From Movement to Models: A Tribute to Professor Alan G. Hannam

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This tribute article to Professor Alan G. Hannam is based on 7 presentations for him at the July 1, 2008 symposium honoring 3 "giants" in orofacial neuroscience: Professors B.J. Sessle, J.P. Lund, and A.G. Hannam. This tribute to Hannam's outstanding career draws examples from his 40-year academic career and spans topics from human evolution to complex modeling of the craniomandibular system. The first presentation by W. Hylander provides a plausible answer to the functional and evolutionary significance of canine reduction in hominins. The second presentation, by A. McMillan, describes research activities in the field of healthy aging, including findings that intensity-modulated radiotherapy improves the health condition and quality of life of people with nasopharyngeal carcinoma in comparison to conventional radiotherapy. The developments in dental imaging are summarized in the third paper by E. Lam, and an overview of the bite force magnitude and direction while clenching is described in the fourth paper by M. Watanabe. The last 3 contributions by G. Langenbach, I. Staveness, and C. Peck deal with the topic of bone remodeling as well as masticatory system modeling, which was Hannam's main research interest in recent years. These contributions show the considerable advancements that have been made in the last decade under Hannam's drive, in particular the development of an interactive model comprising, in addition to the masticatory system, also the upper airways. The final section of the article includes a final commentary from Professor Hannam.
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Alan Hannam completed his dental education at the University of Adelaide in Australia and thereafter gained fellowship training in the UK, where he also obtained his PhD under the supervision of Professor Declan Anderson and his colleagues at the University of Bristol. He then went to an academic position at the University of British Columbia (UBC) in the early 1970s and is currently professor emeritus at UBC. His research interests have centered on orofacial motor control and related biomechanics and modeling.

The Evolution of the Masticatory Apparatus in Early Humans

William Hylander made the initial tribute presentation for Professor Hannam, and first noted that their acquaintance was made and friendship began in the 1980s. Over the years their collegial relationship also led to many scientific interactions and influenced Hylander's thinking on the structure-function relationships of the masticatory apparatus.

The primate fossil record indicates that the earliest members of the human lineage are about 6 to 7 million years old.[1,2] These earliest humans (hominins), which were characterized by ape-sized brains, differed from apes in that they were bipedal and had evolved important modifications of their craniofacial region. These craniofacial modifications included, but were not limited to, *(1)* an overall reduction of canine-size dimorphism (males vs females), including a reduction in the height of their canine teeth (particularly the males), *(2)* a reduced occlusal relief and an increased enamel thickness of the postcanine teeth, and *(3)* an unusually thick mandibular corpus in the transverse direction.

These postcanine and gnathic features have been interpreted as indicative of an important dietary shift that had occurred during the early evolution of hominins from their more ape-like ancestors. An important component of the early hominin diet presumably included unusually hard, difficult-to-chew food items.[3] However, the functional and evolutionary significance of canine reduction in hominins is still an importantly debated issue and there is still no consensus as to the evolutionary significance of canine length reduction in hominins.[4–7] A possible explanation has been put forward by Hylander and Vinyard[8] after having analyzed the functional links between canine length and jaw mechanics in over 600 adult male and female living catarrhines (Old World monkeys and apes) representing 22 different species.

An analysis of maximum jaw gape in sedated catarrhines showed that, relative to mandibular length, adult male nonhuman catarrhines have much larger gape than do females. Thus, during maximum jaw opening, male catarrhines rotate their mandibular condyles more than do con-specific females. Therefore, females likely have more rostrally positioned jaw muscles and relatively shorter muscle fibers. Among the 22 different catarrhine species, there are considerable interspecific differences in the amount of gape relative to mandibular length. For example, adult male baboons (*Papio anubis*) open their jaws over 100% relative to jaw length whereas the opening in female baboons is less than 80% relative to jaw length. Male and female humans open their jaws only about 50% of jaw length whereas male and female hylobatids (gibbons and siamangs) open their jaws about 100% of jaw length. Male long-tailed, lion-tailed, and pig-tailed macaques have much larger gape than do male rhesus and Japanese macaques. Moreover, male chimpanzees, gorillas, and orangutans have less relative gape than do Old World monkeys, but more relative gape than humans. Most importantly, recently collected canine length data showed that those catarrhines with relatively smaller (or larger) gapes have relatively shorter (or longer) canines, respectively.

Relative maximum gape is a function of jaw adductor muscle-fiber length and muscle position. There are important costs and benefits linked to modifying these muscle characteristics. Relative to muscle size, more caudally or posteriorly positioned muscles and/or longer muscle fibers have the benefit of increasing jaw gape (for long canines), but the cost is a reduction in bite force. Conversely, more rostrally or anteriorly positioned muscles and/or shorter muscle fibers increase the production of bite force, but at the cost of a reduced maximum gape.

It may therefore be hypothesized that in the earliest hominins, selection pressures for increased bite force exceeded those pressures for maintaining large gape linked to large canines. Canine reduction and reduced jaw gape was the morphological result of the demand for increase bite force. Thus, canine reduction in catarrhines was linked to the ability to generate larger bite forces with no necessary increase in jaw-muscle size. Finally, this analysis provides us with *(1)* a plausible hypothesis for the benefits of canine reduction and *(2)* additional but independent evidence that the origin and radiation of early hominins is importantly linked to a dietary adaptation that included hard, difficult-to-chew food items.

From Neurophysiology to Oral Rehabilitation

Anne McMillan was Hannam's first PhD student in the newly formed doctoral program in Oral Biology at the Faculty of Dentistry, UBC, in 1986. She recalled that as a prosthodontist who had embarked on a clinical academic career and wished to obtain formal research training that would underpin her future academic endeavors, her single-most important reason for going to UBC was Professor Hannam's outstanding international reputation in the field of orofacial neuroscience. The key to their research was a serendipitous encounter with Dr Andrew Eisen, head of neurology at the UBC, who gave a live demonstration (on himself) of single motor unit (MU) recording techniques as part of a graduate core course in neurophysiology. Hannam supervised her work on MU behavior in the human jaw muscles. It was a very productive time that resulted in numerous publications, and a key part of this activity was Hannam's encouragement to publish outside the dental literature in prestigious journals such as *Experimental Brain Research* and *Muscle and Nerve*. McMillan also remarked on her good fortune to work from 1993–94 with a second "giant" in orofacial neurosciences, Professor Jim Lund at the Université de Montréal. She concluded that these experiences greatly marked her future approach to clinical research.

Cross-disciplinary research is particularly important in the healthy aging research domain, the overarching theme of McMillan's own research. Under the subtheme of xerostomia, a series of studies investigated the impact of intensity-modulated radiotherapy (IMRT) on oral health condition and quality of life (QoL) of people with nasopharyngeal carcinoma (NPC), the efficacy of Cevimeline hydrochloride in the treatment of Sjögren's syndrome, and the efficacy of novel lubricating systems in the management of radiotherapy-related xerostomia. Other studies that underpinned her neurophysiology background investigated the epidemiology and psychosocial impact of orofacial pain in southern Chinese people and the impact of stroke on oral health condition and QoL. These research projects involve collaboration with her colleagues in the Departments of Clinical Oncology, Rheumatology and Clinical Immunology, Rehabilitation Medicine, and the Family Medicine Unit at the University of Hong Kong.

The clinical research on NPC is particularly relevant to the Hong Kong population, as the tumor is common in southern Chinese people.[9] Because the tumor is highly radiosensitive and surgical access is difficult, radiotherapy (RT) is the mainstay of treatment. Conventional RT has been shown to be very effective in the control of NPC, notably in early-stage disease. However, conventional head and neck RT results in serious, frequently irreversible damage to structures within the radiation field, especially the parotid glands. Life-long sequelae such as xerostomia lead to impairment of patient QoL.

Intensity-modulated RT is an advanced form of conformal RT that achieves improved target irradiation while limiting radiation dose to normal tissues leading to reduced treatment side effects.[10] A prospective study involving patients with early-stage disease showed that parotid IMRT achieved good loco-regional control of NPC, and that saliva profile improved in the 2-year post-IMRT period.[11] Thus, given that IMRT-related tumor control for early-stage disease appeared to be at least as good as conventional RT, the effect of IMRT versus conventional RT in terms of saliva quantity and patients QoL was investigated in a prospective study and randomized controlled clinical trial (RCT).[12,13]

In the RCT, patients with early-stage NPC were randomly assigned to IMRT or conventional RT. Stimulated whole and parotid saliva flow were measured, and generic and head and neck cancer health status questionnaires administered before RT treatment and up to 12 months post-RT. Global health scores showed continuous improvement in QoL after both RT treatments, but 12 months post-RT, more than half of the IMRT group patients had recovered at least 25% of the pre-RT saliva flow, compared with less than 10% respectively in the conventional RT group, and they also showed fewer dry-mouth-related symptoms. For early-stage NPC, IMRT was significantly better than conventional RT in terms of parotid gland sparing and QoL.

McMillan concluded her presentation by noting that the healthy aging-related research at the University of Hong Kong has been published in journals such as *Cancer* and the *International Journal of Radiation Oncology Biology and Physics,* thereby reflecting Hannam's early encouragement of cross-disciplinary collaboration and high-impact research outputs that have become a pattern through her research career.

Multi-dimensional Imaging of the Jaws

The next presenter, Ernest Lam, first encountered Professor Hannam when Lam was a dental student at UBC. His interest at the time in magnetic resonance appeared to fit nicely into some of the work that was being done in Hannam's laboratory, so he joined Hannam's group as an MSc student while enrolled in dental school. The years spent in the laboratory launched Lam's career as an academic oral and maxillofacial radiologist.

Lam remarked that developments in computer technology have been largely responsible for many

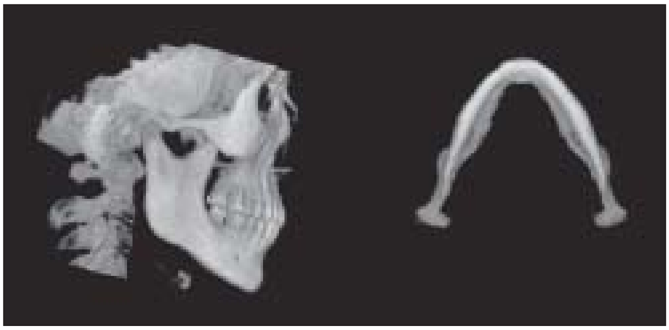

Fig 1 Three-dimensional rendering of the skull from cone-beam CT data. The lateral projection of the skull is shown on the left and a rendering of the mandible alone is shown from below, on the right.

of the most significant advances in diagnostic imaging in the past quarter century. Faster, more powerful computers have facilitated not only the development of digital imaging in dentistry and medicine, but also the widespread use and manipulation of images generated by x-ray computed tomography (CT) and magnetic resonance imaging (MRI) in research and patient care.

The earliest applications of digital 3-dimensional (3D) imaging in dentistry focused on the development of protocols to depict the temporomandibular joint (TMJ) disc by using CT and MRI.[14,15] During this time, many dental researchers as well as oral and maxillofacial radiologists were often challenged by administrative and technical obstacles that prevented them from obtaining the necessary time and resources to develop, test, and implement novel imaging protocols for applications in the masticatory system. Regrettably, this is still the case today in many centers.

Technically, image signal-to-noise ratios were often poor in early CT and MRI systems as voxel sizes were relatively large, and computer memory was limited and expensive. Moreover, renderings of the image data were made more difficult because individual manufacturers of CT and MRI systems used proprietary file formats that made it difficult if not impossible to decode image data, even for research purposes. As a result, clinicians and researchers alike routinely received filmed sheets of images, and the extraction of image data often meant sitting over a light box for many hours and hand-tracing the outlines of structures and digitizing them; a very laborious task.[16]

Since then, 2 important developments have occurred that have permitted more widespread use and application of this technology in dentistry. The first was the creation of a standard for digital picture and image archiving: the Digital Imaging and Communications in Medicine, or DICOM standard (http://medical.nema.org). DICOM was a collaborative effort between the American College of Radiology and the National Electrical Manufacturers Association to develop a uniform standard for the coding of digital image data. Today, DICOM has become the standard format for digital patient records and image files, allowing individual offices and large institutions alike to archive and exchange patient information and technical data related to the images, as well as the actual image data itself. Furthermore, standardized file formats have enabled third-party companies to develop novel and very powerful software for image manipulation and analysis.

The second development was the introduction in the late 1990s of a novel CT imaging technique, cone-beam CT (cbCT).[17] Much less costly to purchase than medical CT systems, cone-beam CT systems utilize a cone-shaped rather than a fan-shaped x-ray beam coupled to a flat panel solid-state detector. As with medical CT, cbCT systems are capable of acquiring large image volumes that are limited only by the size of the detector panel. In comparison to medical CT, cbCT volume acquisition is fast, with far lower radiation dose to the patient.[18]

In a very short period of time, cbCT has been used to investigate jaw and tooth-related pathoses, but its use as a method to quantify craniofacial architecture, primarily in orthodontics and oral and maxillofacial surgery, is still very new. Consequently, the routine use of cbCT for this purpose prior to the establishment of population norms is a topic of considerable controversy.[19]

Routine imaging of the soft tissues of the jaws continues to be problematic in clinical dentistry and dental research. While medical CT has the capability to depict soft tissue structures, it does not do this with great detail. Furthermore, the sensitivity of current cbCT sensors is such that they are unable to resolve soft tissue structures at all. At this time, there are no dedicated MRI systems for dentistry. However, with time, this too may change, and some of the applications that are in widespread use in medicine and medical research may find their way into our hands: functional

MRI,[20] magnetic resonance spectroscopy[21] and angiography, to name just a few. Dr Lam's concluding comment was that the continued advancement of both basic and clinical research utilizing 3D imaging in dentistry will rely on the fostering of new ties and the development of common areas of interest between dentistry and medicine in both the research and clinical settings.

Occlusal Loading in Humans

Makoto Watanabe next gave a brief overview of research at Tohoku University on occlusal loading in humans that was initiated as a result of long-term collaborations with Professor Hannam. The goal of this research was to develop a technique for the in vivo measurement of bite forces to study the normative bite force distribution and orientation.[22]

3-D Bite Force Registration at an Isolated Bite Point

The development of a 3-D bite force transducer was initiated at UBC in 1986. The transducer consisted of 3 subminiature load cells and 3 bearing balls. Each load cell and bearing ball was placed on opposing maxillary and mandibular teeth, respectively. The cells were oriented at a 45-degree inclination in relation to the occlusal plane. When closing, the balls contacted the cells, with forces directed perpendicularly to the cell surfaces. From the 3 force vectors the resultant bite force could be computed. This transducer worked satisfactorily; however, it was inconvenient to use.

Therefore, a newer transducer was designed that was more versatile and could be used for a large number of subjects. Although it still incorporated 3 load cells, the number of bearing balls was reduced to 1 so as to facilitate the setup procedure. This transducer allowed analysis of the activity patterns of motor units (MUs) of the human masseter muscle in relation to the closing force vectors. In vertically and contralaterally directed clenching, more than 90% of MUs were recruited irrespective of their locations. During posteriorly directed clenching, however, the ratio of recruited MUs differed significantly among the different masseter region depths, providing further support for findings by Hannam and others for the functional heterogeneity of this muscle.

3-D Bite Force Registration at Multiple Bite Points

Bite force can be measured simultaneously at different contact (occlusal) points by means of a specially designed pressure-sensitive thin film, Dental Prescale (Fuji Film Co, Tokyo, Japan) that measures bite forces during medium to maximum voluntary clenching. Film insertion leads to a minimal jaw separation. The pressure-sensitive foil is a laminate consisting of a thin film that is coated with a color developer on 1 side. Over this is a color-former layer consisting of a uniformly distributed mixture of microcapsules containing a color former colorless dye. When a bite force is applied, the microcapsules brake and the dye reacts with the color developer, resulting in the appearance of red spots at the points of the applied force. The shade of red spots varies according to the amount of pressure applied on the film. Therefore, by measuring the color density, the applied force can be measured. The shape and distribution of the red spots can then be compared to those recorded by means of occlusal check-bite records in order to identify the point of occlusal contact.

This recording technique allowed calculating magnitude and direction of the bite forces exerted on each single tooth as well as the wrench axis. A "wrench" is the simplest yet most complete representation of the force system. It was assumed that the location of the application point of an occlusal force coincides with the central point of the occlusal contact area and that the direction of a bite force is perpendicular to the contact area.

Features of a normal dental occlusion have been studied with this technique. Results indicated that the second molar was subjected to one-fourth of the total bite force, and the first molar bore 15% of it. In general, greater bite forces were produced on the posterior teeth than on the anterior ones, and bite forces showed a bilaterally balanced distribution. The asymmetry indexes, which are the ratio of the bilateral difference in bite forces to the bite force total, were smaller when calculated for the entire dental arch than for individual pairs of the same type of teeth, indicating that the dentition functions biomechanically as a unit. The wrench axes of the bite forces acting on the posterior teeth were slightly inclined mesially and lingually, and this inclination was greater in the molar than in the premolar teeth area. This inclination's variation corresponded to the orientation of the tooth long axes. The wrench axes calculated for the entire jaw were almost perpendicular to the occlusal plane, and intersected it near the midpoint between the left and right first molars. The wrench axes orientations for the entire jaw showed less fluctuations than those for each single tooth.[23]

Watanabe concluded by pointing out that direct in vivo observations still provide considerable insight into the interrelation between the structure and function of the masticatory system. As bite force is the sole directly recordable force in the masticatory system, its direct measurement seems to be an optimum technique in order to obtain in vivo data for the development and verification of models.

Muscle Function—A Source of (Re)modeling

Geerling Langenbach started his presentation by noting that the interaction between muscle and bone on the macroscopic and microscopic level has been the main focus of his research and that his postdoctoral research with Professor Hannam at UBC gave him the opportunity to enter what was at that time, a new area of dynamic modeling. His presentation then described the influence of muscle function on bone structure, including biomechanical modeling of the jaw system, as well as the remodeling of bone tissue.

He pointed out first that the physical events occurring during function and dysfunction are complex. It is appealing to make biomechanical models, because this approach simplifies the complex reality of the musculoskeletal systems, clarifying their functioning to a comprehensible level. In the early 1990s, computational power had increased such that, for instance, the automotive and aircraft industries were using dynamic modeling for the development of new products. Langenbach and Hannam took up the challenge to apply this technology to examine jaw muscle function in a dynamic way. By collecting averaged anatomical data obtained from previous publications, a typical human jaw system was generated[24] which was then loaded by means of earlier published average activity patterns of masticatory musculature obtained during chewing. The resulting jaw motion was surprisingly similar to the human chewing motion recorded in vivo.

The next step was to individualize such a model. By using CT and MR images, the jaw system of a pig was constructed. Recordings of the jaw muscle activities during chewing in the same animal provided the loading features necessary as force input to the model. The resulting chewing motion showed an alternating incisor point motion characteristic of the pig.[25] These models showed that it was feasible to generate complex biomechanical models simulating movements comparable to those recorded in vivo, predicting motions and forces that are impossible to record in vivo, and allowing virtual experiments to be performed that are too invasive to be executed in vivo.

After Langenbach returned to the Netherlands in the late 1990s, he started looking into the influence of muscle function on the bone tissue itself. In addition to the generation of bone motion, the muscles also generate bone deformations. These deformations, although very small, are essential for the maintenance of the bone tissue by remodeling,[26–29] a process that rejuvenates bone tissue. New bone is minimally mineralized and flexible, but as bone tissue becomes older the mineral content increases making the bone more brittle. While unloaded bone shows low rates of remodeling, which results in highly mineralized tissue, frequently loaded bone shows a high rate of remodeling, thus a low degree of mineralization. This seems odd, as loaded bone should be able to withstand the applied forces, but this goal is reached by increasing the bone mass and not mineralization.

To examine the influence of muscle forces on bone architecture, the naturally occurring masticatory muscle forces can be used. In doing so it is important to record all and not only specific muscle activities performed during the day. Langenbach accomplished this by means of a fully implantable telemetric device (Data Science Int.) enabling the recordings of all jaw muscle activities performed during the whole day in freely moving animals during several weeks. The results showed consistent muscle activity patterns (expressed as burst number and total duration of muscle activity), but large variations between animals and muscles.[30–32] The examination of the bone mineralization degree by means of microCT showed that the muscle attachment sites had a lower degree of mineralization than bone sites without attachments, eg, without any direct muscle loading. This effect generally increased with the number of daily muscle loadings. Although the results seemed to indicate a clear influence of muscle loading on bone architecture, the individual variations in daily muscle activity were not associated with comparable variations in the degree of mineralization.

Langenbach's final point was that it has become possible to register bone deformation by telemetry. A commercially available system (Microstrain, Williston, VT) has been modified in order to be implanted in a rabbit. This technique, which allows simultaneous telemetric registration of muscle activities and bone deformations in vivo, will provide the necessary data to develop and validate a high-resolution FE model of the rabbit's mandible. Such a model would help to further clarify the relationship between local strain distributions and bone architecture, information that is essential for the development of intervention strategies able to prevent bone loss.

Dynamic Jaw and Tongue Modeling with ArtiSynth

Ian Stavness first noted that Professor Hannam provided invaluable mentorship for his master's work on dynamic jaw modeling at UBC in 2004, and that they continue to collaborate on the ArtiSynth and OPAL (Oral, Pharyngeal, and Laryngeal Complex Modeling) projects during his current doctoral studies. He then pointed out that while previous studies have focused on jaw biomechanics,[33,34] efforts are today directed toward the development of an open dynamic computer simulation toolset, called ArtiSynth. (ArtiSynth can be downloaded at www.artisynth.org.) This is capable of simulating the movement of the hard and soft tissues of the upper airway.[35] The function of the upper airway, including the jaws, tongue, pharynx, and larynx, involve complex interactions between hard and soft tissues that are difficult to analyze in vivo due to the inability to measure forces and tissue motion directly. Therefore, dynamic computer simulation can facilitate the understanding of the function of this complex forces-motion interplay. A primary focus of his studies is to develop an interactive toolkit that is usable by nonengineering scientists and clinicians.

ArtiSynth employs a general framework for biomechanics modeling: complex musculoskeletal models can be created by assembling combinations of basic structural components. These basic components include constrained rigid bodies, deformable bodies (volume-preserving finite-element methods), contact and coupling between bodies, and muscle models.[36]

Forward dynamics simulations use muscle activation signals as input and compute motion and forces as output. Manual trial-and-error tuning of individual muscle activations is challenging in redundant multi-muscle systems, such as the jaws and tongue. Functional muscle grouping has been proposed for mastication[37] in order to reduce the control space dimensionality, and ArtiSynth allows for the inclusion of such hierarchical muscle groups. Also, optimization has been used in previous studies to automatically compute activations to create desired forward dynamics simulations.[38,39] Efficient computational methods for kinematic trajectory tracking with biomechanics models have been described,[40,41] and Stavness and his colleagues are incorporating such techniques within their ArtiSynth framework for soft-hard tissue modeling.

At present a dynamic jaw-hyoid model is implemented in ArtiSynth[42] and muscle drive patterns have been created to simulate typical unilateral chewing with the model.[43] The model includes also a dynamic tongue that has been developed based on quasi-linear fast FEM methods.[44] The tongue consists of a 3-D FEM tissue volume with muscle fibers distributed throughout the tongue body that are oriented and organized into the main intrinsic and extrinsic muscle groups.

The final point made by Stavness was that a promising direction for modeling studies is to incorporate biological mechanisms of motor control including peripheral reflexes and central motor commands, such as those generated by the central pattern generator.[45,46] The flexibility and usability of the ArtiSynth toolset makes it a strong candidate platform for pursuing such advances in the near future. Another reason for developing biomechanics simulation tools is to predict the consequences of structural alterations to the musculoskeletal system. Virtual surgery on computer models could, for instance, help determine post-surgical functional deficits. Therefore, interactive model editing capabilities have been implemented into ArtiSynth. These tools are used to develop models of surgical jaw reconstructions in the aim of predicting post-reconstruction deficits in jaw motion and force production in mastication.[36]

Integrating Jaw Models into Clinical Research

The final tribute presentation was by Christopher Peck, whose initial interaction with Professor Hannam was in a virtual environment, with simultaneous audiovisual presentations across Australia on jaw biomechanics. He was then mentored by Hannam from 1994 when he commenced his doctorate on structure-function relationships of the jaw, this time in the virtual environment of mathematical modeling. The biomechanical environment of the human masticatory system is complex. Multiple muscles, many with pennate internal architecture,[47] span the curvilinear TMJs, in which condylar translation and rotation take place.[48] Furthermore, the occlusal interface and contact patterns consist of uneven non-planar contact points and multidirectional cuspal inclines that influence jaw movement with tooth contact.

Mandibular movement is a result of the interactions between the viscoelastic contact properties of the TMJs and dental occlusion, active muscle tensions and passive muscle, fascial, and joint capsule constraints.[34] Consequently the mandible is able to move with 6 degrees of freedom within a border defined by these constraints.[49]

The ability to understand better the relationship between the structural and functional properties of the human jaw is largely limited by the ability to obtain physiological data in extant human subjects. Many recording procedures are invasive, and even if ethically permissible, will themselves likely alter the outcome in question.

Mathematical modeling provides a tool to gain better insight into jaw biomechanics. Modeling can be considered translational research linking the basic oral physiology sciences with clinical research. A model allows the systematic change of variables to explore cause-effect relationships and generate hypotheses that can then be tested clinically.[50] This modeling approach provides a virtual environment that has realized greater insight into knee replacement mechanics,[51] and improved design in the aerospace and automobile industries. Models are constructed using best available physiological human data, and, where this is not possible, animal data or assumptions based on human jaw behavior are applied. With whole jaw modeling, a "black box" approach is often utilized that disregards the detailed structural mechanisms at work. For example, in dynamic models, the jaw is modeled as a rigid body with overall inertial properties (mass and moments of inertia) that can be derived from imaged jaws.[52] These images can also be used to attain key landmarks such as joint morphology and muscle attachment sites.[53] Furthermore, sarcomere mechanics are replaced by whole muscle models which retain essential biological data to perform plausibly when compared to experimental results.[54] Peck's research with Hannam has found that the jaw's passive resistance to wide mouth opening is low at approximately 5 N.[55] When these data are utilized in mathematical models, estimates of the jaw's viscosity (modeled as a velocity-dependent force that resists jaw opening) suggested it was the predominant resistance to motion. This is plausible in such a biological system where lower-speed jaw abduction can be resisted by neuromuscular reflexes, but at higher-speed movements constraint is achieved with the system's viscosity as well.

The jaw is capable of a diverse range of functional tasks that involve power, speed, and/or precise positioning, and there are many more muscles present than are needed for any single jaw task. Thus it is conceivable that a jaw task can be achieved with a number of different but plausible muscle coactivation strategies. To overcome this challenge of redundancy, jaw models have applied restrictions on available muscle-activation strategies such as applying only active tensions from muscles with significant EMG activity or from muscles that only shorten during a task.[56] This simplification process is supported in animal studies which identified groups of muscle triplets according to onset of activity and contribution to activity in mastication.[37] Such a functional set for a motor task suggests that if one knows the activity of a single muscle in that set, then the task can be determined. In simulated bruxing, the surface EMG patterns of the masseter and anterior temporalis muscles were able to predict the specific task (jaw excursions, intercuspal and eccentric clenching) with 96% accuracy.[57]

As the masticatory system is mechanically redundant, there is the potential to change the functional set of muscles for a specific task, and modeling has suggested that task achievement is possible with different plausible muscle coactivation strategies. Of course this will change the dynamic environment of the jaw, including muscle tensions and articular loads, and this may be an important clinical management goal. Preliminary data support this ability to alter coactivation strategies. Eight subjects performed standardized contralateral jaw tasks before and after isometric resistance jaw exercises, and masseter and anterior temporalis activity (as defined by area under the curve of rectified, butterworth filtered EMG signals) before and after the exercises was significantly different ($P < .05$, ANOVA).

Lastly, Peck noted an important clinical advantage of modeling is in the education of future health care providers. The virtual environment of modeling provides complete control for the student to understand better the relationships between structure and function. Apart from the ability to discover systematically the effects of different structural (eg, dental occlusal schemes, jaw joint morphology, muscle positions) and functional (eg, muscle coactivation strategies) variables, the impact of clinical scenarios (eg, maxillofacial surgical procedures, developmental disturbances) can be examined.[58] To realize the maximum benefit of modeling, interdisciplinary teams consisting of engineering and computer scientists, biologists, and clinicians need to be developed. Where interdisciplinary teams have been developed, advanced models including the jaw and other structures have been developed which are based on sound physical and biological principles, as Hannam has espoused.[43]

Hannam response

Professor Hannam commented on each of the presentations, and noted that they exemplify the diverse backgrounds and skills of the many colleagues with whom he had the privilege to work. Hylander already had an international reputation before they met, having produced what is still the seminal literature on primate jaw biomechanics. His paper highlights the impact of physical anthropological and comparative primate studies on our understanding of human jaw function. Hannam further commented that McMillan provides an example of what can be accomplished when an experienced clinician undertakes graduate training in motor unit physiology, then returns to the clinic to guide cross-disciplinary studies, in this case involving intensity-modulated radiation therapy in the management of oropharyngeal carcinoma. He also mentioned that Lam, a graduate student who utilized his earlier experience to work with him on muscle imaging and spectroscopy, subsequently pursued an academic career in oral radiology. His focus on cbCT is pertinent because this imaging approach is used to create patient-specific models of the craniofacial skeleton. Watanabe was the first of many competent Japanese postdoctoral visitors to work with Hannam. Hannam said that his description of 3-D bite-force measurement and its correlation with muscle activation are central to present model assumptions and validation. Langenbach, already a comparative anatomist and his first postdoctoral fellow, pioneered their original model of the human masticatory cycle, and Hannam noted that his current work on chronic recording and the mechanobiology of musculoskeletal growth draws upon a deep understanding of the jaw's biomechanical environment. He also said that Stavness, presently a senior graduate student in electrical and computer engineering at UBC, is a classic example of a cross-disciplinary collaborator. He shows how advanced bioengineering techniques can be used to create fully integrated, dynamic models of the jaw, tongue, and larynx, areas of mutual interest to investigators working in oral physiology, the upper airway, speech, and dysphagia. Finally, Hannam mentioned that Peck, a senior clinical professional who acquired a bioengineering background during his graduate training, discusses the clinical significance of modeling and emphasizes its role in the analysis of structural and functional interactions as well as its potential for predicting clinical outcomes. Hannam concluded that, collectively, the presentations trace a progressive path to the present.

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