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Mammalian Oral Rhythms and Motor Control

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1. Introduction

Mastication is a derived mammalian trait, characterized by rhythmic jaw movements associated with intra-oral food handling, reduction and bolus formation. Hiiemae defined it as "a key feature of mammalian feeding that involves the coordination of complex movements and precise dental occlusion during a distinct power stroke of the chewing cycle (Hiiemae, 2000). Lund and Kolta refer to mastication as the time "during which the food is mechanically broken down and mixed with saliva to create a slurry of small particles or bolus that can be easily swallowed" (Lund & Kolta, 2006).

There is a debate as to whether to define mastication in general or precise terms. The debate focuses on whether to include in its definition the requirements of precise post-canine occlusion, unilateral food bolus placement, and transverse motion of the mandible during the power stroke. Given that feeding in most mammalian and non-mammalian species has yet to be studied and characterized, we opt to use fewer qualifiers and to rely on a more general definition of mastication or chewing in this chapter.

The variety of masticatory kinematics and dentoskeletal morphologies (Ungar, 2010) across mammals is almost as striking as plumage variation is among birds. The increased efficiency afforded by masticatory forms and functions may have been necessary to keep pace with another mammalian synapomorphy, the increased energy demands of endothermy. Alternatively, given that erupted enamel cannot be replaced, and that healthy teeth are requisite for longevity and fecundity, efficiency may be required to maximize the life of teeth.

Whatever the case, mastication is only one of several distinct oral motor behaviors, which also include (a) suckling, a mammalian-specific trait involved in milk ingestion, (b) lapping or sucking which are used to ingest liquids, fruit juices or insects, (c) rumination or chewing of cud, (d) gnawing of bones or tough food items, (e) tongue rasping used by cats as a food softening behavior, (f) incising, chopping or cutting food, (g) tooth sharpening or thegosis, (h) speech, whistling and communication, (i) facial expressions such as smiling or gritting teeth aggressively, (j) protective behaviors such as sneezing, coughing, gagging or vomiting, (k) tool use such as blowing on, holding or catching objects, (l) respiratory behaviors such as breathing and panting (m) sensory pleasures such as tasting or kissing.

2. Significance of masticatory biomechanics

Although motor behaviors "above the neck" are underrepresented in biomechanics studies, the oral apparatus affords several important and compelling features and advantages for such studies, which we discuss in this section.

2.1 Jaw tracking

The dentition is a sturdy set of anchors for kinematic tracking purposes. Teeth are anchored by the periodontal ligament to the mandibular bone, which prevents significant tooth movement in healthy mouths. Orthodontic brackets or custom clutches with small footprints are often attached to teeth for holding jaw tracking markers (Flavel et al., 2002; Gerstner & Fehrman, 1999; Gerstner & Kinra, 1999; Gerstner et al., 1999; Gerstner & Parekh, 1997; Hiiemae et al., 1996; Plesh et al., 1993; Wintergerst et al., 2004). More invasive tracking methods such as anchored bone markers or cineradiography are easily used in non-human mammals (Byrd, 1981; Gerstner & Goldberg, 1991; Hylander et al., 1987; Kobayashi et al., 2002a; Schwartz et al., 1989; Yamada et al., 1988). The development of X-ray reconstruction of moving morphology (XROMM) has been used to study oral movements and promises to revolutionize comparative biomechanical studies of oral function (Brainerd et al., 2010).
It is also possible to track certain jaw movement features with marker-less methods (Gerstner & Goldberg, 1994; Ross et al., 2009). This is possible, because most species remain relatively motionless while masticating. Hence, special equipment is often unnecessary.

2.2 Unique motor control characteristics

Because they involve the movement of a single bone, i.e., the mandible, masticatory movements can be relatively simple to track. Yet, mastication has some complex aspects that can provide significant insights into biomechanical issues. For instance, the mandible crosses the midline and articulates with the temporomandibular joints (TMJ), each of which possesses six degrees of freedom in humans and many other species. The jaw is driven by at least 18 muscle groups, and the masticatory movements, which these muscles generate, are usually asymmetrical. Hence, activity in masticatory muscle pairs is asynchronous, but carefully controlled so that mandibular positions and movements are precise and accurate to sub-millimeter levels especially near tooth-to-tooth contact.

2.3 Unique muscle characteristics

The masticatory muscles contain a number of unique features and properties that need to be further explored to understand their functional significance (for review, see Korfage et al., 2005a, 2005b). These include the presence of Type IIX, α-cardiac and neonatal myosin heavy chains in fairly high levels in all adult human masticatory muscles. Furthermore, > 40% of jaw-closer muscle fibers are hybrids, consisting of two or more myosin heavy chain types. Also, whereas in the limbs and trunks, type IIA fibers have larger diameters than type I fibers, the opposite is true in masticatory muscles. Type I fibers are about the same diameter in jaw muscles as they are in limb and trunk muscles; however, the masticatory type IIA fibers are three times smaller in diameter than they are in limb and trunk muscles. The reasons for these unique features remain unclear; however, candidate hypotheses include: (1) the need for fine jaw motor control, (2) energetic demands of jaw function and posture maintenance, (3) the heavy daily use of the jaw, and/or (4) unique adaptive requirements.

2.4 Unique proprioception

Masticatory proprioception has several unique features. For instance, although jaw closer muscles are populated by muscle spindles, jaw opener and tongue muscles have few to no muscle spindles. Tendon organs are absent in jaw closer muscles, but occur in jaw openers albeit at relatively low densities. Mechanoreceptors in the periodontal ligaments, the

connective tissue that holds the teeth in their sockets, likely play important proprioceptive roles, essentially replacing the tendon organs in this function.
Also, the mesencephalic nucleus (MeV) is essentially a dorsal root ganglion residing in the brain stem. It contains the cell bodies of primary afferents involved with proprioception of the face and jaw and of mechanoreceptors from the teeth. Interestingly, the MeV is found in all vertebrates with jaws, whereas it does not exist or exists in very rudimentary form in vertebrates without jaws. This suggests that its unique design is somehow tied to jaw function requisites. Cells within the nucleus are electrically coupled, with chemical synapses being absent from the nucleus. Spindle afferents, whose cell bodies are in MeV, are unipolar and form a monosynaptic jaw closing reflex with jaw closer motoneurons.
Skin and hair receptors especially around the corners of the mouth play a role in proprioception; however, they are mostly rapidly-adapting and appear to require tactile stimulation. Proprioception also plays unique and important feedback and feed-forward roles in masticatory control as will be discussed below.

2.5 Central pattern generation and timing

Mastication is controlled by brainstem central pattern generator circuitry (Section 4). The circuitry develops from rhombomeres distinct from respiration, and it has some unique features in the adult. Interestingly, the rhythm generator is anatomically distinct from circuitry that orchestrates muscle activity patterns. Why the rhythm and muscle activity pattern generators are separate is unknown, but probably neurobiologically significant. We believe it may be related to the fact that chewing cycle rhythmicity is relatively invariant. This invariance is curious, given that rhythmic behaviors such as locomotion, heart rate and respiration can vary considerably with changes in functional demands.

2.6 Comparative studies

Although mastication is a mammalian derivation, other non-mammalian species chew rhythmically including teleost fishes (Gintof et al., 2010), some larval amphibians (Larson & Reilly, 2003), and many invertebrates (Marder et al., 2005). Although larval amphibians manifest rhythmic feeding, the adult forms manifest mainly non-rhythmic forms of feeding (Deban et al., 2001). The diversity of chewing patterns among all animals is striking; however, this chapter will focus on mammalian chewing or mastication.
It is generally believed that the masticatory motor program is conserved across mammals (Langenbach & Van Eijden, 2001) and other vertebrate classes as well (Gintof et al., 2010). Although little comparative work at the neurobiological level has been done, it is likely that the fundamental brain stem circuitry that produces mastication is found in many if not most mammals and other vertebrate classes. For the comparative biomechanists, this provides a potentially rich source of questions to address including: (1) does the nervous system constrain evolutionary pathways involving the masticatory apparatus, (2) how are dentoskeletal form and masticatory function interrelated, and (3) how does the centrally generated rhythm differ among species.

2.7 Biomechanics

Oral and mandibular biomechanics are complex due to numerous features including the six degrees of freedom of movement in both TMJs, the 3-dimensional shapes of the mandible the TMJs and the occluding dental surfaces, the material properties of the periodontal

ligaments, the complexity of the force-producing muscles including their mechanical redundancy and pennation, and the largely unknown forces generated by muscles of the cheeks, tongue and lips that are in play during rest and function.

Because of these complexities, experimental and modeling studies have made slow inroads to understanding oral biomechanics. Recent finite element modeling (Korioth & Versluis, 1997; Strait at al., 2007), dynamic modeling (Peck & Hannam, 2007), experimental work (Herring et al., 2001) and combinations of experimental and modeling techniques (Gallo, 2005; Peck & Hannam, 2007) have begun to show promise. One of the greatest challenges is to achieve reasonable agreement between experiments and models (Daegling & Hylander, 2000). Biomechanical data and issues with respect to the oromandibular complex are discussed in detail elsewhere (Daegling & Hylander, 2000; Douglas, 1996, Gallo, 2005; van Eijden, 2000). Examples of some of the challenges and issues will be presented, below.

It is tempting to think of the mandible as a Class III lever, with the TMJs serving as fulcra. However, this is an oversimplification, and there is a long-standing alternate argument that the mandible serves as a link with the dentition bearing the load rather than the TMJs (Douglas, 1996). A recent model of the TMJs using MRI and 3-D kinematic data suggests that the joints are loaded during mastication, with the balancing condyle loaded more than the working condyle (Gallo, 2005). The model has not yet captured all functional movements, however, and so it remains possible if not likely that the mandible can act as link, Class III lever or even Class II lever under appropriate conditions (Douglas, 1996). Importantly, biomechanical parameters of interest, e.g., stress, strain, shear, tension, compression, torsion, bending in mandibular corpus, condyles and alveolar bone can be very sensitive to experimental designs or model assumptions.

Of interest to us is whether the time during which opposing teeth are either in contact or are forcibly working on food stuffs, i.e., the occlusal phase of chewing, is related to the rate of tooth wear over the lifetime of an individual. Hence, the forces achieved during mastication are critical parameters to know. These forces have been reported as being 3 – 18 N (reviewed in Douglas, 1996). These are considerably less than the maximum voluntary forces that can be produced in humans, which average about 350 N, with males being able to produce higher (> 400 N) forces on average than women (~ 260 N). Human bite forces are considerably less than those reported in other mammals. Moreover, the maximum voluntary bite forces, above, are higher when the posterior molars and premolars on both left and right sides of the arch are simultaneously maximally intercuspated, as during clenching; maximum voluntary forces drop sharply when the teeth are in eccentric positions, e.g., when anterior teeth are edge-to-edge, where fewer teeth remain in contact.

More investigations are needed to determine how tooth position and bone morphology may be influenced by functional and resting forces, as the above-reported forces are within the range of forces used by orthodontists to move teeth and to alter bone growth patterns.

One of the most promising biomechanical models of the oral complex has been developed in conjunction with the Artisynth project at the University of British Columbia (Peck & Hannam, 2007). This "whole-jaw" modeling project uses morphological and muscle attachment data obtained from imaging real subjects and functional models of muscle physiology, the latter of which can vary in complexity from Huxley-type to Hill-type models. Recently, flexible finite-element model methods have been incorporated to study tissue distortion in the TMJs and tongue associated with function. Jaw movements have been integrated with laryngeal models to explore swallowing and even speech. The ultimate

promise is to create subject-specific models and to understand joint loading, movement constraints and neuromotor activation strategies associated with real function. The project is of interest to the issues presented in this chapter, because it is likely that inertial and neuromotor properties of the tongue and hyoid complex may impact chewing rate and rhythmicity. Therefore, a more complete understanding of chewing motor control will require insights from biomechanical models such as those available through Artisynth.

2.8 Clinical significance

There are numerous clinical issues of the orofacial complex, which require biomechanical insights. These include congenital dentoskeletal and neuromuscular anomalies, such as cleft lip and palate, as well as abnormal jaw growth and tooth eruption patterns. Other often serious neuromotor conditions include oral dyskinesias, akinesias, bradykinesias, dystonias, and neurological problems such as aphasias, tics, swallowing disorders and speech disorders. Several common chronic pain conditions occur including temporomandibular disorders (TMD), which are second in prevalence to lower back pain only, and TMD co-morbidities ranging from tinnitus to fibromyalgia. There are issues of physical rehabilitation for denture wearers and cancer survivors who have lost oral structures. Numerous age-related changes in muscle tone, muscle fiber type, oral coordination and eating habits also occur. Several sleep disorders involve the oral apparatus including nocturnal bruxism, sleep-related eating disorder, nocturnal eating syndrome, somniloquy, and obstructive sleep apnea. Many psychosocial disorders involve the orofacial region including facial expressive disorders and eating disorders among others.

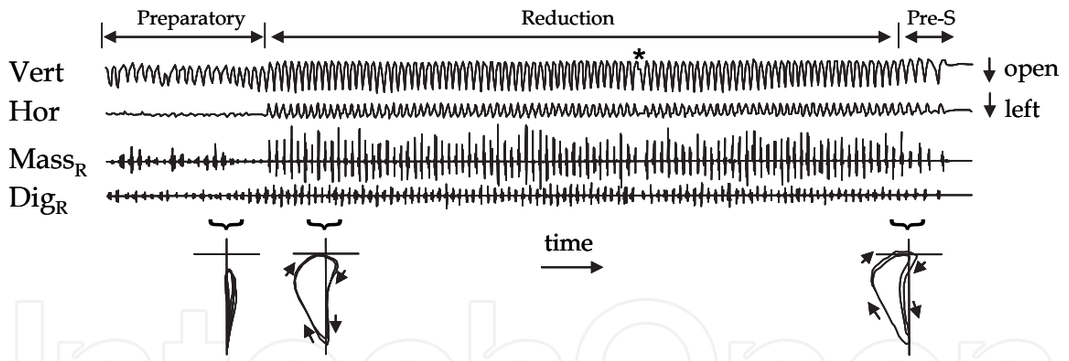


Fig. 1. A chewing sequence. Top: Sequence divided into preparatory, reduction and pre-swallow (Pre-S) series. Traces top to bottom: vertical (Vert) and horizontal (Hor) jaw movement components, right masseter (Mass$_R$), right digastric (Dig$_R$). Asterisk (Vert trace) identifies an O_2 phase. Bottom: Frontal plane projections of jaw movements from each series. Arrows depict jaw movement directions. Crosses on each of the three projections identify the animal's midline (vertical line), and jaw position at maximum closure (horizontal line). Modified and redrawn from Yamada & Yamamura, 1996.

3. Nomenclature: Chewing sequences, series, cycles and phases

Chewing typically occurs in **sequences** beginning with food ingestion and ending with swallowing of the bolus (Fig. 1). A typical chewing sequence is made up of rhythmical chewing **cycles**, which involve successive jaw openings and closings (Fig. 2). Each cycle is

then made up of a jaw opening component and a jaw closing component. Many investigators further divide chewing cycles into four **phases** (Fig. 2), viz., slow opening (SO), fast opening (FO), fast closing (FC) and slow closing (SC). We should add that, although these phase names have become fairly commonly used, they may be somewhat misleading. For instance, in some cases, investigators have demonstrated that SO velocities can be faster than velocities occurring during FO (Lund & Enomoto, 1988).

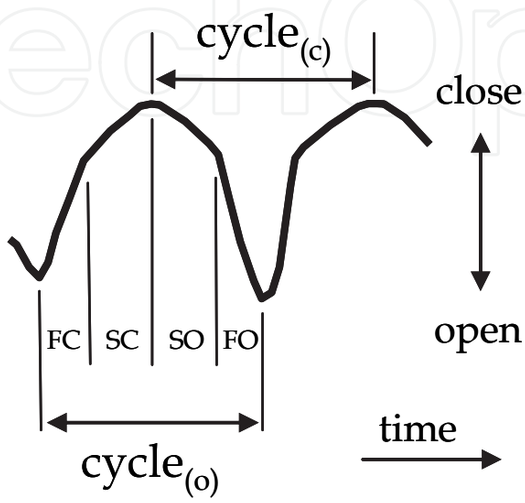


Fig. 2. Masticatory cycles and phases, defined by the vertical jaw movement component using the anterior midpoint of the jaw as a referent (see also Fig. 1). Cycles can be defined from successive maximum jaw closures (cycle($_c$)) or maximum gapes (cycle($_o$)). The phases, fast close (FC), slow close (SC), slow open (SO) and fast open (FO) are also shown.

Chewing cycles that introduce food into the mouth are the **preparatory series** (Fig. 1). These cycles are also called Stage I chewing (Masuda et al., 1997; Morimoto et al., 1985), the food preparatory period (Narita et al., 2002; Ootaki et al., 2004; Yamamura et al., 2002), or Type I chews (Schwartz et al., 1989). Those involved with working the food into a bolus are the **reduction series,** Stage IIa chewing (Masuda et al., 1997; Morimoto et al., 1985), rhythmic chewing period (Narita et al., 2002; Ootaki et al., 2004; Yamamura et al., 2002), or Type II chews (Schwartz et al., 1989). Those involved with preparing the food for swallowing by introducing the food into the pharynx are the **preswallow series**, Stage IIb chews (Masuda et al., 1997; Morimoto et al., 1985), the preswallow period (Narita et al., 2002; Ootaki et al., 2004; Yamamura et al., 2002), or Type III chews (Schwartz et al., 1989).

3.1 Type I chews

During a sequence, the food is manipulated initially in the incisor, canine and pre-molar region with a series of rhythmic jaw movements that have been called the preparatory series (Fig. 1). These Type I jaw movement cycles bring the food into the mouth and allow it to undergo initial handling by the anterior teeth as it is moved backwards towards the molars to begin the reduction of the food into a bolus. The preparatory series typically do not involve tooth contact or strong jaw closer muscle activity. They may often have high jaw opener muscle activity. They also tend to be relatively short-duration cycles, i.e., the cycles occur at a relatively fast frequency.

3.2 Type II chews

The rhythmic jaw movements that reduce the food to a bolus are termed the reduction series (Fig. 1). The cycles that constitute this series are the prototypical chewing cycles and involve tooth intercuspation and strong jaw closer muscle activity. Each of these chewing cycles typically consists of FC and SC phases. Whether the opening consists of a single phase, or has two (SO and FO) or even three phases (the third one involves a short pause in jaw movements, see asterisk in Fig. 1) varies, both within chewing sequences and probably across species. The SC phase is the power stroke during which jaw closing muscle force increases to handle the food resistance. Feedback from proprioceptors is used to recruit muscle at a rate that is directly proportional to the resistance offered by the food; the tougher the food, the faster the muscle recruitment rate. This results in each chewing cycle being relatively similar in duration, despite variation in load and concomitant variation in muscle force. This phenomenon is a main part of the discussion in Section 5.

3.3 Type III chews

As the food is reduced and mixed with saliva to form a bolus, tongue movements prepare the food for swallowing by moving the bolus towards the pharynx. The chewing cycles that occur at this time in the sequence are called the pre-swallowing series (Fig. 1) and tend to be the longest duration chewing cycles.

Some chewing cycles may involve a brief pause occurring during opening. When this happens, three opening phases occur, viz., O_1, O_2 and O_3. O_1 and O_3 are similar to SO and FO, respectively, with O_2 being the brief pause (Fig. 1, asterisk). Alternatively, the O_1 and O_2 phases may be lumped together into the SO phase (Lund & Enomoto, 1988). The O_2 phase is associated with a significant increase in cycle duration.

3.4 Caveats

Chewing sequences, cycles and phases can vary considerably, especially under free-roaming conditions, when reduction, ingestion and swallowing can occur at varying time points in a sequence. Under laboratory conditions when a single bite of food is given, the chewing series often proceeds in the order described, above.

Also, it is likely that future investigations will identify species-specific differences in food processing that will be characterized in chewing sequences. One of the future challenges will be to identify what commonalities exist in chewing sequences across species and within species under free-roaming conditions.

We are presently refining methods for use in comparative masticatory studies (see chapter entitled Functional data analysis for biomechanics, in Biomechanics / theory). One of the main goals of this work will be to use these advanced statistical methods to identify functionally and kinematically distinct chewing cycles, to determine why these distinctions exist from biomechanical, developmental, evolutionary and functional perspectives, and ultimately to use the categories to help refine neurophysiologic work so that it becomes possible to address issues regarding how the nervous system switches between chewing cycle forms.

3.5 Summary

A chewing sequence involves ingesting a food morsel and reducing the particle sizes while mixing them with saliva to create a bolus with properties that allow it to be swallowed (Fig. 1).

The chewing sequence consists of rhythmically-occurring chewing cycles (Fig. 2). Over the course of a chewing sequence, the functional nature of chewing shifts from ingestion and initial food handling in the front or anterior part of the mouth (preparatory series) to grinding and reducing the food in the molar region (reduction series) to introducing the food into the pharynx in preparation for swallowing (pre-swallow series). Chewing cycles tend to have the shortest durations during the preparatory series and the longest durations during the pre-swallow series as detailed in (Schwartz et al., 1989).

4. The neuromotor basis of mastication

This section provides a very brief overview of the central and peripheral neural mechanisms involved in the control of oral rhythmic behaviors.

4.1 Central pattern generators (CPG) and central timing networks (CTN)

As is the case for locomotion and respiration, rhythmic oral behaviors including mastication, suckling and licking are controlled by CPG circuits. Unique features to be emphasized below include: (1) anatomical distinctions between CTN also called central rhythm generators (CRG) and the circuits that coordinate output to lower motoneurons, (2) relative invariance in the rhythmicities produced, (3) relatively high variation in the duration of the phases that make up the fundamental cycles.

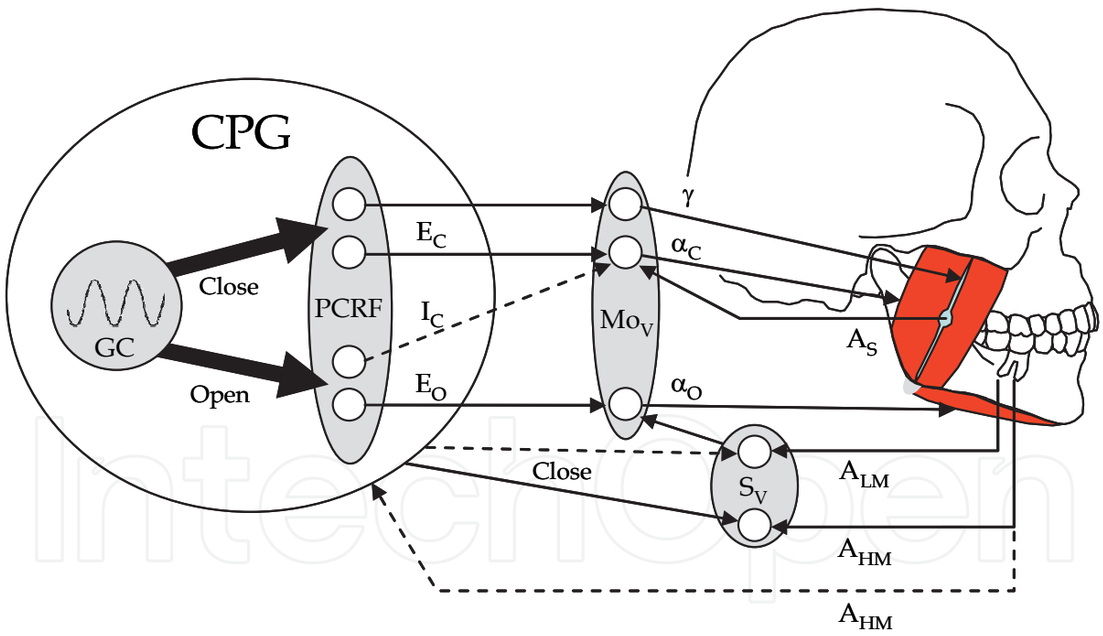


Fig. 3. Simplified diagram of neural components of mastication. Gray ovoids are brain stem nuclei. Solid arrows are excitatory and dotted arrows inhibitory pathways. Abbreviations: Central pattern generator (CPG), nucleus gigantocellularis (GC), parvocellular reticular formation (PCRF), trigeminal motor nucleus (Mo_V), trigeminal sensory nuclei (S_V); afferents: spindle afferents (A_S), low (A_{LM}) and high (A_{HM}) threshold mechanoreceptors; premotoneurons: excitatory to jaw closers (E_C) and to jaw openers (E_O), inhibitory to jaw closers (I_C); lower motoneurons: gammas (γ), alphas to closer (α_C) and opener (α_O) muscles.

4.1.1 Mastication

Fig. 3 shows a diagram of a popular model of CPG circuitry involved in the production of mastication (Nakamura, 1985; Nakamura & Katakura, 1995), reviewed also in (Lund & Enomoto, 1988). The model is based on sophisticated and elegant *in vivo* labeling and electrophysiological work done mainly in the guinea pig and domestic cat. Mastication appears to be largely under the control of CPG circuits located in the pontine and medullary brain stem. Input from higher cortical sites descends through a corticobulbar tract that is a part of the pyramidal system and synapses in the nucleus paragigantocellularis (PGC, not shown in Fig. 3; however, see Fig. 4). The PGC appears to act as a relay between corticobulbar and CPG circuits, because an experimental stimulus frequency applied to the pyramidal tract is recorded in the PGC without modification. However, in the nucleus gigantocellularis (GC), an experimental stimulus applied to the pyramidal tract is packaged into bursts that recur at the rate at which the animal chews. This region within the GC has been termed the central timing network (CTN) or central rhythm generator (CRG).

Output from the GC goes to premotoneurons in the parvocellular reticular formation (PCRF, Fig. 3). These premotoneurons organize output to lower motoneurons, which are located in the trigeminal motor nucleus (Mo_V, Fig. 3). Three main premotoneuron populations have been identified. This includes two excitatory populations, one that synapses on jaw opening lower motoneurons (E_O) and one that synapses on jaw closing motoneurons (E_C). A third population is inhibitory to the jaw closing lower motoneurons (I_C). The E_O and I_C populations burst in synchrony and are involved in jaw opening. The I_C population is believed to suppress the spindle-mediated jaw closing reflex during jaw opening, so that opening is unencumbered by this monosynaptic stretch reflex. The E_C premotoneuron pool bursts out of phase with the other two populations and is involved with jaw closing.

It is likely that there are premotoneurons regulating gamma (γ) motoneuronal activity in spindles; this pathway is depicted as an unlabeled pathway from the PCRF to the γ motoneuron pool in Fig. 3. Both dynamic and static γ motoneurons have been identified (reviewed in Lund, 1991); the dynamic γ motoneurons are tonically active during mastication, whereas the static γ motoneurons are active during jaw closing only. It is likely that α–γ co-activation plays an important role in maintaining a relatively constant chewing cycle frequency in the face of varying loads associated with the ever changing physical properties of ingestants (Ross et al., 2007b).

4.1.2 Licking and suckling

Although most work has focused on the masticatory CPG, there is also interest in the neural correlates of other rhythmic oral behaviors such as spontaneous licking and suckling. Based on evidence from acute animal studies, investigators have suggested that licking and chewing (and other oral rhythmic behaviors) share a common CTN (Carvalho & Gerstner, 2004; Gerstner & Goldberg, 1991; Goldberg & Chandler, 1990). Evidence exists that the licking CTN is located at the same site as the masticatory CTN (Brozek et al., 1996). The concept of a shared CTN probably does not conflict with the more recent model presented by Lund and Kolta describing how CPG circuitry could be modified to produce distinct chewing forms (Lund & Kolta, 2006); at issue is whether the modifiable masticatory CPG output of the Lund-Kolta model in fact produces the licking "form".

There is also debate among scientists about the relationship between suckling and mastication. Iriki, et al. (Iriki et al., 1988) have demonstrated that suckling and mastication

are represented at anatomically distinct cortical sites (Fig. 4). In the guinea pig, suckling can only be evoked by stimulation to cortical sites anterior to those that stimulate mastication in adult animals. Stimulating the cortical suckling area (CSA) in adults induces no rhythmic movements. However, in pre-weaned neonates, stimulating the CSA sites produces rhythmic movements that resemble suckling. Stimulating cortical masticatory areas (CMA) in neonates produces no rhythmic jaw movements; however, in the same animals upon weaning, stimulation of these CMA sites produces rhythmic chewing-like movements.
Although suckling and chewing are distinct at the cortical level, the brain stem sites involving the two appear to overlap (Fig. 4, bottom). Future work is required to determine if suckling and chewing share brain stem circuitry.

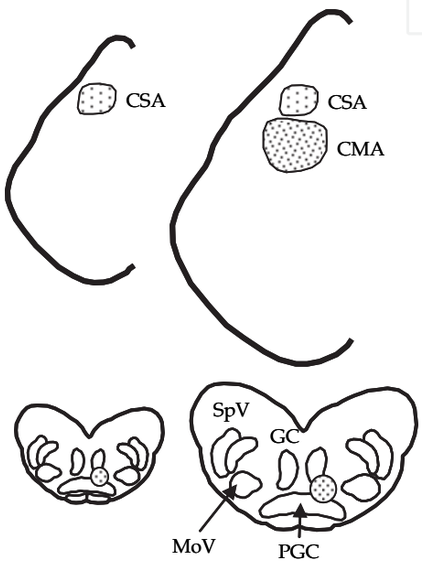


Fig. 4. Top. Left cortical hemispheres of neonate (left) and adult (right) guinea pigs. Bottom. Brain stem sections of neonate (left) and adult (right) guinea pigs. Abbreviations: CSA, cortical suckling area; CMA, cortical masticatory area; SpV, spinal trigeminal system (nucleus is medial, tract is lateral); MoV, trigeminal motor nucleus; GC, nucleus gigantocellularis; PGC, nucleus paragigantocellularis. Modified from Iriki et al., 1988.

4.1.3 Tooth eruption and the transition from suckling to chewing

The above findings (Iriki et al., 1988) are interesting, given that guinea pigs used in the experiments, are born with erupted teeth, which show wear from intra-uterine grinding. However, neonatal guinea pigs do not feed or chew until weaning, indicating that tooth eruption is not sufficient to produce chewing. Rather, events surrounding weaning are apparently required to make the transition from suckling to chewing. What the events are that induce the transition are presently unknown. In any case, discoveries in this area will contribute importantly towards understanding the development of motor systems.
A developmental study of dogs demonstrated that the normal weaning period was prolonged when either the tooth buds were enucleated or the trigeminal afferents to the teeth were blocked (Iinuma et al., 1994). In the case of the afferent block, the puppies ultimately made a transition from suckling to rhythmic chewing. However, in the enucleated group, rhythmicity never developed. The puppies in the enucleated group ate

food by "biting" rather than by chewing. In a third experimental group, puppies' teeth were removed after they had erupted and after the puppies had learned to chew rhythmically; this group maintained a rhythmic chewing pattern after the removal of the teeth.
These findings suggest that the teeth and associated afferents are important for developing a normal chewing rhythm, even if chewing starts considerably after tooth eruption. Carefully designed future experiments may be able to uncover a critical developmental window when the brainstem CTN circuits are most responsive and adaptive to such peripheral feedback or cues. This could also be useful for insights into allometric scaling (see Section 5).

4.2 Afferent systems

There are also several afferent systems that regulate and are, in turn, regulated by the CPG circuitry. Among these are muscle spindles found mainly in the jaw closer muscles, tendon organs found in small numbers in jaw opener and tongue muscles, joint receptors (e.g., Ruffini and Pacinian receptors, ligamentous organs and free-nerve endings), high- and low-threshold mechanoreceptors in the oral mucosa, tongue and periodontal ligaments around tooth roots, skin and hair receptors, temperature receptors and nociceptors. For simplicity, Fig. 3 only shows spindle afferents in the masseter, a jaw closer (A_S), and high (A_{HM}) and low (A_{LM}) threshold mechanoreceptors from the periodontal ligament of a lower molar. The spindle and mechanoreceptor afferents are believed to play important roles in minimizing tooth breakage and wear during mastication among other functions (Ross et al., 2009).
Feedback from afferents is carefully modulated by CPG circuitry throughout the masticatory cycle (for review, see Lund, 1991). During jaw opening, the monosynaptic spindle-mediated jaw closing reflex (A_S to α_C, Fig. 3) must be inhibited, and this duty is performed by the inhibitory premotoneuron pool (I_C, Fig. 3). Likewise, during closing the CPG modulates feedback from afferent mechanoreceptors (A_{LM} and A_{HM}, Fig. 3). These afferents mediate a multisynaptic jaw opening reflex, which plays a protective role so that teeth and mucosa are not damaged during jaw closing. Generally, feedback from the A_{LM} is inhibited by the CPG, probably so that low loads do not result in jaw opening during food reduction, whereas feedback from the A_{HM} is enhanced by the CPG, probably so that the opening reflex responds efficiently when potential damage is most likely to occur.
Fig. 3 also shows that feedback from the A_{HM} probably directly inhibits CPG activity so that chewing is halted when potential damage has occurred (Fig. 3, bottom). Similar inhibitory feedback to CPG circuitry probably involves other mechanoreceptors, nociceptors and joint receptors. Activation of these inhibitory feedback arms is responsible for the familiar responses that occur when the tongue or cheeks are accidentally bitten or when something too hard for chewing is bitten.

4.3 Model limitations

The above description is a considerable simplification. Moreover, most of the known details of brainstem control of mastication stem from work involving guinea pigs, cats, rabbits, rats and mice. Hence, knowledge of masticatory neuromotor control is based on a few, mainly inbred laboratory animal models. Virtually nothing is known about the control of mastication in humans or the other 5400+ mammalian species.
There is a broadly-held assumption that masticatory neural circuitry is conserved among mammals. On the other hand, the variation in mammalian dentoskeletal and masticatory muscle forms is striking. It seems likely, therefore, that masticatory neural circuitry would

show equally variant characteristics across species. More comparative work is required before the assumption of conserved masticatory neural circuitry can be substantiated.

5. Problems and issues

This section introduces issues involving chewing rate, F_C, or its inverse chewing cycle duration, T_C. We discuss first the surprising relationships between T_C, which is relatively invariant, and the durations of chewing cycle phases, which are relatively variant. Functional and developmental issues with respect to these relationships will be discussed. Next, we tackle issues and experiments relating the scaling of T_C across species and finish by introducing experiments that beg for better biomechanical models of chewing rhythmicity.

5.1 Chewing cycle invariance and phase variance

Ross, et al. (Ross et al., 2010; Ross et al., 2007b) have described chewing variability via the coefficient of variation, CV,

$$CV = SD / \bar{Y} \quad (1)$$

where SD is the standard deviation of a sample and $\bar{Y}$ is the mean. CV standardizes variation for comparison purposes. It has been used as an uncorrected statistic (equation 1) (Ross et al., 2010; Ross et al., 2007b) or corrected (Gintof et al., 2010),

$$CV = (1 + 1/4n) * SD / \bar{Y} \quad (2)$$

where n is the sample size used in the calculation (see Sokal & Braumann, 1980).

Of interest are two important facts. First, the CV for cycle duration, T_C, is surprisingly low in mammals (21%) compared with lizards (32%) (Ross et al., 2007b). Second, the CVs of the phases, which constitute a cycle (cf. Fig. 2) are relatively high, ranging on average from 38% for FC to 73% for FO. In fact, FO and FC phases are significantly more variant in mammals than they are in lizards, and SC variability is similar in mammals and lizards (Ross et al., 2007b). These findings suggest that time-sharing must occur among cycle phases so that T_C remains relatively constant in mammals.

Investigators have extensively studied the correlations between chewing cycle durations and phase durations and the correlations among phase durations. Below, we review work in this area, which reveals as yet resolved complexities. Further work in this area will provide important insights into neural control mechanisms.

5.1.1 Phase modulation and chewing series (preparatory, reduction, pre-swallow)

Work with cats (Hiiemae, 1976; Thexton et al., 1980) and rabbits (Morimoto et al., 1985) suggested that the durations of opening phases (particularly SO, Fig. 2) were correlated with T_C. By contrast, the durations of the closing phases did not correlate with T_C.

However, further work in rabbits demonstrated that correlations between phase durations and T_C depended on cycle type, viz., Type I (preparatory series), II (reduction series), and III (pre-swallow series) (Schwartz et al., 1989). These investigators found positive correlations between opening phases and T_C during Type I and III chews, but not during Type II chews. Likewise, FC and T_C were positively correlated during Type I and III chews, but not during Type II chews. Also SC and T_C were positively correlated during Type II chews, but negatively correlated during Type III chews. It was concluded that three major changes occurred in the chewing motor program during a chewing sequence (Schwartz et al., 1989).

Although these results suggest that kinematic and functional distinctions are important considerations in understanding phase modulation, there are several other important factors that have profound effects on phase modulation as well (see below).

5.1.2 Phase modulation and food properties

It has been shown in rabbits that food properties can influence the relationship between phase durations and T_C. During Type II (reduction series) chews, the opening and FC phases were positively correlated with T_C when the animals chewed bread, whereas these correlations were not present when the animals chewed rice or rabbit chow (Yamada & Yamamura, 1996). By contrast, SC was positively correlated with T_C when the animals chewed rice; however, this correlation was absent when the animals were chewing on bread or rabbit chow (Yamada & Yamamura, 1996).

5.1.3 Phase modulation in driven chewing

A few studies have been done to determine how individual phases are modulated during driven mastication in humans. This typically involves chewing to the beat of a metronome, starting at speeds similar to that of "natural" chewing and increasing the frequency to several times that of natural chewing. Morimoto, et al. (Morimoto et al., 1984) determined that, although the duration of all phases was reduced as driven chewing speed was increased, it was mainly the durations of the opening phase and the occlusal phase (the occlusal phase being the time when the teeth on both arches are crushing the food) that were most significantly correlated with the reduction in T_C. The duration of closing was not as shortened as were the durations of the opening and occlusal phases during the experimental reduction in T_C via increased metronome speeds. The authors suggested that their results for the opening phase corroborated the findings for the cat (Thexton et al., 1980), which findings we presented in Section 5.1.1; however, because the cat lacks an occlusal phase, the cat would not be expected to have an occlusal phase to modulate.

On the other hand, in a similar experiment performed by Plesh, et al. (Plesh et al., 1987), all phases showed similar reductions in duration as the driven speed of mastication was increased. These investigators concluded that all phases were variant.

We believe it is important to recognize that the metronome-driven chewing studied by these investigators is probably controlled or strongly modulated by the cortex (and possibly by cerebellar circuits). It is highly likely that the cortex plays little role in ongoing mastication of the sort being studied in animal models. Hence, what these human experiments demonstrate is that, even with the cortex heavily involved in the production of mastication, there can be complex phase modulation relationships.

5.1.4 Phase modulation individuality

Many if not all of the studies, above, report considerable variation in mean phase and T_C durations at the individual level. We have recently completed a study of data used in a previous publication (Gerstner & Parekh, 1997), in which 22 healthy adult subjects chewed an 8-10 mm diameter gum base pellet first on the right side and then on the left. Twenty-second samples of right-sided and 20-s samples of left-sided chewing were digitized, and then filtered and processed using the functional data analysis methods we present in our chapter on Functional Data Analysis for Biomechanics.

The results revealed individual differences in phase-T_C correlations. Specifically, of the 44 trials (22 subjects x left- and right-sided chewing trials), 18 had positive correlations between SO and T_C, 15 had positive correlations between FO and T_C, one had a negative correlation between FO and T_C, 7 had positive correlations between FC and T_C, and 14 had positive correlations between SC and T_C. Interestingly, in no case were the same correlations found for the left and right-sided chewing trials for a given subject. These findings suggest two things: (1) that left and right-sided chewing within individuals is unique in terms of phase modulation and (2) that phase modulation is unique among individuals. It is important to recognize that all subjects were chewing gum with the same material properties and probably performing mainly Type II (reduction series) chewing cycles.

This suggests several possibilities to us. First, these findings may be unique to humans. Humans have a dense corticobulbar tract relative to other species. If this tract played a role in modulating chewing phases in our human subjects, it may impart individual-specific characteristics in the form of unique phase modulation patterns.

Alternatively, phase modulation patterns may be species-specific and vary across species. Any species-specificity tendencies that may exist may be further amplified by the heavy inbreeding that occurs among laboratory animals, the various results from which were presented, above. We believe it will be important in future work to determine (a) whether the correlations observed within individuals are stable through time, (b) whether there is evidence of heritability in the patterns, and (c) whether the patterns are species-specific.

Perhaps the most intriguing issues are, why does phase modulation vary within chewing sequences, between foods and between individual humans? And what can comparative studies and carefully-designed experiments tell us about the function, stability and behavior of rhythmic motor programs?

5.2 Why and how is chewing rate allometrically-scaled across mammals?

Chewing cycle duration, T_C, scales with body mass across mammalian species (Druzinsky, 1993; Gerstner & Gerstein, 2008; Ross et al., 2009). The scaling takes the mathematical form:

$$y = aM^b \tag{3}$$

or its logarithmic transformation:

$$\log(y) = b*\log(M) + \log(a) \tag{4}$$

Where y is, for instance, T_C or its inverse F_C, and M is usually a size variable, e.g., body mass, M_B, jaw mass, M_J, or jaw length, L_J. The logarithmic transformation linearizes the relationship between y and M, so that log(a) is the y-intercept and b is the slope. Among mammals, the scaling exponent, b, ranges from 0.14 - 0.20, when $y = T_C$ and $M = M_B$ (Druzinsky, 1993; Gerstner & Gerstein, 2008). Among primates, the scaling exponent ranges from 0.514 – 0.583, when $y = T_C$ and $M = L_J$ (Ross et al., 2009).

The slope or scaling exponent is important for several reasons. For one, it describes the relationship between size and the dependent variable, y, over as many as 10 orders of magnitude in M (e.g., Turvey et al., 1988). Furthermore, in comparative studies, the exponent suggests the existence of laws governing biomechanical, morphological, physiological or behavioral variation within taxa. Also, allometric scaling probably represents the manifestation of general organizing principles. Therefore, the promise is that an understanding of allometric scaling may lead to a better understanding of many biological relationships, including those governing many motor control problems.

F_C ranges from < 1 Hz for large species such as elephants and giraffes to > 7 Hz for small species such as mice. Although the scaling of chewing rate with size makes intuitive sense, there are no unequivocal reasons why or how the scaling comes to be. This opens up several interesting questions, which will form much of the remaining discussion in this chapter.

Biologists believe that the masticatory CPG, including the rhythm-generating CTN discussed previously (Fig. 3), is highly conserved among mammals. If one takes this literally, then all mammalian species should possess a CTN that produces a similar masticatory rhythmicity, i.e., the mean and variance in F_C should be nearly the same within individuals of a species, between individuals of a species, and between species.

Secondly, studies to be discussed, below, have demonstrated that the masticatory rhythm adjusts to load variation, probably via feedback from proprioception during chewing. If we take these results at face value, then all mammals should chew at about the same rate because the masticatory system is designed to hold chewing rate constant despite variation in load, including presumably load variation due to jaw mass.

Obviously, what we are omitting from this literal interpretation is whether size-dependent variation in such things as CTN circuitry, peripheral nerves, muscle contractile properties, the size of orofacial structures, tooth biting surface area, metabolic and vascular properties, etc., can influence the fundamental rhythm generated by the CTN. However, in order to shed light on our issue of interest, we are focusing on the observations and claims reported in the literature that: (1) chewing rate is centrally generated by the CTN, (2) the frequency generated by the CTN is relatively invariant, (3) the CTN is a conserved phenotype across mammals, and (4) proprioception serves to hold frequency relatively constant against variation in load. Given these observations and claims, it is unclear how neurobiological factors are being adjusted so that the size-dependent scaling among mammals occurs. In other words, that chewing rate scales with size indicates that there are details with respect to the timing of chewing and chewing rhythmicity, which need to be elucidated.

5.2.1 Acute oral rhythmicity experiments

An obvious missing 'detail' of the model presented in Section 4 is the possibility that cellular or molecular mechanisms exist that adjust chewing rhythmicity to match load variation due to, say, jaw mass independent of load variation due to food properties. Numerous experiments seem to refute this possibility, however.

Using an anesthetized guinea pig model, which can be made to produce rhythmic chewing upon stimulation to a specific region of the cortex known as the cortical masticatory area (CMA, Fig. 4), Chandler and Goldberg were able to demonstrate that affixing 20- and 50-g weights to the lower jaw did not significantly change the rate of oral rhythmicities, although it did increase both the amplitude and duration of masseter (jaw closer) EMG activity (Chandler et al., 1985). The authors believed this was most likely due to an increase in the excitability of jaw closer motoneurons produced by activation of muscle spindles within the jaw closer muscles.

Similarly, Ross' group recently demonstrated that bite force was modulated during SC, primarily by varying the rate at which force was generated in the jaw closers of macaques (Ross et al., 2007a). In other words, as the resistance in food properties increased, not only did the number of recruited muscle fibers increase, but the rate at which muscle fibers were recruited increased as well, so that the increased load did not significantly impact the

duration of jaw closure. The group hypothesized that the reported low variance in chewing cycle durations might be attributable at least in part to rate modulation of bite force during SC (Ross et al., 2010).
These acute experiments demonstrate that, in the short term, the masticatory neuromotor system seems designed to hold chewing rate constant.

5.2.2 Chronic oral rhythmicity experiments

The above experiments demonstrate that chewing rate adjusts to acute load variations. But what about chronic load variations? Is it possible that chronic-tonic changes in load could lead to rhythm adjustments? That is, might the rhythm adapt to load due to jaw mass by slowing or speeding up accordingly, whereas it would adapt to load due to food stuffs by varying jaw closer muscle recruitment levels?
In order to test this, we placed submandibular gold implants in test rats, which doubled the weight of the jaws, and acrylic implants in control rats, which increased the weight of the jaws by only 10%. We then monitored licking rates for 3 months (Carvalho & Gerstner, 2004). (Licking rates are also relatively invariant. Also, as we presented, above, licking and chewing are believed to share the same CTN.) The licking rates remained not significantly different between test and control animals. Interestingly, each animal maintained an individual-specific licking rate such that individuals could be identified at the study's end by reference to their baseline licking rates.
This study showed that chronically loading the jaws for 3 months did not lead to changes in licking rates. However, this experiment was done in grown rats. Perhaps there is a critical window in development when CTN circuitry is particularly plastic and adaptable to jaw mass or load properties. Two such studies, one using a mutant mouse strain and one using dog breeds of various sizes, have been done that shed light on this issue.
Work has been done with the osteopetrotic mouse (op/op), a genetic mutant that results in unerupted teeth and the lack of an important proprioceptive feedback from mechanoreceptors around the dental roots (Kobayashi et al., 2002b). The question was, do these animals chew similarly to normal mice? Although some aspects of feeding were different between the mutant and normal mice, one surprising feature was that the mean ± SD duration of T_C for the mutant mice was similar to that of normal mice (205.6 ms ± 20.5 vs. 205.5 ms ± 34.0, respectively). The authors concluded that these results suggested that the CPG may be genetically pre- programmed, needing no feedback from peripheral receptors to develop.
We evaluated 31 dog breeds in conjunction with 31 size-matched non-domestic mammalian species as a control group with body masses ranging from about 2 kg – 50 kg in both groups. For the dog breeds, T_C did not scale to M_B ($r = 0.299$, $P > 0.1$) nor to L_J ($r = 0.33$, $P > 0.05$); however, T_C did scale to M_B among the mammalian species ($r = 0.63$, $P < 0.001$). We interpreted the results for the dogs to mean that the CTN rhythmicity does not necessarily adjust, even in developmental time scales to the size of the adult animal. The fact that we did see T_C - M_B scaling in the size-matched non-domestic mammals suggested to us that we should have seen scaling in the dogs if scaling necessarily occurred.

5.2.3 Hypothesis 1: Scaling is a result of natural selection

The dog-study results suggested to us that allometric T_C - M_B scaling may be due to natural selection, based on the following arguments. First, the non-domestic mammals manifested

T_C - M_B scaling, indicating that non-domestic species possess chewing rates that scale to M_B. Moreover, all members of a given non-domestic species manifested similar T_C durations and M_B. These results would most likely occur via one of two means: (1) if M_B and T_C were genetically inherited, or (2) if T_C came to scale with M_B as a result of neural feedback in developmental time scales.

If the results had occurred via the first means, i.e., that M_B and T_C were genetically inherited, then M_B and T_C could either be regulated by independent genes, or they could be regulated by the same genes, and thus represent a pleiotropy.

If both M_B and T_C were regulated by independent genes, then the observed T_C - M_B scaling would suggest that the scaling was a result of selection. Alternatively, if T_C - M_B scaling were a pleiotropy, then the scaling should have been observed in the dog breeds. This is because, as breeders select for specific M_B, T_C would have been modified as well. This was not the case, suggesting that M_B and T_C are genetically independent.

It is also important to note that we specifically evaluated L_J in the dogs. Breeders have selected for variation in head size independently of M_B in many breeds. Hence, it is revealing that the dog breeds manifested a lack of either T_C - M_B scaling or of T_C – L_J scaling, because this argues against both the pleiotropy hypothesis and the neural control hypotheses. Based on these results, it would appear that chewing rate may be genetically inherited, and that the scaling occurs as a result of natural selection mechanisms.

5.2.4 Hypothesis 2: Chewing rate is fixed during a critical developmental window

The "selection" hypothesis, above, is primarily based on work with adult animals. It is important to stress that the developmental studies of dogs and guinea pigs presented in Section 4.1.3 suggest an alternative hypothesis, which considers infant size.

The infants of most dog breeds are similarly sized for several weeks before weaning (Hawthorne et al., 2004). If canid T_C were adjusted to scale with L_J or M_B during an early developmental window prior to weaning, then T_C - M_B scaling would not be observed among adult dogs representing breeds differing significantly in adult M_B.

By contrast, there is a correlation between adult M_B and infant M_B among many mammals (Calder, 1996). As for the dogs, if T_C were adjusted to L_J or M_B during an early developmental window prior to weaning in the mammals we studied, then T_C - M_B scaling would be observed among the adult mammals as a result of the correlation between adult and infant M_B.

Given that the erupting teeth appear to play a role in the development of rhythmicity (Section 4.1.3), it seems plausible that the duration of the adult T_C could be determined during a critical developmental window. We would hypothesize that during this window, the nascent CTN circuitry could have its rhythmic output adapted to load due to jaw size, tongue size, oral cavity size, size of a mouthful of ingestant, etc. via peripheral feedback. After this critical window closes, the CTN would only be able to adjust to load variations by modulating muscle recruitment to hold the rhythm constant. The rhythm frequency carried into adulthood would then reflect the time at which the CTN circuitry reached a critical maturation point and/or the time at which the sensory systems modulating muscle recruitment matured.

To begin evaluating the potential role of development, we have undertaken studies of humans between the ages of 4 – 6 yrs (n=20), 11 – 13 yrs (n=20) and 18 - 21 yrs (n=20), sampling mean chewing rates by videotaping gum chewing for 2 minutes and calculating L_J

using lateral cephalograms, a radiograph of the head in the sagittal plane used by orthodontists to perform morphometric analyses of jaw sizes. Our preliminary results suggest that T_C continues to slow down during childhood and adolescence. Hence, a critical developmental window does not appear to occur in human chewing rhythmicity.

However, as introduced earlier in the chapter, humans are characterized by a large corticobulbar fiber tract, which is not present in most other mammalian species. It is possible that this tract provides a means, relatively unique to humans, for continuous adaptation of the oral rhythm. Intriguingly in this regard, the changes in chewing rhythm appear to correlate better with biological age than with L_J among our subjects. This may suggest that CTN maturation is delayed among humans but not indefinitely so.

Why would adjustments leading to T_C – LJ or T_C – M_B scaling during development be critical? Mammals as endotherms require significant energy for sustenance, and maternal milk production in conjunction with infant suckling are two inextricably linked mammalian characteristics necessary for mammalian infant survival. Efficient ingestion of milk is, therefore, critical to individual survival. It has been suggested that the invariant rhythmicity of chewing, with the rhythmicity matched to the natural resonance frequency of the jaw, are necessary for efficient energy acquisition and food processing (see Ross et al., 2010 for a review). Although this suggestion has been made for chewing in adult animals (Ross et al., 2010), it is arguable that an efficient suckling rhythm is even more critical for infant survival.

To evaluate the efficiencies associated with masticatory rhythmicity, we have begun studies of the metabolic costs of chewing at various rates. These have proven somewhat challenging, as the increase in metabolic rate associated with chewing is very small compared to resting metabolic rate. This, however, may be rather telling; if metabolic costs associated with chewing are easily lost in the fluctuations of resting metabolic rate, how metabolically costly can chewing be? If we confirm that chewing at different rates does not result in significant metabolic changes, it will be important to turn our attention to metabolic issues associated with suckling in infancy. If metabolic issues are more significant in infant suckling than in adult chewing, this would provide some important clues as to why the rhythmicity would be determined in infancy and not in adulthood.

5.2.5 Other chewing rhythm observations

Numerous biomechanical models have been presented in the literature to predict the relationship between L_J and T_C (Druzinsky, 1993; McMahon, 1975, 1984; Ross et al., 2009; Turvey et al., 1988). These models predict that L_J is directly proportional to T_C and, therefore, inversely proportional to F_C. In other words, as the length of the jaw lever arm (L_J) increases, F_C should decrease and T_C should increase.

As the food shifts from the front of the mouth during preparatory series chews to the back of the mouth during pre-swallow series chews, L_J, defined by where the food is with respect to the jaw joint fulcrum, gets progressively shorter (Fig. 5). Therefore, if chewing could be approximated by any of the lever-arm models, one would expect that the preparatory series chews would have relatively long durations and pre-swallow series chews would have relatively short durations. However, this is the opposite of what is seen, as the shortest-duration chews occur at the beginning of chewing sequences and the longest-duration at the end of chewing sequences (Fig. 1). This observation indicates that, within individuals, T_C does not appear responsive to feedback regarding the functional L_J; rather, T_C is being

determined by the cycle type. Therefore, whatever is responsible for modulating cycle type is key in this regard.

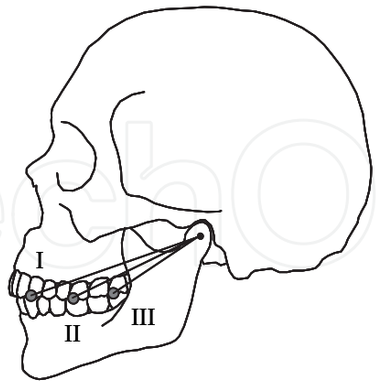


Fig. 5. Jaw lever lengths for preparatory (I), reduction (II) and pre-swallow (III) series cycles.

In humans, males have larger jaws (longer L_J) than females. Therefore, the lever-arm models would predict that males should chew more slowly than females. However, adult human males chew more rapidly than age-matched young adult females (F_C = 1.4 Hz ± 0.3 for 45 males versus 1.2 Hz ± 0.3 for 44 females; our unpublished observations).

Males tend to have more masticatory muscle mass, and male masticatory muscle tends to have more fast fatigable fibers than does female masticatory muscle. Thus, an important set of studies should be performed to identify the relationship between gender, chewing rate and muscle fiber characteristics. Additionally, if results of other studies determine that the rhythmicity is determined during infancy (Section 5.2.4), it would be critical to identify relationships between gender and suckling with respect to gender-specific chewing rates.

These observations suggest some of the intellectual challenges to understanding masticatory control. One important challenge is to develop appropriate biomechanical models of mastication and/or suckling. Another challenge will be to understand the role and function of chewing cycle phases, especially with respect to why phases are added or deleted from ongoing chewing sequences. Finally, it will be critical to identify why and how chewing cycle rhythmicity is so tightly controlled.

6. Conclusion

Rhythmic oral behaviors are under-represented in biomechanics studies; however, the neural mechanisms that produce them, coupled with the biomechanical issues of moving the jaw, tongue and teeth during behaviors such as mastication, licking and suckling present challenges to traditional biomechanical modeling and thinking. Oral rhythmicities are generated by a central timing network, CTN, and associated proprioception, which together produce a relatively invariant rhythmicity. Load variability results in modulation of the rate of muscle recruitment, which results in a chewing rhythm with low variability. Most of the variability in the chewing rhythm is linked to shifts between chewing cycle types. Numerous studies and observations indicate that traditional pendulum and mass-spring biomechanical models are inadequate. The rhythm may be set early in infancy during suckling or it may be genetically pre-programmed and matched to jaw size via natural selection to produce efficient chewing. The problems with understanding the jaw system

may expose limitations in other biomechanical models and provide new challenges to more traditional biomechanics studies and paradigms. Future studies will require approaches as diverse as neuroscience, evolutionary, developmental, and comparative biology in order to address biomechanical problems effectively. Because the oral system is a feature shared among humans, mammals and most vertebrates, these studies promise broad impacts and insights to biomechanical issues.

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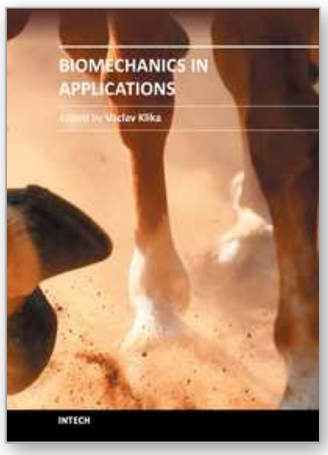
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During last couple of years there has been an increasing recognition that problems arising in biology or related to medicine really need a multidisciplinary approach. For this reason some special branches of both applied theoretical physics and mathematics have recently emerged such as biomechanics, mechanobiology, mathematical biology, biothermodynamics. The Biomechanics in Application is focusing on experimental praxis and clinical findings. The first section is devoted to Injury and clinical biomechanics including overview of the biomechanics of musculoskeletal injury, distraction osteogenesis in mandible, or consequences of drilling. The next section is on Spine biomechanics with biomechanical models for upper limb after spinal cord injury and an animal model looking at changes occurring as a consequence of spinal cord injury. Section Musculoskeletal Biomechanics includes the chapter which is devoted to dynamical stability of lumbo-pelvi-femoral complex which involves analysis of relationship among appropriate anatomical structures in this region. The fourth section is on Human and Animal Biomechanics with contributions from foot biomechanics and chewing rhythms in mammals, or adaptations of bats. The last section, Sport Biomechanics, is discussing various measurement techniques for assessment and analysis of movement and two applications in swimming.

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