J Musculoskel Neuron Interact 2003; 3(4):391-394

Hylonome

Review Article

TMJ anatomy and animal models

S.W. Herring

Department of Orthodontics, University of Washington, Seattle, WA , USA

Keywords: Temporomandibular Joint, Biomechanics, Animal, Mastication

General and specialized characteristics of the TMJ

The temporomandibular joint (TMJ) is a cardinal feature that defines the class Mammalia and separates mammals from other vertebrates. As befits its late evolutionary origin, the TMJ also makes a tardy developmental appearance[1]. The TMJ is interesting because its constituent bones, the mandible and the squamous temporal, are intramembranous in origin. Thus, the tissue that covers each articulating surface is a secondary cartilage with a fibrous skin, derived from the periosteum. Another nearly constant feature is the intra-articular disc. The disc, even when incomplete, is associated with the lateral pterygoid muscle[2], which has led some authors to speculate that it arose as a tendon which became pinched by the new joint[3].

An additional interesting feature of the TMJ is its role in growth. Intramembranous bones do not have epiphyseal plates, but their growth is effected (or at least affected) by nearby cartilaginous structures. In the cranium, the cranial base cartilages and the nasal septum are thought to be the major drivers of growth at cranial sutures[4]. It seems likely that in most vertebrates, Meckel's cartilage performs a similar role for the multiple bones of the lower jaw. The evolution of the TMJ accompanied the almost complete removal of Meckel's cartilage from the sutureless lower jaw of mammals, thus eliminating this mechanism of growth. The substitute is the secondary condylar cartilage, which is a major growth site in addition to being an articular covering.

Despite its status as a mammalian identifier, the TMJ shows remarkable morphological and functional variation in different species, reflecting not only the great mammalian adaptive radiation in feeding mechanisms, but also a freedom from constraints such as bearing body weight. The most extreme evolutionary variants include: (1) loss of the synovial cavity in some baleen whales; (2) loss (or possibly primitive absence) of the disc in monotremes, some marsupials, and some edentates (anteaters and sloths)[2,5]; (3) variations in the orientation of the joint cavity from parasagittal (many rodents) to transverse (many carnivorans); and (4) reversal of the usual convex/concave relationship so that the mandibular condyle becomes the female element (many artiodactyl ungulates such as sheep and cattle[6]). In addition, the relative size of the joint is exceedingly variable. Soft tissue details such as capsular ligaments[7] and collagen orientation in the disc[8] are also highly species-specific.

The striking anatomical differences in TMJs are clearly tied to biomechanics. The features mentioned above are either correlates of loading (e.g., size of articular surfaces) or movement (e.g., orientation of the joint) or both. Loading of the TMJ is a reaction force arising from the contraction of jaw muscles; its magnitude depends strongly on the position of the bite point relative to the muscle action line. The evolution of the TMJ is thought to have coincided with a period of low reaction loads, with higher loading having evolved repeatedly in different lineages[9], including our own. Many commonly used laboratory animals, especially rodents, fall in the category of minimal TMJ loading, especially during chewing. In contrast, carnivorans such as dogs probably sustain TMJ loads that are higher than those in primates[10]. Complex movement in three planes of space is also a primitive characteristic of the TMJ, at least if embryology is any indication[3], but there is no uniformity in how movements are accomplished. Opening of the jaw usually involves a combination of forward sliding and rotation around a transverse axis, but some carnivorans have lost the ability to slide and some specialized anteaters instead use a rotation around the long axis of the curved mandible[5]. Similarly, transverse movement is usually accomplished by moving one condyle forward and the other one backward, but carnivorans use a combination of lateral sliding and rotation around the long axis of the mandible[11].

Animal models for TMJ research - a literature survey

TMJ research on animal models has not lagged in com-

The author has no conflict of interest.

Corresponding author: Susan W. Herring, Ph.D., Professor, Orthodontics, University of Washington School of Dentistry, Box 357446, Seattle, WA 98195-7446, USA
E-mail: herring@u.washington.edu

Accepted 1 August 2003

parison to other joints. A May, 2003 Medline search for "TMJ and animal" yielded 952 hits overall, a distant second place to the number of citations for the knee but well ahead of those for other body parts (Table 1).

In the last 20 years, animal-based publications on TMJ research have increased from 17 papers per year in 1968-82 to an average of over 80 per year in 2000-02. At the same time, there have been striking changes in the species used. Interestingly, the genetic revolution has not revolutionized TMJ research. The proportion of TMJ publications using mice has remained steady at 6-7% over the entire time period. Probably this reflects the physical difficulty of working on tiny mouse joints, but in addition it surely points to a lack of interest in the TMJ on the part of geneticists.

What has changed the most is use of primates. In 1973-82, monkey studies accounted for 37% of animal TMJ work, but in 1998-2003 this percentage dwindled to 6%. Work on dogs and cats also declined, from 18% to 6%. The slack has been taken up by rats (from approximately 22% to 37%), rabbits (from 6% to 22%), and surprisingly, artiodactyl ungulates (pigs, sheep, goats and cattle, increasing from approximately 10% to 24%). The most likely reason for this changeover is pressure from animal protection groups.

Although harder to characterize, some of the changes in species chosen are related to changes in research questions. The increased use of rats is largely related to a burgeoning of research involving nociception and the nervous system (32 papers in 1998-2003 vs 4 in 1973-82). Rabbits were introduced as models for TMJ disease, including disc displacements and inflammatory conditions. The ungulates are mostly favored for material property measurements and for the more elaborate surgical procedures that formerly utilized primates and carnivorans.

Search Term	Number of Citations
Knee Joint and Animal	3649
TMJ and Animal	952
Hip Joint and Animal	800
Tarsus and Animal	728
Ankle Joint and Animal	448
Shoulder Joint and Animal	310
Intervertebral Joint and Animal	198

Table 1. Results of a Medline search.

Are rats, rabbits, pigs, sheep, goats and cattle adequate as TMJ models?

Whether or not a given animal model is appropriate obviously depends on what problem the model is supposed to address. On a basic biological level, for example, the response of mesenchymal cells to a certain type of loading or a certain cytokine, the species may not matter. Indeed, for such general problems, one might not need a TMJ. Despite their unusual origin, it has not been demonstrated that TMJ cells are physiologically different from cells of other joints. Some "TMJ research" could probably be conducted using more conveniently located joints such as the knee. For more specific questions, however, the joint and the species clearly do matter.

One might ask, in view of my earlier comments on mechanics, whether a switch from primate and carnivoran models to rodents, lagomorphs and artiodactyls has been wise. These species have emerged as preferred TMJ models for practical reasons, not because their TMJs are particularly similar to those of humans. I would argue, however, that we are better off with these diverse groups. The relative proximity of the monkey and human lineages is no guarantee of similarity in TMJ function. If representatives of three different mammalian orders (Rodentia, Lagomorpha and Artiodactyla) all support a given finding, the chances are good that the finding will be valid for humans too[12]. A comparative approach will be especially useful to determine the generality of genetic influences, pain mechanisms, and inflammatory responses.

The one area which remains a problem is function, because muscles, movements, and joint loads are so species-dependent. A perfect animal mimic of human function is an impossibility, because the human TMJ is unique in several features, such as the comparatively enormous lateral pterygoid muscle[13]. However, it will clearly help if researchers have a good understanding of how the TMJ functions in their model organisms. Thus, I will conclude with short descriptions and key references for the TMJs of the currently most popular species.

Sheep, goats and cattle are closely related ruminant artiodactyls and have essentially identical TMJs. This group of ungulates has a distinctive jaw apparatus specialized for an herbivorous diet[14,15]. As mentioned above, the condyle is the concave element. The TMJs are specialized for great mobility in the transverse plane but limited opening. The mandibular symphysis is patent and flexible, permitting long axis rotation of the mandible. Although the TMJ has not received much attention, muscle activity patterns and loading of facial bones have been well described[16-18].

Despite belonging to the same order (Artiodactyla) as the ruminants, pigs have a totally different TMJ, actually surprisingly similar to that of higher primates. For this reason, their jaw joint anatomy and function have been well investigated[7]. Moderate movements in all planes are permitted[19], and the symphysis is fused, as in humans. The condyle is compressed and probably twisted during chewing[20], whereas the lateral surface of the temporal bone is bent[21]. More general features of pig oral behavior and muscle contraction are known as well[22-25].

Rabbits have converged with the ruminants in terms of their occlusal pattern and masticatory movements[14] but the condyle is rounded (more so than in primates and pigs) and the symphysis is immobile (but unfused). Rabbit TMJs have a pronounced antero-posterior component which is utilized in certain masticatory movements[26]. There is a rich literature on masticatory function in rabbits[27-30], including calculations of TMJ loads based on muscle activity[26,31]. Interestingly, the working side condyle may be completely unloaded during the power stroke of chewing in rabbits[26].

The rat (and mouse) TMJ is highly specialized for extensive protrusive movements, much more so than the rabbit. The rounded condyle travels in a trough-like temporal fossa and the power stroke is in the protrusive direction with only a minor medial component[32]. Long-axis rotation can occur around a mobile symphysis. Calculations indicate that neither the working nor the balancing side TMJ is loaded during mastication[33]. Although rat masticatory mechanics are a far leap from those of primates, practical considerations have led to a database which is both deep and broad[34-37].

Summary

The TMJ is unique to mammals, but among different mammalian groups its morphology and function vary enormously. Practicality dictates that animal models will not be the closest mimics of the human condition. Currently, the most used species are rats, rabbits, pigs, and ruminant ungulates. Each has distinctive TMJ adaptations. Except for pigs, it is likely that these species show less loading of the jaw joints during chewing than do humans.

References

1. Smith KK. The evolution of mammalian development. Bull Mus Comp Zool 2001; 156:119-135.
2. Sprinz R. A note on the mandibular intra-articular disc in the joints of Marsupialia and Monotremata. Proc Zool Soc London 1965; 144:327-338.
3. Du Brul EL. Evolution of the temporomandibular joint. In: Sarnat BG (ed) The Temporomandibular Joint. Charles C Thomas, Springfield, IL; 1964:3-27.
4. Scott JH. Dento-facial Development and Growth. Pergamon, Oxford; 1967.
5. Naples VL. Morphology, evolution and function of feeding in the giant anteater (*Myrmecophaga tridactyla*). J Zool 1999; 249:19-41.
6. Bermejo A, González O, González JM. The pig as an animal model for experimentation on the temporomandibular articular complex. Oral Surg Oral Med Oral Pathol 1993; 75:18-23.
7. Herring SW, Decker JD, Liu ZJ, Ma T. The temporomandibular joint in miniature pigs: anatomy, cell replication, and relation to loading. Anat Rec 2002; 266:152-166.
8. Gillbe GV. A comparison of the disc in the craniomandibular joint of three mammals. Acta Anat 1973; 86:394-409.
9. Crompton AW, Parker P. Evolution of the mammalian masticatory apparatus. Am Sci 1978; 66:192-201.
10. Herring SW. Animal models of temporomandibular disorders: how to choose. In: Sessle BJ, Bryant PS, Dionne RA (eds) Temporomandibular Disorders and Related Pain Conditions. IASP Press, Seattle; 1995:323-328.
11. Scapino RP. The third joint of the canine jaw. J Morphol 1965; 116:23-50.
12. Herring SW. How can animal models answer clinical questions? In: Carels C, Willems G (eds) The Future of Orthodontics. Leuven University Press, Leuven, Belgium; 1998:89-96.
13. Herring SW. Critical Commentary 1: The role of the human lateral pterygoid muscle in the control of horizontal jaw movements. J Orofac Pain 2001; 15:292-295.
14. Maynard Smith J, Savage RJG. The mechanics of mammalian jaws. Sch Sci Rev 1959; 40:289-301.
15. Becht G. Comparative biologic-anatomical researches on mastication in some mammals. Konink Nederl Akad Wetensch Ser C 1953; 56:508-527.
16. 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.
17. Lieberman DE, Crompton AW. Why fuse the mandibular symphysis? A comparative analysis. Am J Phys Anthrop 2000; 112:517-540.
18. De Vree F, Gans C. Mastication in pygmy goats *Capra hircus*. Ann Soc Roy Zool Belg 1976; 195:255-306.
19. Sun Z, Liu ZJ, Herring SW. Movement of temporomandibular tissues during mastication and passive manipulation in miniature pigs. Arch Oral Biol 2002; 47:293-305.
20. Liu ZJ, Herring SW. Masticatory strains on osseous and ligamentous components of the jaw joint in miniature pigs. J Orofac Pain 2000; 14:265-278.
21. Rafferty KL, Herring SW, Artese F. Three-dimensional loading and growth of the zygomatic arch. J Exp Biol 2000; 203:2093-3004.
22. Herring SW, Rafferty KL, Liu ZJ, Marshall CD. Jaw muscles and the skull in mammals: the biomechanics of mastication. Comp Biochem Physiol A Mol Integr Physiol 2001; 131:207-219.
23. 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.
24. Herring SW, Wineski LE. Development of the masseter muscle and oral behavior in the pig. J Exp Zool 1986; 237:191-207.
25. Herring SW, Scapino RP. Physiology of feeding in miniature pigs. J Morphol 1973; 141:427-460.
26. Weijs WA, Dantuma R. Functional anatomy of the masticatory apparatus in the rabbit (*Oryctolagus cuniculus L.*). Neth J Zool 1981; 31:99-333.
27. Van Eijden TMGJ, Turkawski SJJ, van Ruijven LJ, Brugman P. Passive force characteristics of an architecturally complex muscle. J Biomech 2002; 35:1183-1189.
28. Langenbach GEJ, Weijs WA, Brugman P, Van Eijden

TMGJ. A longitudinal electromyographic study of the postnatal maturation of mastication in the rabbit. Arch Oral Biol 2001; 46:811-820.
29. Langenbach GEJ, Weijs WA. Growth patterns of the rabbit masticatory muscles. J Dent Res 1990; 69:20-25.
30. Weijs WA, de Jongh HJ. Strain in mandibular alveolar bone during mastication in the rabbit. Arch Oral Biol 1977; 22:667-675.
31. Widmer CG, English AW, Carrasco DI, Malick CL. Modeling rabbit temporomandibular joint torques during a power stroke. Angle Orthod 2002; 72:331-337.
32. Weijs WA. Mandibular movements of the albino rat during feeding. J Morphol 1975; 145:107-124.
33. Weijs WA, Dantuma R. Electromyography and mechanics of mastication in the albino rat. J Morphol 1975; 146:1-34.
34. Bresin A, Kiliaridis S, Strid K-G. Effect of masticatory function on the internal bone structure in the mandible of the growing rat. Eur J Oral Sci 1999; 107:35-44.
35. Liu ZJ, Ikeda K, Harada S, Kasahara Y, Ito G. Functional properties of jaw and tongue muscles in rats fed a liquid diet after being weaned. J Dent Res 1998; 77:366-376.
36. Sato I, Konishi K, Kuramochi T, Sato T. Developmental changes in enzyme activities and in structural features of rat masticatory muscle mitochondria. J Dent Res 1998; 77:1926-1930.
37. Byrd KE. Opto-electronic analyses of masticatory mandibular movements and velocities in the rat. Arch Oral Biol 1988; 33:209-215.