < 0.01 *	51 % 388 49 % 371 p < 0.01 *
Papio	60	85 % 51 15 % 9	35 % 21 65 % 39 p < 0.01 *	27 % 16 73 % 44 p < 0.01 *
Macaca	834	64 % 536 36 % 298 p < 0.01 *	48 % 436 52 % 398 p < 0.01 *	49.5 % 413 50.5 % 421 p < 0.01 *
Pan	225	87 % 195 13 % 30	80 % 180 20 % 45	90 % 202 10 % 23

Fig. 20.10 The prevalence of the triplet motor pattern in five primates quantified using proportion of masticatory cycles. At onset, peak, and offset, the number and percentage of cycles that follow the triplet motor pattern are shown in blue text and blue segment, while the number and percentage that do not are given in gray. If the number of cycles that follow the triplet motor pattern is significantly greater (*$P \leq 0.05$) than the number expected by random probability (16.66%), then the P-value is depicted below the pie chart and the box is shaded

poids with the transverse motor pattern characteristic of other herbivorous mammals (Hylander 1984). Hylander and colleagues have established strong links between increased recruitment (larger EMG amplitudes) of balancing-side muscles (expressed as lower ratios of working/balancing, or W/B, EMG amplitudes) during mastication and greater relative depth and width of the mandibular corpus and symphysis (Hylander 1979b, c; Hylander et al. 1998, 2000b, 2004, 2005; Ravosa 1991, 1996a, b, 1999) and greater condylar areas (Vinyard et al. 2006, 2007, 2008). Strong support for this hypothesis comes from the independent evolution in *Propithecus verreauxi* of postnatal symphyseal fusion and lower W/B ratios (Hylander et al. 2011). However, when these comparisons are extended to other mammals and performed in a phylogenetic context, relationships between mandible morphology and W/B ratios in superficial masseter and temporalis are not significant (Vinyard et al. 2011). The strength of the relationship among primates, along with a strong biomechanical explanation for the existence of the pattern, suggests that the lack of a similar pattern in other mammals reflects differences in feeding system biomechanics between mammalian clades.

Late activity and lower W/B ratios of the bDM and bPT have also been linked to symphyseal robustness and fusion in primates because they produce transverse components of bite force that contribute to the wishboning deformation regime of the mandible late in the power stroke (Hylander and Johnson 1994; Hylander et al. 2000b, 2011; Vinyard et al. 2005, 2006, 2007; Ravosa et al. 2000). This hypothesis is further corroborated by the fact that *Propithecus verreauxi* also exhibits late activity in the bDM during mastication (Hylander et al. 2011).

Ravosa et al. (2000) identified several other suborder differences in feeding system morphology that may be linked to anthropoid/strepsirrhine differences in muscle activity patterns. Compared with most strepsirrhines, anthropoids have both a taller ramus and a condyle positioned higher above the occlusal plane, more isodontic molars (similar BL width of uppers and lowers) and greater isognathy. Ravosa et al. (2000) suggest that these features augment the ability of anthropoids to generate transversely oriented bite force (lingually directed on the working side) with their bDM, in part necessitated by decreased ability of the superficial masseters to generate transverse forces. In the context of the enhanced transverse component of the power stoke hypothesized by Kay and Hiiemäe on the basis of occlusal analysis, this might be related to either larger transverse displacements during occlusion, or greater forces. The fact that *Propithecus* resembles anthropoids in having both a taller ramus and a condyle positioned higher above the occlusal plane (Ravosa et al. 2000; Ravosa pers. comm.) adds extra weight to the idea that muscle firing patterns and these morphological features are linked. A more recent biomechanical analysis by Reed et al. suggests that when the resultant muscle force is anteriorly directed, as is the case in primates, elevation of the jaw joint decreases joint reaction forces and increases bite force. However, they also noted that a more vertical muscle resultant moderately increases vertical joint reaction forces, decreases total joint reaction forces, and increases bite force (Reed et al. 2016). Exactly how these effects trade off in primates remains to be determined.

The relationships between muscle firing patterns and feeding system morphology at the suborder level have been linked to diet. The increased bite force associated with lower W/B EMG ratios (i.e., increased balancing-side muscle activity) have been linked to mastication of harder, tougher, more resistant food items in extant animals (Hylander 1979b, 1985). Hylander and Johnson (1994) have also shown that, in baboons and macaques, although rise times in activity of masseters and medial pterygoids are not greatly affected by food type, fall times in these muscles are longer when chewing hard and tough foods (monkey chow and popcorn kernels) than when chewing apple with skin. Notably, the balancing-side deep masseter shows the largest increase in these fall times, suggesting that the requirements of different diets may affect bDM activity. These results suggest possible links among variation in diet, chewing mechanics, and mandible symphysis morphology (Ravosa and Hylander 1994; Hylander 1979b; Hylander et al. 1998, 2000b, 2005).

20.8 Phylogenetic Patterns of Variance in Feeding System Functional Morphology

It is noteworthy that large proportions of variance in muscle mechanical advantage, muscle firing patterns, mandibular corpus bone strain magnitudes, symphyseal morphology, and corpus morphology are nested at high taxonomic levels—at the base of major primate clades (Hylander et al. 2000b, 2005; Ravosa et al. 2000; Vinyard et al. 2011; Williams et al. 2011; Ravosa 1990; Ross et al. 2012b). These conclusions from experimental and comparative studies are mirrored in recent broad scale analyses employing phylogenetically informed comparisons. Several separate studies on strepsirrhines (Baab et al. 2014), platyrrhines (Marroig and Cheverud 2001; Rocatti et al. 2017; Perez et al. 2011), guenons (Cardini and Elton 2008), and macaques (Grunstra et al. 2018) reveal that, once phylogenetic relationships are taken into account the relationships between cranial morphology and diet are weak (see also Edmonds 2016). Most of the shape differences in primate cranial morphology seem to have emerged early in extant primate clades, many of which have subsequently expanded into a range of ecological niches exploiting a range of diets. Weak relationships between diet and cranial morphology are perhaps to be expected given the experimental results summarized at the beginning of this chapter, but the same pattern is also seen in primate mandibles. In the widest ranging study to date, Meloro et al. found strong phylogenetic signal in mandible size across Primates as a whole, as well as across strepsirrhines, anthropoids, platyrrhines, and catarrhines. Phylogenetic signal in mandible shape is strongest in strepsirrhines and platyrrhines. They report significant but weak relationships between diet and mandible shape across primates as a whole (diet only explained 10% of the variance) and no significant relationship between them among anthropoids and catarrhines (Meloro et al. 2015). They did find diet to be an important factor in the evolution of shape diversity in the mandibles of strepsirrhines (32% of variance) and platyrrhines (49%).

These results for relationships of diet with cranial and mandibular form stand in contrast to the relationships of diet to dental morphology when controlling for phylogeny. Within clades of primates, folivores and insectivores have relatively longer shearing crests than frugivores, and feeders on hard foods have shorter crests and cusps that are more bulbous (Anthony and Kay 1993; Kay and Covert 1984; Meldrum and Kay 1997; Strait 1993a, b; Ungar 2011); differences in diet and food processing behaviors explain differences in maxillary tooth root areas among four species of closely related platyrrhines (Spencer 2003); and folivorous anthropoids have larger postcanine teeth relative to facial size than closely related nonfolivores (Scott 2011). The evidence suggests that a large proportion of the variation in cranial and mandibular form was established at the bases of the major clades of extant primates and that crania and mandibles have subsequently evolved less quickly than dental morphology in response to changes in diet.

If these patterns are real, what drove them? Did dietary diversification drive early diversification in cranial and mandibular morphology? If so, what were those dietary drivers and why is dietary variation not closely related to craniomandibular morphology in extant primates? A possibility we think worth considering is that variation in diet at the base of primate clades was associated with significant variation in feeding behavior—e.g., anterior dental food processing versus chewing; wide gape behaviors versus narrow gapes; gouging versus non-gouging—and that this variation resulted in the family and subfamily level variation in feeding system morphology we see today. To evaluate this hypothesis, better data are needed on the mechanics of different feeding behaviors—beyond simple chewing—in a range of extant primates, as well as a comprehensive data set on the relationships between feeding behavior and the rich data on food geometric and material properties being collected in the field.

Another possibility is that these patterns are not real but artifacts of sampling and or measurement methods. Recent emphases on geometric morphometric methods reap the advantages of pure measurements of shape at the expense of rigorous biomechanical applicability: shape space is not biomechanical space, making functional interpretations of geometric morphometric patterns quite challenging. To eliminate this possibility, it is important to revisit functional hypotheses derived from GM analyses using biomechanically relevant variables, such as lever arms, load arms, torques, and cross-sectional areas, to determine what patterns in shape space actually mean.

20.9 Conclusions

This review suggests several ways in which integration of results from new and improved methods for experimental study of primate feeding biomechanics will significantly enhance our understanding of the biomechanical determinants of primate feeding performance. Integration of data on high resolution jaw kinematics with occlusal fingerprinting analysis and computational modeling promises significant advances in our understanding of the relationships between occlusal mechanics, jaw kinematics, and food break down. In particular, it will enable evaluation of the utility of the “shearing, crushing, and grinding” terminology to specific tooth facets, as well as the (probably dubious) value of this terminology for understanding food fracture mechanics (Lucas 2004). Moreover, a better understanding of the relationships between dental microwear and jaw and tooth kinematics is certainly needed to fully explicate the meaning of dental microwear for understanding the role of diet, grit, and feeding behavior in dental evolution.

Integration of 3D data on jaw kinematics with data on muscle architecture and XROMM-based measures of muscle architecture dynamics promises to offer insight into the mechanisms whereby primate biting performance is impacted by muscle gearing. The fundamental constraints on primate feeding systems—the trade-off between muscle fiber length and muscle force, the third-class lever arrangement of the jaw muscles, and the constraint that the jaw elevator muscle resultant must pass through the triangle of support—impose a gape–force trade-off on primate feeding systems. The exact nature of that force–gape relationship is a function of relationships between feeding behavior (where on the tooth row animals are biting objects of what size) muscle architecture established during ontogeny and muscle architecture dynamics—changes in pinnation angle, fiber, and sarcomere lengths change during jaw movement—during feeding. How these variables are related and distributed across primate phylogeny will hopefully provide insight into the drivers of diversity in craniomandibular morphology at the base of the major clades of primates.

It is also clear that better data are needed on relationships between patterns of recruitment of jaw and hyolingual muscles and patterns of jaw and hyolingual movement. The optimality criteria driving these relationships are unknown. Some workers argue or assume that muscles are recruited to minimize muscle stress (Curtis et al. 2008), but there are currently no data to support this hypothesis in primates. Studies by Wall and colleagues on energetics of feeding in a wide range of primates promise significant insight into these questions as avoidance of muscle fatigue may be one goal of primate feeding systems. However, it is also clear that primate jaw muscle firing patterns cannot be shoe-horned into the "triplet" model. Exactly what criteria are used by the central nervous system to select different firing patterns remains unknown. More data on EMG activity across a range of behaviors would be informative in this regard.

One of the most exciting areas for future work is the integration of data on wild primate feeding behavior with the geometric and material properties of the foods they are eating. Strong relationships have not emerged between these properties and craniomandibular morphology, probably because feeding behavior intervenes in ways that makes these relationships multidimensional and complex (Taylor et al. 2008; Vogel et al. 2014; McGraw and Daegling 2012). The amount of time that different species of primate spend on different behaviors when feeding on foods with different food geometric and material properties is not well enough known (McGraw et al. 2010). Whether answers to questions about the drivers of craniomandibular diversity are to be found in these data remains to be seen. Comparative analyses from a number of independent research groups suggest that much of the variation in primate feeding system biomechanical variables is nested at the base of major extant clades. It will be exciting to learn whether this reflects a paucity of the relevant data on variation in feeding biomechanics and performance within closely related primate species, "constraints" imposed by phylogeny, and/or the robustness and adaptability of primate feeding system design.

Acknowledgements Richard Kay and Myra Laird provided detailed comments on the manuscript. Matt Ravosa clarified the position of *Propithecus* in the data set for Ravosa et al. (2000). This work was funded by NSF HOMINID and Physical Anthropology BCS 0240865, 0504685, 0725126, 0725147, 0962682, 1732175; by NSF DBI 1338066; and by NIDCR R01-DE023816 and T32-HD009007. We thank several colleagues who have contributed significantly to our research, including David Reed, Andrea Taylor, Olga Panagiotopoulou, and David Strait.

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