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MASTICATORY MUSCLES AND THE SKULL: A COMPARATIVE PERSPECTIVE

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Abstract

Masticatory muscles are anatomically and functionally complex in all mammals, but relative sizes, orientation of action lines, and fascial subdivisions vary greatly among different species in association with their particular patterns of occlusion and jaw movement. The most common contraction pattern for moving the jaw laterally involves a force couple of protrusor muscles on one side and retrusors on the other. Such asymmetrical muscle usage sets up torques on the skull and combines with occlusal loads to produce bony deformations not only in the tooth-bearing jaw bones, but also in more distant elements such as the braincase. Maintenance of bone in the jaw joint, and probably elsewhere in the skull, is dependent on these loads.

Keywords

mastication; masticatory muscles; mammals; bone strain

INTRODUCTION

Although mastication is a hallmark attribute of mammals, there is great diversity of all its components. Ignoring very specialized feeding systems such as those of whales and anteaters, this discussion will concentrate on typical mastication, addressing differences among species commonly used in research. Masticatory muscle activation and coordination determine the direction of jaw movement, control occlusal force, and deform the skull in a variety of ways. The critical features to understand, then, are action line, force production, and relationship to the cranium. Action line and force production are not as straightforward in the complicated masticatory muscles as in limb muscles, which tend to be arranged more linearly. Similar difficulties with the irregularly shaped skull make the effect of muscles on the bones challenging to model. Thus this short review will emphasize empirical data from electromyography (EMG) and *in vivo* recordings of bone strain.

COMPLICATED MUSCLES

One feature in common among mammals is the size and complexity of the muscles of mastication, which occupy much of the head. In terms of size, it is customary to examine the relative mass of individual jaw muscles as a percentage of the whole.¹ This procedure illuminates the contrast between species whose masticatory apparatus is dominated by the temporalis muscle (typically generalized species and specialized carnivores with a hinge-like

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TMJ like cats) and those that emphasize the masseter and medial pterygoid (typically omnivores like primates or herbivores like rabbits, with anteroposterior mobility of the TMJ). However, standardizing each muscle mass to the total masticatory mass obscures whether there are differences in the relative size of the total masticatory mass relative to head size, which remains an unanswered question.

Although the same basic terminology (e.g., “masseter” and “lateral pterygoid”) is used for all mammals, it is important to realize that these names are based on bony attachment areas and not on function. The anteriorly directed, fascially subdivided superficial masseter muscle of rodents has little functional resemblance to its relatively vertical and unitary human counterpart.

The jaw muscles have broadly distributed origins and insertions on the skull and mandible, but the main factor that contributes to functional complexity is the fact that most muscle fibers attach to internal aponeuroses rather than to the bones directly. Necessarily, fibers that attach to different surfaces of an aponeurosis must have different orientations, raising the possibility that differential contraction of fibers could change the direction of muscle pull, a possibility that has been confirmed in a variety of masticatory muscles.^{2–5} Thus, action line is not a constant, but varies dynamically throughout a masticatory cycle. Distortion of aponeuroses from stretching or folding could alter fiber direction even more, but results from one muscle, the pig masseter, indicate that aponeurotic stretching is limited to no more than about 5% linear strain.⁶

MUSCLES AND MOVEMENTS

Both the muscles and the dentition are determinants of the direction of the power stroke. Teeth play a larger role when they provide an inclined plane, keeping the direction of jaw movement medial even the muscle resultant is vertical or slightly lateral.⁷ Examples include rabbits and many ungulates and rodents. Muscles become more significant when irregular occlusal surfaces do not define a plane, i.e. the low-cusped molars of pigs. Age changes in power stroke are independent of occlusal development in pigs but may relate to muscle vectors.⁸

Muscle anatomy both causes and reflects jaw movement. Muscles (or parts of muscles) may be mostly rotatory (open/close) or mostly translatory (anterior/posterior or medial/lateral). The relative importance of upward, medial, and anterior components in the power stroke is associated with startlingly different muscle anatomy. Thus we can explain why the lateral pterygoid is small and unimportant in carnivorans such as cats and ferrets but huge in humans, and why the masseter of rodents is specialized and subdivided. There are some surprises. Parts of the medial pterygoid and/or masseter in several species open the jaw rather than closing it,^{2, 9} raising some interesting questions about neural circuitry (Fig. 1).

Most mammals with transverse masticatory excursions use a combination of muscles referred to as either “couples”¹⁰ or “triplets”¹¹, consisting of the superficial masseter and medial pterygoid of one side and the temporalis of the opposite side, with the jaw moving toward the temporalis side. This clearly reflects the fact that temporalis-side condyle is moving posteriorly relative to the masseter-side condyle, i.e., the movement is a rotation. The deep masseter, which typically has a posterior vector, usually acts with the temporalis rather than the superficial masseter. In recognition of this functional difference, comparative anatomists often use the name “zygomaticomandibularis” for the deep masseter.

MUSCLES, MASTICATION AND THE BIOMECHANICS OF THE SKULL

Masticatory muscles, through their direct action on bony attachments and their indirect action in loading the teeth and the jaw joints, constitute the major biomechanical challenge to the

skull. Direct vs. indirect effects differ. Direct effects of a muscle attachment are sensitive to the particular muscles used and to the pattern of muscle coordination. For example, the temporalis and masseter twist the pig braincase in opposite directions,¹² and because these muscles usually act in opposite-side “couples”, the effect is exaggerated rather than cancelled.

Indirect effects depend on global features such as total muscle force and the particular teeth in occlusion. With regard to total muscle force, the point is simply that the muscles collide the mandible with the upper jaw and thus engender reaction forces at points of contact, specifically the teeth and the TMJs. The former is occlusal force, and its major influence on the skull is to shear the maxilla upward and the mandible downward.¹³ The reaction force on the TMJs arises from lever mechanics and the fact that the resultant muscle force rarely if ever passes through the bite point.¹⁴ Depending on the particular species, however, it is clear that there are major differences in the geometry of the muscle resultant and hence the relative magnitude of the TMJ reaction load. In particular, rodents and rabbits likely unload at least one TMJ during chewing,^{15, 16} whereas carnivorans probably have relatively large TMJ loading.¹⁷

The creation of occlusal force is, of course, the reason we have jaw muscles. For deformation of the skull, an important determination is whether occlusion is unilateral or bilateral. Many mammals have jaws so anisognathous that only one side at a time can be in molar occlusion. Strain gage readings from the mandible and braincase are highly asymmetrical during chewing in such animals. For example, working and balancing mandibular bodies show opposite directions of bending because of the influence of the unilateral bite point.¹⁸ Other groups, including many rodents, pigs, and higher primates, have some probability of occlusal contact occurring on the balancing side, and may even have a bilateral bolus and true bilateral chewing. Thus in pigs, mandibular and maxillary strains are identical on the working and balancing sides.¹³ In fact, the only part of the pig skull that strains differently depending on the side of chewing is the premaxillary, because incisor occlusion, unlike molar occlusion, is one-sided.¹⁹

Like occlusal force, TMJ loads are reactions to muscle pull. The balance between occlusal and joint force is a product of muscle anatomy and contraction pattern. In pigs, with their bilateral occlusion and similar magnitudes of EMG on the two sides, bone strains at the TMJ are symmetrical.¹³ In contrast, mammals with anisognathous occlusion or asymmetrical muscle forces are expected to have heavier loading on the balancing side.²⁰

A final location of interest is the mandibular symphysis. An unfused symphysis is the primitive condition and can act either as a facilitator of unilateral occlusion²¹ or as the means by which a bilateral occlusion can be maintained throughout the duration of the power stroke.²² Symphyseal fusion has been independently acquired in a number of lineages, including that leading to humans, and is associated with the timing and level of recruitment of the balancing side muscles. Like higher primates, pigs have strong recruitment of balancing side muscles as part of the force couple mechanism for moving the mandible laterally. The pig symphysis begins to ossify at about the time of complete weaning. Strains recorded from the unfused symphysis are large, generally similar in magnitude to those from unfused sutures. After fusion begins, strain magnitudes drop to the same level as typically seen for solid bones. During jaw opening the pattern of deformation is generally consistent with medial transverse bending, which has also been reported in macaques²³ and humans.²⁴ This deformation is attributed to the medial pull of the lateral pterygoid muscles.²⁵ However, during closing the pattern of strain is not the simple lateral transverse bending expected,²³ but rather reveals a tendency of the mandibular bodies to rotate around their long axes.²⁶ In large part, this is also likely to be a direct effect of muscle contraction, particularly the rotational forces arising from the masseter.

HOW DOES THE MASTICATORY SYSTEM COPE WITH LOSS OF A MUSCLE?

The choreographed interplay within and between the complicated masticatory muscles focuses attention on whether, and how, mastication would be changed if one muscle or even just one muscle compartment were incapacitated. This question might seem arcane, because most neuromuscular diseases attack indiscriminately and would not target single muscles. However, it is increasingly common these days for patients to have single muscles paralyzed, not only for therapeutic, but also for cosmetic reasons.^{27, 28}

To some extent, the answer depends on which muscle and species. The loss of one muscle may be less of a problem for those taxa in which the inclined planes of the teeth guide the power stroke (such as rabbits) than for those that depend on muscle choreography (such as pigs). Unilateral paralysis of the masseter muscle in rabbits using botulinum toxin did not prevent the animals from chewing on both sides,²⁹ perhaps because the inclined plane of the occlusion sufficed to control movement. In contrast, pigs in which the masseter was temporarily inactivated by procaine exaggerated their jaw movements although they also continued to use both sides.³⁰

In order to maintain occlusal force, however, all species would be expected to increase the recruitment level of synergists. Muscle weights suggested that the unparalyzed masseter in the rabbits had hypertrophied.²⁹ The pig experiment was short-term, but EMG showed that the masseter's synergists for transverse movements, i.e. the ipsilateral pterygoids and the contralateral temporalis, were overactive,³⁰ a condition that would be expected to lead to hypertrophy.

It is also likely that such changes in muscle usage would alter skull loading. Both the masseter and medial pterygoid create similar strain magnitudes on the pig mandibular condyle, but the orientation of strain is unique for each muscle.³¹ Therefore, if one masseter were incapacitated, total joint load would not only be reduced, but also re-oriented. If such conditions were long maintained, as for example with botulinum toxin, bony adaptations would be likely. The growing rabbits in the study by Matic²⁹ developed smaller condyles on the paralyzed side, presumably because of decreased loading. Our own preliminary data on adult rabbits suggest that bone strain in the condyle is indeed reduced by paralysis of the ipsilateral masseter, and that this unloading leads to massive bone loss in the condyle (Fig. 2).

CONCLUSION

Muscle action and skull biomechanics are inextricably intertwined. In the evolutionary sense, the muscles of mastication are co-adapted with dental morphology and jaw movements to produce species-specific chewing patterns. In the physiological sense, masticatory muscles comprise the major loading on the skull, influencing its growth and controlling its strength.

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References

1. Turnbull WD. Mammalian masticatory apparatus. *Fieldiana: Geology* 1970;18:149–356.
2. Herring SW, Grimm AF, Grimm BR. Functional heterogeneity in a multipinnate muscle. *Am J Anat* 1979;154:563–576. [PubMed: 433798]
3. Wood WW. A review of masticatory muscle function. *J Prosth Dent* 1987;57:222–232.

4. Blanksma NG, van Eijden TMGJ, van Ruijven LJ, Weijs WA. Electromyographic heterogeneity in the human temporalis and masseter muscles during dynamic tasks guided by visual feedback. *J Dent Res* 1997;76:542–551. [PubMed: 9042076]
5. Turkawski SJJ, Van Eijden TMGJ, Weijs WA. Force vectors of single motor units in a multipennate muscle. *J Dent Res* 1998;77:1823–1831. [PubMed: 9786639]
6. Herring, SW.; Agazzi, M.; Emry, PK.; Peterson, JA. Mammalian jaw muscles: growth and *in vivo* behavior of an aponeurosis. In: Aerts, P.; D'Août, K.; Herrel, A.; Van Damme, B., editors. *Topics in Functional and Ecological Vertebrate Morphology*. Maastricht: Shaker Publ BV; 2002. p. 105-124.
7. Becht G. Comparative biologic-anatomical researches on mastication in some mammals. *Konink Nederl Akad Wetensch Ser C* 1953;56:508–527.
8. Obrez A. Mandibular molar teeth and the development of mastication in the miniature pig (*Sus scrofa*). *Acta Anat* 1996;156:99–111. [PubMed: 8993629]
9. Chen EK, Herring SW. An unusual function for the medial pterygoid muscle in the guinea pig. *Arch Oral Biol* 1986;31:781–783. [PubMed: 3479066]
10. Herring SW, Scapino RP. Physiology of feeding in miniature pigs. *J Morphol* 1973;141:427–460. [PubMed: 4760635]
11. Weijs, WA. Evolutionary approach of masticatory motor patterns in mammals. In: Bels, VL.; Chardon, M.; Vandewalle, P., editors. *Biomechanics of Feeding in Vertebrates*. Berlin: Springer-Verlag; 1994. p. 281-320.
12. Herring SW, Teng S. Strain in the braincase and its sutures during function. *Am J Phys Anthropol* 2000;112:575–593. [PubMed: 10918130]
13. Herring SW, Rafferty KL, Liu ZJ, Marshall CD. Jaw muscles and the skull in mammals: the biomechanics of mastication. *Comp Biochem Physiol A* 2001;131:207–219.
14. Hylander WL. The human mandible: lever or link? *Am J Phys Anthropol* 1975;43:227–242. [PubMed: 1101706]
15. Weijs WA, Dantuma R. Electromyography and mechanics of mastication in the albino rat. *J Morphol* 1975;146:1–34. [PubMed: 1171253]
16. Weijs WA, Dantuma R. Functional anatomy of the masticatory apparatus in the rabbit (*Oryctolagus cuniculus* L). *Netherlands J Zool* 1981;31:99–147.
17. Herring, SW. Animal models of temporomandibular disorders: how to choose. In: Sessle, BJ.; Bryant, PS.; Dionne, RA., editors. *Temporomandibular Disorders and Related Pain Conditions*. Seattle: IASP Press; 1995. p. 323-328.
18. Thomason JJ, Grovum LE, Deswysen AG, Bignell WW. *In vivo* surface strain and stereology of the frontal and maxillary bones of sheep: implications for the remodeling and mechanical optimization of cranial bones. *Anat Rec* 2001;264:325–338. [PubMed: 11745088]
19. Rafferty KL, Herring SW, Marshall CD. The biomechanics of the rostrum and the role of facial sutures. *J Morphol* 2003;257:33–44. [PubMed: 12740894]
20. Greaves WS. The jaw lever system in ungulates: a new model. *J Zool* 1978;184:271–285.
21. Scapino RP. The third joint of the canine jaw. *J Morphol* 1965;116:23–50. [PubMed: 14294954]
22. Weijs WA. Mandibular movements of the albino rat during feeding. *J Morphol* 1975;145:107–124. [PubMed: 1111422]
23. Hylander WL. Stress and strain in the mandibular symphysis of primates: a test of competing hypotheses. *Am J Phys Anthropol* 1984;64:1–46. [PubMed: 6731608]
24. Chen DC, Lai YL, Chi LY, Lee SY. Contributing factors of mandibular deformation during mouth opening. *J Dentistry* 2000;28:583–588.
25. DuBrul, EL.; Sicher, H. *The Adaptive Chin*. Springfield, IL: Charles C. Thomas; 1954.
26. Herring, SW.; Rafferty, KL.; Liu, ZJ.; Sun, Z. A nonprimate model for the fused symphysis: *in vivo* studies in the pig. In: Vinyard, CJ.; Ravosa, MJ.; Wall, CE., editors. *Primate Craniofacial Function and Biology*. Kluwer; Accepted
27. Bakke M, Moller E, Werdelin LM, Dalager T, Kitai N, Kreiborg S. Treatment of severe temporomandibular joint clicking with botulinum toxin in the lateral pterygoid muscle in two cases of anterior disc displacement. *Oral Surg Oral Med Oral Pathol Oral Radiol Endod* 2005;100:693–700. [PubMed: 16301150]

28. To EW, Ahuja AT, Ho WS, King WW, Wong WK, Pang PC, et al. A prospective study of the effect of botulinum toxin A on masseteric muscle hypertrophy with ultrasonographic and electromyographic measurement. *Br J Plast Surg* 2001;54:197–200. [PubMed: 11254408]
29. Matic, DB. MS Thesis, Medical Biophysics. London: Ont.: Univ. West. Ont.; 2005. The effects of masseter muscle paralysis on facial bone growth in a rabbit model.
30. Huang X, Zhang G, Herring SW. Alterations of muscle activities and jaw movements after blocking individual closing muscles in the miniature pig. *Arch Oral Biol* 1993;38:291–297. [PubMed: 8517800]
31. Rafferty KL, Sun Z, Egbert MA, Baird EE, Herring SW. Mandibular mechanics following osteotomy and appliance placement. II. Bone strain on the body and condylar neck. *J Oral Maxillofac Surg* 2006;64:620–627. [PubMed: 16546641]

Figure 1.

Anatomy and EMG of the masseter muscle in the caviomorph rodent, *Kerodon rupestris*. A. Superficial view; the arrow indicates the posterior masseter, which inserts on the condylar process. B. Overlying layers of the masseter removed to show the posterior masseter (asterisk). C. EMG of right-side muscles during ingestion and mastication. The posterior masseter is mainly active in protrusion during ingestion (open arrows) and acts with the digastric in opening the jaw. MedPt: medial pterygoid; Mlat: lateral masseter; Mmain: main (middle) masseter; Mrefl: pars reflexa of superficial masseter; Mpost: posterior masseter; Dig: digastric muscle.

Figure 2. Coronal μ CT slices through the mandibular condyles of a rabbit (*Oryctolagus cuniculus*) that had received an injection of type A botulinum toxin into one masseter 29 days before sacrifice. A. Intact side condyle. B. Paralyzed side condyle. The relative volume of trabecular bone on the paralyzed side is 17% less than on the intact side.