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Human mastication

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Human mastication is a complex biomechanical process. Many different structures, tissues and functional units are involved. The great variability observable in the procedures of crushing and lubricating food constrains the clear distinction between physiologic and pathophysiologic chewing pattern. Diagnostic procedures on masticatory performance are still lacking clear definitions and classifications. The use of individual chewing performance data in restorative dental procedures is not yet established.

The purpose of this article is to provide an overview on human mastication. Interdisciplinary teamwork is frequently quoted. Patients are claimed to represent the center of all activities. Mastication is essential for proper nutrition. The link between chewing ability and nutrition is evident. Nevertheless, deficiencies in nutrition, especially in elderly, even in nursed situation, are reported in the scientific literature not only on the base of few cases; a systemic nonconformity, involving all health care providers, may be assumed. The transfer within this article illustrated facts into daily routine should be encouraged.

Keywords: human mastication, standard food model, mandibular movement, condylography, biomechanics, temporo-mandibular joint, chewing, swallowing, food size, elastic food properties, plastic food properties, chewing muscle activity, EMG, nutrition, systemic disease, tooth loss

Introduction

Mastication places a functional demand on the stomatognathic system throughout life [22]. Chewing is one of the most common rhythmic behaviors, along with respiration and locomotion, in mammals [60]. Mammalian mastication is a process combining simultaneous food comminuting and lubrication [71]. The ability of the stomatognathic system to crush and preprocess food can be related to vital functions of the body and is associated with general health [85].

Ingestion in mammals starts with food capture, defined as the process of catching and ingesting food or prey into the oral cavity. Vertebrates use their dentition in combination with lips and/or tongue for food capture. In humans, food capture is a combined action of hand/arm and stoma, but lips and tongue are involved as well. Lips, cheek, tongue, and soft palate take active part in oral transport. Shift and movement of food within the oral cavity are essential to locate food between teeth, so occlusal breaking forces can be applied to the bolus. Oral transport can be separated into a stage I transport (before mastication starts) and a stage II transport (during mastication, before swallowing). The goal of masticatory actions is to bring occlusal structures forcefully against the food bolus, which breaks into smaller pieces and is lubricated with saliva. Mammals typically perform a unilateral mastication. Transverse jaw and tooth movement are variable parameters. Mastication is stopped at a specific moment (yet the neurophysiologic mechanism for the stopping mechanism of chewing is not completely understood and clarified) and swallowing (deglutition), a complex neuro-motor reflex involving more than 25 muscles and 5 different cranial nerves, is performed. The swallowing reflex is unique in mammals, not seen in other vertebrates. It is initiated at gestation weeks 10–12. Intrauterine swallowing and mandibular movement do have an important role in developing jaw joint structures and tissues.

Chewing pattern of children with primary dentition is characterized by wide lateral movement toward the working side on opening and a more inward directed path during closing phase of the chewing cycle. On the contrary, adults show different chewing movements. The opening movement is performed more or less in the mid-sagittal plane. The closing movement is characterized by a wide lateral movement toward the working side. The closing trajectories of working side molars move toward intercuspal position from a retrusive direction. In the adult, the working side molars on closing are approaching intercuspal position that from a retrusive, inferior, and lateral position. Molar cusps therefore are heading anterior, superior, and median [20, 21, 85]. This observation is detectable only in adults, but not in children. Children are approaching intercuspal position directly. Working side and non-working side movements of molar cusps show different trajectories (Figs. 1 and 2). Pure hinge movement during mastication is neither seen in adults nor in children. Quality of occlusion has a dramatic impact on mandibular movements during mastication [20, 85]. Range, coordination, and fine motor control are jeopardized in situations of

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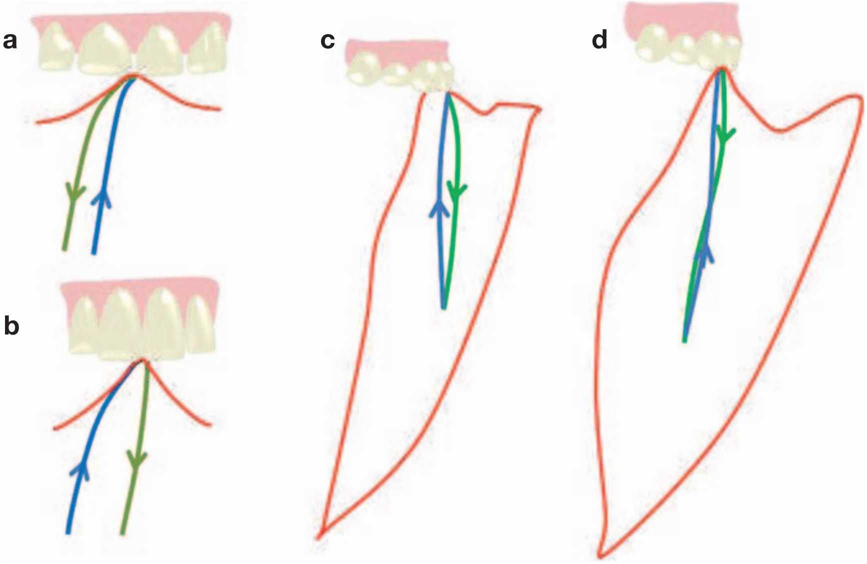


Fig. 1: Lower incisor edge trajectories in children with mixed dentition (a, c) and adults (b, d) during mastication. The red line indicates the border movement of the lower incisor edge, the opening phase of the chewing cycle is shown in green, the closing stroke shown in blue (adapted from Refs. [20, 22]). (a, b) frontal view; (c, d) lateral view

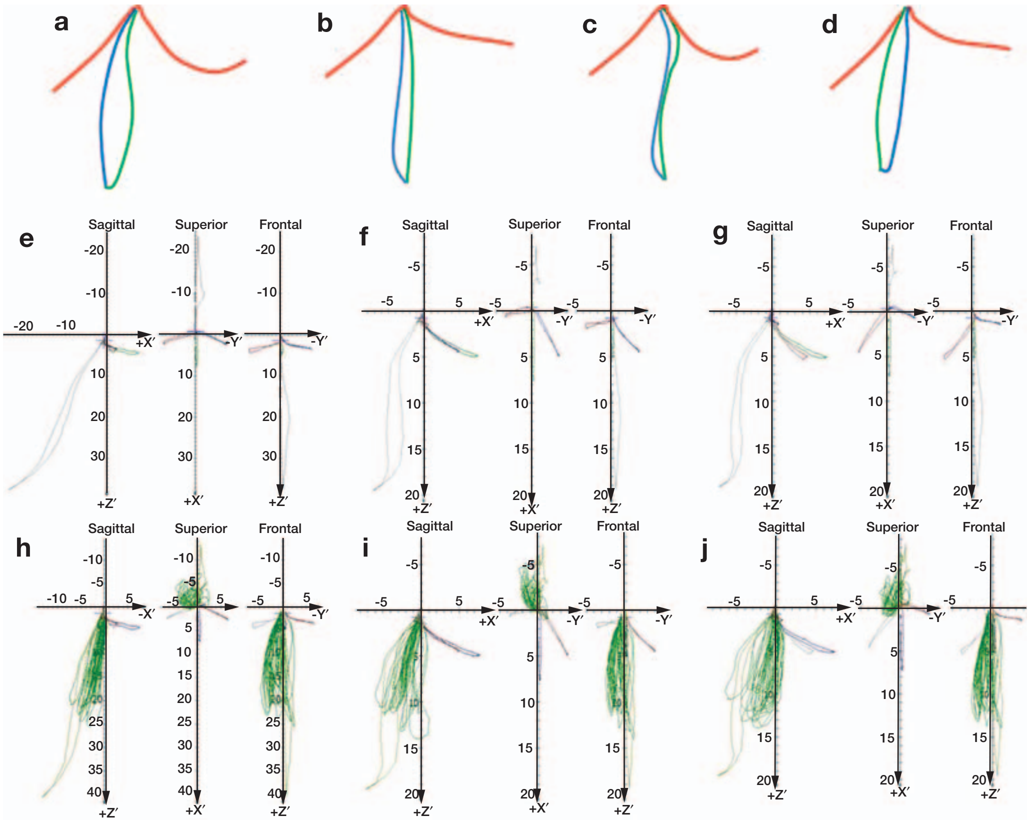
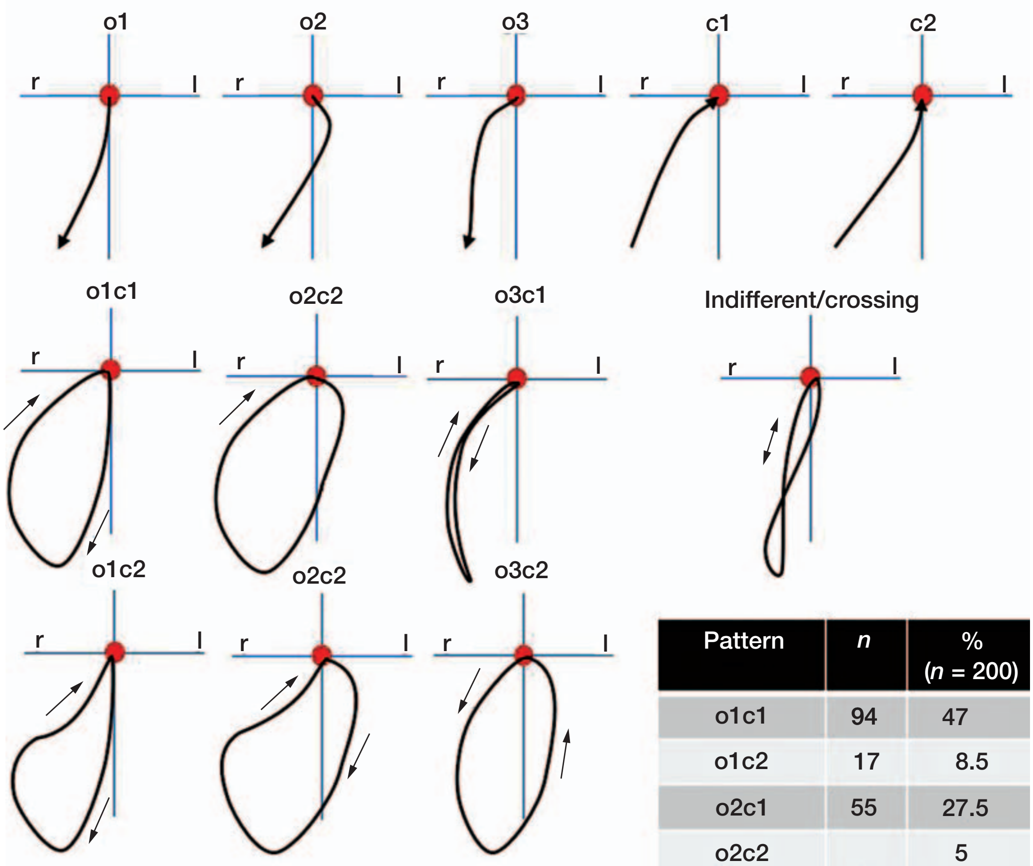


Fig. 2: Lower molar cusp trajectories in adults (a, b) and children with mixed dentition (c, d) during mastication. The red line indicates the border movement of the lower jaw, the opening phase of the chewing cycle is shown in green, the closing stroke shown in blue, (a, c) working side; (b, d) non-working side (Adapted from Refs. [20, 22]). (e–g) Border movements of the mandible; (e) lower incisal edge (coordinates sagittal $x = 70$, transversal $y = 0$, vertical $z = 30$); (f) right molar ($x = 30$, $y = -30$, $z = 30$); (g) left molar ($x = 30$, $y = 30$, $z = 30$). (h–j) Chewing sequence (right side mastication, soft model food, 18 sec) in relation to the border movements; (h) lower incisal edge; (i) right molar, representing working side; (j) left molar, representing non-working or balancing side



Pattern	*n*	% (*n* = 200)
o1c1	94	47
o1c2	17	8.5
o2c1	55	27.5
o2c2		5
o3c1	9	4.5
o3c2	6	3
Indiff./cross.	9	4.5

Fig. 3: Lower incisor edge trajectory patterns (adapted from Ref. [40]). The table shows the distribution of the different paths as reported by Kobayashi et al. [40]. The "typical" chewing cycle, as described by Gibbs et al. [20, 22], corresponds to path o1c1 and was found in 94 out of 200 subjects (47%).

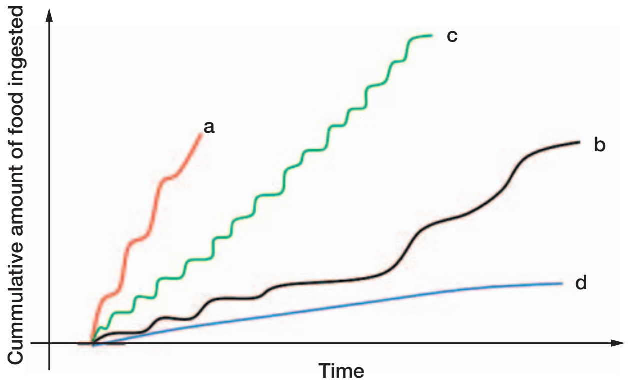


Fig. 4: Food intake as function of food intake and mastication: feeding sequences with food intake, chewing, and swallowing are recorded in different settings and animals: (a – red): carnivore eating small prey (or canned food); (b – black): carnivore eating large prey; (c – green): herbivore grazing; (d – blue): animal is drinking/lapping (adapted from Ref. [77])

malocclusion and occlusal aberrations. The neuromuscular system exerts fine control during chewing to avoid particular occlusal interferences. Present restorative procedures based on lateral border registrations are applicable to functional chewing pattern [20].

Gibbs et al. analyzed chewing pattern with different types of food. When standard foods [45, 85] or commercially available chewing gums [40] are used to analyze human mastication, a single type of a typical chewing cycle in adults – as described by Gibbs et al. – could not be identified. Seven movement patterns have been recognized (Fig. 3) [40]. However, it has to be highlighted, that the typical chewing cycle, as described by Gibbs et al., was the most common type ($n = 94$, 47%) within the observed study population. More details on the distribution of the chewing types described in the study of Kobayashi et al. are presented in Fig. 3. A gender difference could not be found within the subjects within the same study [40].

High forces are produced during chewing. The highest forces during a chewing cycle appear when teeth are close in contact (= occlusal phase of a chewing cycle). The importance of occlusal stability in the intercuspal position, seen from this particular aspect, is of utmost clinical significance [21]. Forces created during chewing are affected by the consistency of the food. Complete denture wearers, for

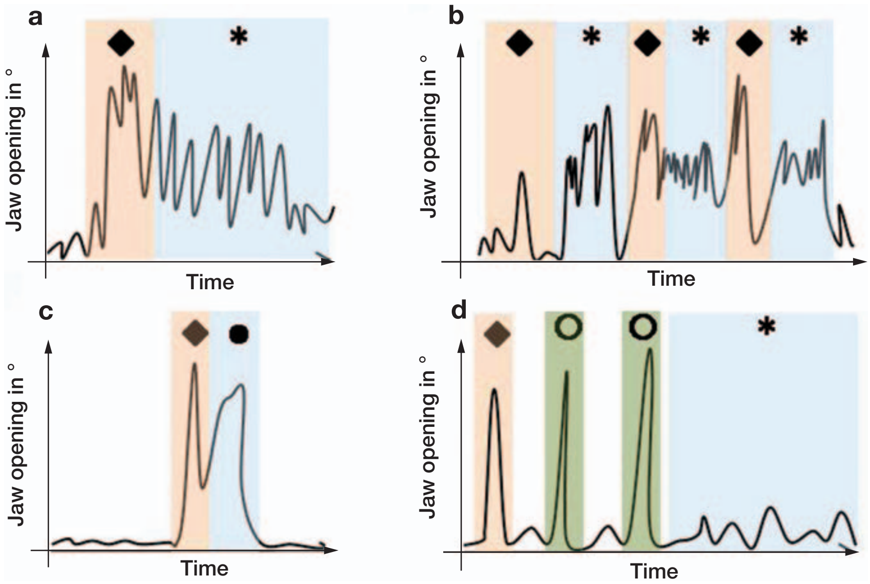


Fig. 5: Food intake, chewing and swallowing in carnivores (a) dog eats large prey, substantial and frequent bites (♦) to secure the morsel, followed by obvious chewing and swallowing (*); (b) sea lion ingesting live fish, the decreased size of the morsel secured by a reduced number of bites (♦) is chewed and swallowed with a reduced amount of chewing cycles (*); (c) penguin ingesting (♦) and swallowing (●) without chewing, one typical behavior in marine animals; (d) turtles show a variation of carnivorous pattern: grabbing the morsel is succeeded by several vacuum motions (), which are created by expansion of the buccal cavity with closed beak and subsequent opening of the beak. The prey is transported into the oral cavity due to this vacuum motions. Chewing motions (*) are performed with low frequency (*) (adapted from Ref. [77])

example, do not reach the force level of natural dentition subjects [21].

Modeling human mastication

Animal studies serve as source for new insight on human diseases or targeting novel treatment strategies. Fundamental research is often conducted with animals. The principle question on transferability arises immediately and is of highest importance.

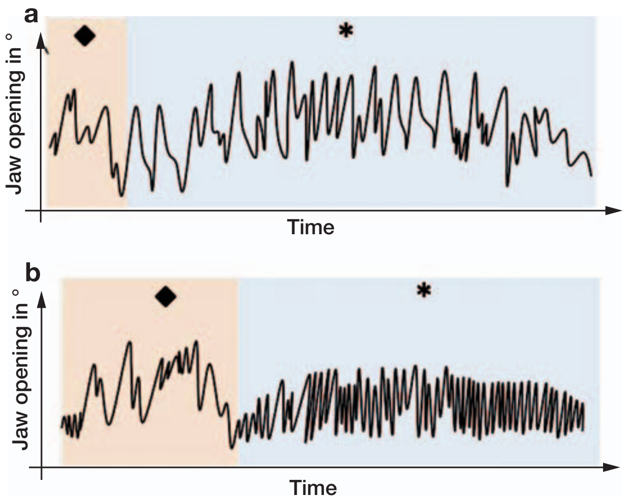


Fig. 6: Food intake, chewing, and swallowing in herbivores (a) horse is grazing and plucking (♦), followed by chewing cycles with large vertical strokes and a decelerated frequency (*); (b) goat is grazing and plucking (♦), followed by chewing cycles with reduced vertical strokes and high frequency (*) (adapted from Ref. [77])

Different mandibular movements occur during mastication in rodent, carnivore, and herbivore (Fig. 7). Anatomical, occlusal, and functional coherence on different species has been described in detail ([63] and further readings). Prominent canines, present in species such as macaque or carnivores are believed to restrict the lateral movement. This would prohibit the transfer of results from animal studies to human mastication. Jaw movements are restricted in lateral direction in macaque. Manipulations in anesthetized animals clearly demonstrate the limiting role of the canine. But these limitations of the lateral component of chewing movements remain present even after canine extraction. Lateral limitations of mandibular movements are not only due to canines, but also due to anatomical factors such as jaw joint morphology, muscle orientation and post canine occlusal relation [38]. Lazzari et al. concluded in their recently published study on the change of tooth morphology during evolution: “It does not appear reasonable to use animals of such phenotype for modeling human mastication. The reverse orders of the changes involved in these different pathways reveal a mosaic evolution of mammalian dentition in which direction of chewing and crown shape seem to be partly decoupled. Either can change in respect to strong functional constraints affecting occlusion which thereby limit the number of the possible pathways. Because convergent pathways imply distinct ontogenetic trajectories, new Evo/Devo (evolution of development) comparative studies on cusp morphogenesis are necessary” [44].

Food is minced during mastication by a process of selection and breakup. The chances of a component of food being “selected” between the teeth may be viewed in relation to the size of the individual unit of food. The actual breakup of food may be described as a cumulative dividing function. Computer simulations based on these two processes could be

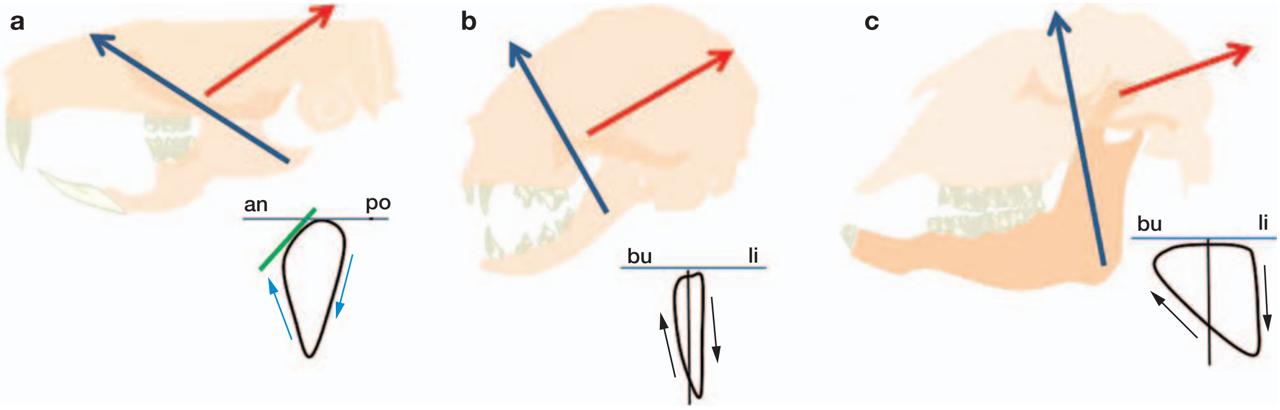


Fig. 7: Different skeletal form and direction of muscle pull (red: temporalis muscle, blue: masseter) (a) rodent, (b) carnivore (dog), (c) herbivore. A characteristic (schematically) chewing cycle is presented for each skull. Consider the different view, the chewing cycle for herbivores and carnivores are presented as frontal projection, the movement in the rodent is displayed as lateral projection. The green line represents upper front teeth, the direction of the movement is forward–backward (= gnawing, propalinal motion) (adapted from Ref. [95]). *bu* buccal; *li* lingual; *an* anterior; *po* posterior

used to describe the individual's efficiency of mastication [80]. The efficiency of mincing food may also be determined with the aid of filter methods. A functional model based on a model of human mastication describes the qualitative abilities of the masticatory organ [80].

Human mastication serves as resource for functional data assessing the effectiveness of occlusion and the functional status of the stomatognathic system prior to restorative or prosthetic intervention. For this purpose, it is necessary to standardize the investigation and the registration procedure of mastication. The use of a standardized model of food in combination with mandibular movement recordings is highly recommended in future studies. Principles of standard model food and standard procedures of chewing recording are described elsewhere [85].

Temporomandibular joint movement during mastication with possible loading and unloading of joint structures is subject matter of many hypothetical models; yet, many questions remain unanswered. In one of the initiator studies of the functional pathways of the condyle, it has been shown, that opening and closing trajectories of the temporomandibular joint are not identical during chewing [22]. However, the observations have been made from a reconstructed hinge axis point. A single pre-adjusted point may represent the rotational center of the condyle during hinge axis rotation, but cannot correspond with the real rotational center of the mandible during opening and closing movements [5, 64, 72]. Loaded closing movements of the mandibula (e.g., biting on a chewing gum, manual downward directed force on the lower front teeth) result in a reduced intra-articular distance within the temporomandibular joint [27]. The minimum distance between the condylar surface and the surface of the articular eminence was found to be smaller on closing than on opening [64]. But, huge interindividual differences of jaw movements, recording with electronic devices, make it difficult to come to a final solution [85–88]. Furthermore, the exact definition and examination technique of the so-called joint loads are not established and further studies need to be done on that particular subject. A principle model on temporomandibular joint loading patterns was introduced by Colombo et al. Practical application of the theoretical fundamentals on human mastication will serve to provide deeper knowledge on charges of different jaw joint structures [6].

A stable center of rotation during normal mastication in rabbits has been described by using cineradiographic data [97]. A stable center can be seen for masticatory opening/closing movements between 0° and 15° jaw-opening angle. The position of this rotational center is independent from animal size and food property. The center of rotation was found more than halfway between the temporomandibular joint and the lower margin of the mandible. Ligaments and joint capsule structures do not seem to be of importance for protecting and restricting jaw movement during chewing. Interestingly, the role of the joint capsule and associated ligaments in humans play an important role in this respect [97]. Elastic properties of chewing muscles in humans and their influence on the rotational center of the mandible is not covered by the scientific literature and further investigations are needed to clear up this particular point.

The endpoint for mastication and the trigger for swallowing are difficult to predict: food particles get smaller and smaller, the lubrication of the food bolus accumulates. But at what point chewing is stopped and deglutition is initiated? The intake of enough food (calories) per day is essential and life sustaining for any creature. During the chewing sequence, intake of more food is difficult and limited. From this viewpoint, the endpoint for mastication (= swallowing) is of high importance for survival. In humans and higher primates, the swallowing process is initiated, when the food particles are formed into a bolus. The formation of a food bolus can be described as function of cohesive forces of food particles [71]. When a subject is forced to chew on beyond the point where swallowing would normally have been triggered, the bolus began to fall apart. This is because of an increased lubrication due to the excessive saliva. The particle size distribution seems to be a key factor in initiating deglutition. An optimization model for mastication and swallowing has been described, suggesting that there is an optimum moment for mammals to swallow, defined in terms of a peak cohesive force between food particles. The peak cohesive force may be different in different foods, but the prediction estimates an initiation of swallowing after similar number of chews despite very different food particle size achieved at that stage [71].

Fluid addition to foods influences mastication and swallowing [66]. Sufficient production of saliva is essential for chewing, swallowing, and digestion [11, 17, 18, 35, 48]. On the other hand, the impact of saliva as threshold or initiator for swallowing is still unclear and controversial discussed in the literature [14, 70, 71, 96]. Inconsistent results of previously performed studies suggest inter- and intra-individual differences among subjects with regard to masticatory performance and salivary flow rate. It has to be admitted that these differences in saliva production are only minimally correlated to the number of chewing strokes until initiating swallowing. Good masticatory performance does not mean automatically less chewing cycles until swallowing. And likewise, an increased frequency during a chewing sequence cannot be correlated to impaired chewing ability one to one. Maybe it is possible to define good chewers as subjects which swallow a food bolus at the correct time, which means that the breakage of food particles reached the maximum coherence level and the amount of fluid is optimal for further digestion and this chewing performance of a chewing sequence is performed with a minimum of energy investment because of good coordination and interaction of chewing muscles and occlusion. If fluid is added to natural foods during the chewing process, muscle activity and swallowing threshold decreases. This is distinct especially in dry foods [66]. The main effect of adding fluids to food during mastication is dilution [10]. The findings of this study are relevant to improve quality of life especially in elderly or persons with impaired mastication ability. Patient management and nursing are highly influenced by this fact [43].

Movements of the human jaw are complex and hard to describe. Analytic approaches are difficult because of the compound of the possible actions and the multifarious characteristics in individuals. The smoothness of movements was effectively used for a model of human limb actions [100]. Fundamental principle of such an approach is the assumption that the central nervous system as the main controlling unit of muscle activity is looking for optimization of smoothness and harmony of movements. Smoothness of movement can be quantified by using jerk – cost model. In this context jerk is defined as the rate of change in acceleration during a given time. Maximum smoothness and minimum jerk costs are of the same tenor. But even jaw movements during chewing of healthy adult volunteers with good occlusion and class I molar relationship and no clinical signs of dysfunction could not be sufficiently described with the maximum smoothness/minimum jerk cost model [100]. The authors of this study concluded that a cycle by cycle modification of the jaw movement influenced by tongue and lip actions to manipulate the food bolus that takes place and causes differences in time profiles for the position of the jaw opening/closing phases between the model and observed data [100]. Studies showed the influence of food properties such as plasticity and elasticity influences the chewing movement patterns. Jaw movements are shaped by different groups of neurons of cortical and brain stem origin. The preprogramed organization is adapted to rheologic behavior of the food. An ongoing feedback circle controls the chewing sequence, based on knowledge and experience, modified by food properties [15, 20, 21, 67, 99]. But chewing muscle feedback alone is not the only input, which influences and modifies mastication. The complexity of masticatory control mechanism includes modifiers such as tongue and check activities. Bilateral gum chewing modulates activation in the primary sensory cortex. This activation occurs differentially in each hemisphere, depending on the chewing side preference. This fact supports the existence of short-term memory for a recently practiced movement [84].

The reduction of food particle sizes during mastication is considered to be the composite result of a selecting and breakage process. The chance of a food particle being selected between teeth is related to the particle's size, whereas the breakage of food particles can be described as a cumulative distribution function. Computer simulated influence of selection and breakage of food on the chewing efficiency of humans can be used, in combination with data obtained from clinical experiments to analyze human chewing efficiency [94].

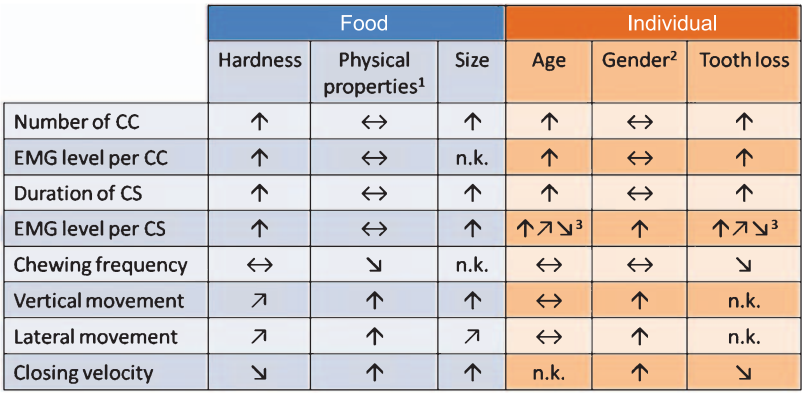
The effect of food properties on chewing parameter

Properties of food such as hardness, plasticity, elasticity, and size of ingested food directly influence afferent input to central nervous control system. Age, gender, and dental status are intrinsic modulators. All of these factors may influence the sequence of mastication. The hardness of food affects chewing parameters in healthy volunteers [67]. Masticatory time (length of a chewing sequence) increases with cumulative hardness, whereas chewing frequency remains almost unchanged. Muscular work (working and non-working side masseter and temporalis muscles) is affected and enhances with increased food hardness. Vertical amplitude increases with increasing hardness; other parameters such as lateral amplitude, opening and closing velocities and duration of the different phases of the masticatory cycle are influenced as well, but to a lesser extent. An overview is given in Table 1 (adapted from Ref. [99]). The most significant determining parameters can be observed within the first 5 chewing cycles. Especially the duration of the occlusal phases of a chewing cycle is elongated with increased food hardness [67]. On the contrary, food perception is dynamic and monitored for changes throughout the whole chewing process [29]. A general three-dimensional model has been postulated: degree of structure, degree of lubrication and time. Each food is changed after ingestion into the mouth; a breakdown path, right through the three dimensions, exists for each food [29].

Food size influences mandibular movement during chewing likewise [55]. Opening and closing phase time and chewing cycle time were significantly longer when food of increased size (10 g vs. 5 g gummy jellies have been used in this study) was chewed. Maximum velocities of jaw closing and jaw-opening activity during chewing were significantly faster and larger when the bigger test food was used. These phenomenons have been observed for both working and non-working side molars. The maximum opening movement on the working side is directly related to food size [55]. Food intake and the first chewing cycle seem to be afferent controlling inputs for precise coordination of chewing movements.

Individual chewing pattern has been demonstrated in many studies [45, 85–88]. The origin and amount of variation in chewing patterns were identified: number of chewing

Tab. 1: Overview on particular parameters of food or individuals with an impact on human mastication (adapted from Ref. [99])



	Food			Individual		
	Hardness	Physical properties[1]	Size	Age	Gender[2]	Tooth loss
Number of CC	↑	↔	↑	↑	↔	↑
EMG level per CC	↑	↔	n.k.	↑	↔	↑
Duration of CS	↑	↔	↑	↑	↔	↑
EMG level per CS	↑	↔	↑	↑↗↘[3]	↑	↑↗↘[3]
Chewing frequency	↔	↘	n.k.	↔	↔	↘
Vertical movement	↗	↑	↑	↔	↑	n.k.
Lateral movement	↗	↑	↗	↔	↑	n.k.
Closing velocity	↘	↑	↑	n.k.	↑	↘

CC Chewing cycle; *CS* chewing sequence; *n.k.* not known; [1]Physical properties of the food are applied from elastic towards plastic; [2]from female to male; [3]a distinct correlation does not exist, the influence on chewing parameters is depending on the food (for details see text)

strokes, mean muscular work, masticatory frequency, opening duration, closing duration, occlusal duration, vertical amplitude, lateral amplitude, and opening and closing velocity. Vertical and lateral amplitudes as well as the velocity of jaw movements during mastication are parameters that can be used for a targeted analysis of determinants that are expressive of the adaptation abilities of healthy individuals and volunteers. In addition, the first cycle appeared to be very different from the subsequent for all parameters except for occlusal duration [45].

On the other hand, the impact of age may not be as significant as was initially assumed. The number of masticatory cycles needed to grind a standardized unit of food increases with age, but the ability to adapt oneself to the properties of food is retained even by elderly individuals [68]. The author concluded: “Although we can make no direct comparison to other motor systems, it would seem that, as long as people keep their teeth, the masticatory system is relatively well preserved. This is perhaps the result of the fact that this motor system is exercised daily, even by people who have difficulty walking. Furthermore, enthusiasm for this type of exercise usually increases as we grow old” [68].

Muscular activity and the frequency of masticatory cycles may be influenced by the hardness of food in the initial stage of mastication [15]. Flow properties and the plastic behavior of food influence the entire masticatory cycle. This initial phase is controlled by a programed pattern steered by the cortex and the brain stem, which adjusts the initial masticatory cycles to the food introduced into the mouth [15]. Chewing forces are greater for hard food than for soft foods, chewing forces decreased during the chewing sequence for hard foods. Closing forces are equal for hard and soft foods immediately before swallowing [20]. In contrast, Kohyama et al. [41] reported that masticatory parameters did not correlate with the physical properties of food measured for small deformation. The discrepancy in the findings of the study maybe explained by the different solid foods used within the project (dry bred, elastic konjac gel, dry sausage, soft candy, raw radish, pickles radish, boiled carrot, and raw carrot). In contrast, the use of a standard food model in clinical trials investigating human mastication showed the dependency of masticatory jaw movement on food properties [15, 45, 68, 85, 99].

The properties of food influence masticatory cycles not only in adults but also in children. Hard food enhances the lateral component in the adult, and increases the medial one in children. Neither in the adult nor in the child does one find a pure hinge movement during mastication [22].

An interesting and novel approach for the use of masticatory movements to analyze feeding habits and behaviors in animals has been described recently (Fig. 4). Food properties can be investigated by data logging devices to monitor jaw movements using a magnet/hall sensor device in animals [77]. Species of mammals, birds, and turtles, with carnivorous and herbivorous feeding habit have been investigated either in marine or terrestrial environments. The so collected data allow estimations on quality and quantity of the food. Carnivores feeding on large prey perform substantial and frequent bites. The prey is secured in this way. These bites are followed by apparent chewing strokes for cutting. The deglution action is less obvious because of the position of the recording system used within this particular study. As the size of the prey is decreased, the number of bites to capture and to chew is decreased. In extreme, e.g., if dogs are fed with canned food, only one single bite followed by immediate swallowing can be observed in carnivores. This behavior is not seen in sea lion, ingesting live fish. In marine animals, the ingestion of small pray does not involve any mastication pattern. Swallowing follows directly the large grabbing peak. This behavior can be observed in Penguins swallowing sardines. A variation of carnivorous feeding pattern can be seen in turtles. Grabbing and chewing motions are separated by vacuuming motions (Figs. 5 and 6) [77]. A complete different prey intake and swallowing in toto requires different morphology of the skull and directions of jaw muscle vectors: pointed, re-curved and hinged teeth, highly mobile mesokinetic and hypokinetic joints and an extraordinarily elongate skull. Such modifications during evolution seem to be an adaptation mechanism to increase the ability to seize, handling, and ingestion of large prey [65].

Mastication, occlusal interference, and jaw joint load

Occlusion, occlusal interferences, and the severity of craniomandibular disorders (CMD) appear to be associated with mastication. Masticatory function is frequently limited in individuals with CMD [12, 79]. The higher the quantity of occlusal interferences detected in the patient's mouth, the more advanced the CMD, the longer chewing time for a specific type of food and the more pronounced are atypical masticatory movements [13]. These results may be interpreted as follows: compensatory masticatory patterns occur on a reflex basis, but the effectiveness of such masticatory patterns is doubtful and it may be presumed that these patterns accelerate a progression of CMD [13]. Several masticatory types have been identified within this study: alternate bilateral, simultaneous bilateral, chronic unilateral, preferentially unilateral, and anterior chewing. Chronic unilateral chewing was defined if more than 95% of the chewing sequence happened on the same side, while preferentially unilateral chewers used one side of the oral cavity for more than 66%. Chewing type was negatively correlated with the number of chewing strokes, with CMD severity and with the number of occlusal interferences on the balancing side. Chewing time was positively correlated with the number of chewing strokes, with CMD severity and with the number of occlusal interferences on the balancing side. The subject's age was positively correlated with CMD severity. In conclusion, CMD patients tended to present a unilateral chewing type pattern, while healthy controls chewed bilateral [13, 56]. Seen under this aspect, chewing side preferences appear in new light. It has to be mentioned that the correlation between chewing side preference and CMD has not been found in all studies [90]. As mentioned before, mammals typically perform a unilateral mastication. A final conclusion cannot be stated on the base of the current literature. Not surprisingly, occlusal interferences cause altered and asymmetrical muscle activity during chewing in the masseter and temporalis muscle [1, 59, 69].

Occlusal interferences are suspect to increase habitual activity in the jaw muscles and especially in the masseter muscle. This hypothesis was tested by establishing active (occlusal) or dummy interferences (vestibular) by means of artificial interferences. A double blind randomized crossover study was performed. Masseter activity remained unchanged during the dummy interference period, while the active occlusal interference caused a significant reduction in the number of activity periods per hour and in their mean amplitude [53]. Initiation of increased muscle activity and development of temporomandibular disorders requires apparently more than one elicitor. The adaptive capacity of the stomatognathic system does not seem to be fully utilized by a single occlusal interference for a short period.

Mastication is a concrete load for the mandible and the craniomandibular joint. Loads on the mandible during the closing action reduce the intra-articular distance in the craniomandibular joint [27]. Ipsilateral (working side) craniomandibular joints are loaded less during mastication than contralateral (non-working side) joints [58]. When subjects chew, the distances tracked by the condylar kinematic centers were found to be shorter on the ipsilateral side than on the contralateral side. The kinematic centers of all contralateral joints showed a coincident movement pattern during chewing and chopping, while on the ipsilateral side the number of joints with coincident movement pattern is significantly less compared to the contralateral side [58].

Masticatory muscle activity during maximum voluntary clench was reported in connection with the research diagnostic criteria for temporomandibular disorder (RDC/TMD) groups [92]. Normal subjects (healthy volunteers, serving as controls) and myogenous, arthrogenous and psychogenous patients were compared within the study. Standardized muscular activity was measured during maximum voluntary clenching (MVC). Normal subjects showed the largest standardized muscular activity during MVC, followed by myogenous and arthrogenous patients. The lowest value was found in psychogenic patients. The percentage overlapping coefficient (POC) has been used as a second outcome parameter. Significant differences between the groups were found for the temporalis muscle only. Controls had a better symmetry in their temporalis muscle compared with TMD patients. Myogenous patients presented with the largest symmetry within all patient groups, but the symmetry was significantly less than the controls. The psychogenic group again showed the lowest value in temporalis symmetry [92]. RDC/TMD subgroups could be objectively discriminated with the aim of surface electromyography of masticatory muscles. Interestingly, no differences were found for masseter muscle symmetry within this study population.

Chewing muscle activity might be influenced not only by local occlusal factors. Electromyographic activity and maximal molar bite force have been investigated in women diagnosed with osteoporosis in upper and lower jaw regions [81]. Individuals with osteoporosis had greater EMG activity in masseter and temporalis muscle when keeping mandibular posture, but lesser EMG activity during clenching and maximal molar biting. Facial osteoporosis can interfere on the patterns of masticatory muscle activation and should be taken into consideration in clinical and experimental settings [81].

Chewing forces acting on the jaw during masticatory movement have been investigated. It was found that maximal forces are achieved in the vicinity of the intercuspal position. The forces are lowest when the jaw is opened [21]. The consistency of food is a major factor that modulates muscle strength: harder food reduces closing strength during mastication, but this is not the case when soft food is chewed. The latter causes no significant changes. Persons who wear full prostheses have lost their ability to react adequately to the quality of food [21]. Chewing forces are influenced by the intraoral situation, but not by gender [23]. Subjects with natural dentition had the highest bite force, followed by pure implant or implant-natural teeth supported prosthesis. Subjects with removable partial dentures and full dentures showed significantly reduced occlusal forces. Notable, all groups showed wide ranged biting forces [23].

Central control of mastication

Mastication is one of the most common rhythmic behaviors, along with respiration and locomotion, in mammals [60]. The steering and controlling mechanism for chewing and swallowing have been discussed and investigated in many studies.

Two simple brain-stem reflexes have been postulated for coordination and rhythmicity of mastication. These reflexes are active alternatively. The jaw-opening reflex is activated by tooth pressure (or tooth – food bolus – tooth contact) or tactile stimulation of wide areas of the mouth and lips. The jaw closing reflex is released by the stretch of the elevator muscles during opening [36, 37, 82, 83]. Two principle models have been postulated for the rhythmic mastication pattern: electrical stimulation of corticofugal pathways selectively excited jaw-opening motoneurones – the jaw-opening reflex is seen as being permanent in this model. An intermittent inhibition of tonic jaw opening is initiated by an activation of closing muscles. This activation could be initiated by a muscle stretch of the closing muscles [76]. On the contrary, a stimulation of suprabulbar sites activates a rhythmic bulbar center controlling mastication [49]. The later model turned out to be sound and the evidence is quite solid that rhythmic mastication pattern occurs within the brain stem and is activated by higher central nervous system centers and/or from the oral cavity [8, 99]. There is evidence for central timing of rhythmical mastication [8]. The authors concluded that mastication is controlled by a brain-stem pattern generator, which can be activated by adequate inputs from certain higher center and from the oral cavity itself. The brain-stem pattern was confirmed by others, among others by Lund [47].

Masticatory patterns seem to differ from person to person, and appear to be markedly dependent on intraoral and neuromuscular sensory feedback controls. A high reproducibility may be presumed, provided the chewed object has similar or identical properties [45]. However, it was shown that even healthy volunteers with class 1 occlusion and no major deviations or missing teeth, and no signs or symptoms of a functional disorder, vary to a certain extent even under standardized conditions [45]. The frequency of mastication, the speed of shift, the amplitude of motions, and the duration of closure were found to differ. Psychologic and physical variables such as emotional status, irritation, or fatigue may play a role in this context, but an explicit statement on this particular subjects cannot be made yet [45].

A mechanism with sensory feedback from the structures of the stomatognathic system is located in the brain stem. This mechanism takes over the function of modifying the muscle strength of the following masticatory movements to the quality of the ingested food. Chewing muscle activities are significantly affected by an increase in hardness regardless of the food type. The circumference of the chewing cycles is depended on the rheologic properties of the food type [15]. The authors proposed a dual hypothesis. First a cortical brain-stem preprogramed mechanism to adapt the shape of the jaw movements to the rheologic properties of the food and second, a brain-stem mechanism with mainly sensory feedback from the mouth to adapt muscle force to the food hardness [15].

Registration of masticatory movements by the use of electronic systems provides deeper insights into the motion and dynamics of the mandible and, at least indirectly, into movements of the craniomandibular joint. Mastication is characterized by gliding of teeth, a pause in intercuspal position or near-intercuspal position, and wide lateral movements [22]. This is true for children as well as adults. Masticatory movements in the occlusion of milk teeth are marked by a pronounced lateral motion during opening. The extent of lateral movement during opening is typically larger than that during closure. In deciduous teeth, the extent of lateral movement reduces when opening while lateral excursion increases during closure. The adult reveals an entirely different masticatory pattern: medial opening and wide lateral closure characterize the adult masticatory pattern [22]. Separation of the molars on the working side is closely related to the size of the food bolus. This corroborates the hypothesis that opening does not occur incidentally during mastication, but is controlled by various feedback systems in order to minimize effort during mastication [55].

Swallowing and mastication are closely related to each other. The production of saliva is a basic prerequisite for successful mastication. However, the additional intake of fluid during a masticatory cycle influences mastication positively only when the individual ingests very dry food (for instance, cake); this is not the case when fatty (such as cheese) or watery foods (such as carrots) are ingested [66]. The optimal time point for mastication was investigated, and an optimized mastication and deglutition model was developed [55]. Interestingly, the number of masticatory cycles until the first act of swallowing was very constant in the individual volunteer, independent of the type of food, such as nuts compared to carrots. In fact, the number of masticatory cycles until the first act of deglutition was strongly correlated with the quantity of produced saliva [55].

Periodontal mechanoreceptors are an important source of tactile sensory input. In dentate subjects, such mechanoreceptors are playing a key role in controlling mandibular movements [39]. Oral tactile function is highly impaired in case of a reduced dentition. In case of edentulous individuals, periodontal mechanoreceptors are completely absent [30]. In such situations, feedback information (afferent input) are transferred to osseoperception. There is a shift from periodontal structures to peripheral mechanoreceptors in oro-facial and temporomandibular tissues. Osseoperception is defined as mechano-receptive input in the absence of a functional periodontal mechano-receptive input but derived from temporomandibular joint, muscle, cutaneous, mucosal, and periostal mechanoreceptors. At least in part, osseoperception is able to compensate periodontal tissue loss in case of full dentures or implant supported restorations [39].

Intrauterine movement seems to be an important factor in the development of joint development in humans. Pre-natal movements of the lower jaw such as sucking, swallowing, and chewing like movements are an important factor in the development of the mandibular condyle. The endo-chondral bone formation is restricted in case of prohibited intrauterine jaw movements, resulting in condylar cartilage reduced in size and ill-defined bone cartilage margin [24].

As previously stated mastication is one of the most common rhythmic behaviors, along with respiration and locomotion, in mammals [60]. To study human diseases, animal models are helpful and often used. Gene targeted mice are used to model the consequences of over expression, under expression and complete inactivation of a particular gene. Such animal models have been developed for Alzheimer's disease and epilepsy among others. Serotonin receptor deficient mice are used as animal models for eating disorders and are linked to oral dyskinesia. It is possible to distinguish a mouse's chewing pattern by the pattern of jaw movements. A chewing cycle of mice consists of 3 phases: an opening movement, a closing movement and a protruding movement. The protruding movement is performed with high muscle activity and in close relation to occlusion. The mice chewing cycle is comparable with the human chewing cycle. Chewing sequence, chewing cycle, muscle activity, and vertical and lateral amplitude of the chewing strokes are altered by food consistency and food properties in similar way as described for human mastication pattern. A mouse model for studying masticatory disorders can be used, because jaw motor behaviors are describable in terms of movement and muscle activity and sensory feedback on jaw behavior are evaluable. Comparison between normal mouse and transgenic mouse with behavioral dysfunction can therefore be used to investigate brain behavior relationships. A new approach for a better understanding of oral motor disorders is conceivable [60].

Electromyographic studies are used to analyze the masticatory muscles. A hypothetical model was used: simultaneous activation of the jaw openers during mastication leads to additional activation of the muscles involved in closing the jaw [73, 74]. During mastication, additional and simultaneous activation of the digastric muscle was much more pronounced during closure than it is in isometric tension. However, such activation was mild compared to the maximum possible activation potential of the digastric muscle. Therefore, it may be concluded that simultaneous activation of the openers has no more than a mild impact on the additional activation of masticatory muscles. It was also found that muscle activity measured with EMG does not always permit consistent conclusions about masticatory strength. The higher muscle activity during mastication, as seen on EMG, is not directly associated with an increase in muscle strength – as compared to the activity of bruxism. Additional EMG measurements are needed to analyze the actual masticatory strength. It would not be permissible to draw conclusions about loads on the craniomandibular joints on the basis of muscle activity on EMG [73, 74]. The hardness or consistency of food modulates EMG activity, especially during the initial masticatory movements [67].

Mastication and brain activity

Recent brain mapping studies have revealed activation in the pre-frontal cortex associated with memory during chewing [42, 57, 61, 62, 84, 91]. Mastication and brain activity are closely interrelated. With the aid of functional magnetic resonance imaging (fMRI) it was shown that mastication involves a bilateral increase in the activity of the sensomotor cortex, the thalamus, the amygdala and the cerebellum [78]. In elderly persons, the magnitude of the increase was less in the first three above-mentioned regions, but greater in the cerebellum. Therefore, in the elderly the function of mastication is integrated in the neuronal circuits of the hippocampus and appears to play an important role in preventing age-related disorientation. Mastication may serve as useful therapy to prevent senile dementia [78]. Human mastication is supported to a great extent by the tongue. Positioning the food, exploring its consistency and size, as well as aiding the process of changing sides, are essential functions without which mastication would be impossible. Bilateral mastication of chewing gum modulates the activity of the primary sensomotor cortex during tongue movements, as determined on fMRI investigations. This activation appears to differ in the hemispheres, depending on the preferred side of mastication. These data support the postulated existence of short-term memory functions which store the recently executed movement pattern. Stimulation of the brain in the elderly or rehabilitation of injured brains can be supported by controlled mastication activity [78].

Chewing activity increases cerebral blood flow. This effect was greater on the working side. The blood flow was measured by bilateral transcranial Doppler ultrasound. Clenching, gum chewing and tooth tapping have been selected as tasks in healthy volunteers. Clenching was used to simulate high muscle activity, while gum chewing should represent moderate muscle activity. Low muscle activity was simulated by tooth tapping. Base line level for cerebral blood flow was measured in rest position of the lower jaw. Cerebral blood flow was greater on the working side during the intensive isometric contraction of the masseter muscle in clenching. These results suggest that task-induced change in cerebral blood flow during jaw movement is influenced by the change in peripheral circulation evoked by muscle contraction [26].

Chewing performance and nutrition

Mastication is the mechanical crushing of foods in the oral cavity prior to swallowing. Mastication plays an essential part in the process of digestion. Mammalian mastication is a process combining simultaneous food comminution and lubrication [71]. The ability of the masticatory organ to mince and process food is related to the individual's vital functions and general state of health. Loss of teeth and the reduced ability to chew have a significant impact on an individual's nutritional condition, health, gastrointestinal disorders and digestion [19]. An altered choice of food and a changed nutrient intake is correlated with the dental status. Missing teeth lead to a reduced chewing efficiency. The evidence indicates reduced consumption of meat, fresh fruit, and vegetables in situations of reduced dentition. Plasma parameters such as Hemoglobin and Vitamin C level may be altered. However, confirmed evidence of these associations is scarcer than one would expect it to be: key co-factors and variables are yet unknown or only partially identified. In the existing studies, the nutritional habits of the study participants have been poorly or fragmentarily documented. Extrapolation of data from animal experiments is such that the results may be poorly applicable to the human setting. Lifestyle, morbidity, and the individual's socioeconomic status are major factors influencing nutrition and oral health. Especially in elderly, cofactors and confounders (known and unknown) have to be taken into consideration in studies investigating mastication, dental conditions, and general health [19].

The quantity of the consumption of certain foods was investigated in a Finnish population aged between 18 and 82 years. Information on dietary ingredients (such as bread, porridges, potatoes, dried peas, fruit, root and green vegetables, milk and milk products, eggs, meat, sausages, fish, etc.) were obtained from personal interviews and questionnaires.

Not surprisingly, at least from a today's point of view, significant differences have been reported for subjects, when dental status was used to assign into groups. Soft diets, avoiding hard and fibrous foods, less fruits, raw vegetables and meat have been identified as typical dietary patterns in subjects with partial or total absence of teeth [50–52]. The tendency to avoid meat due to lack of teeth was reported in elderly subjects as well. Interestingly, the same effect of missing teeth on diet was observed even under nursed or fostered health care surroundings [3]. Chewing difficulty and subsequent weight loss was demonstrated to be associated, but an association could not be detected between specific oral health problems and weight loss. However, oral health problems were based on a standardized nursing assessment form, which might not have been reliable or detailed enough for oral assessment [2].

Nutrition is a mediator in the relation between oral and systemic disease. A literature review [75] highlights the contemporary evidence on this topic. Impaired dentition may contribute to weight change; potential confounders are age and socioeconomic status. The effect of dental prostheses and dental restorations is still uncertain: dentures appear to improve dietary quality somehow but do not really compensate missing teeth. The role of implants on chewing performance and nutrition remains unclear and further studies with dental interventions and acquisition of dietary pattern, chewing efficiency and food consumption are required [16, 25].

Diet and health is discussed habitually emotional and often from a subjective viewpoint; this is true not only for popular publications [98]. Beside all trends and fashion, several serious studies have established associations among nutrient intake, nutritional status, and various systemic diseases as well as the confounding potential of altered chewing efficiency due to missing teeth in regard to systemic diseases [4, 28, 31–34]. Anyhow, interpretation and clinical implementation still have to be done with great care and caution. Subjects concerned with their health might be more conscious about both oral health and eating behaviors, and that might explain the differences in dietary patterns among those with different dentition status. Without adjusting for these confounding effects, we cannot evaluate the independent association between oral health and dietary intakes. Adjusting nutrient intake for total caloric intake is important because people with higher intake of calories may be expected to have higher intake of most foods and nutrients. It is difficult to interpret differences in nutrient intake when total caloric intake is not controlled. In addition, controlling caloric intake helps to reduce unrelated variation in nutrients during such studies. In summary, most of the studies relating tooth loss and nutrition suggest that qualitative nutrient intake deteriorate with fewer teeth. These changes, observable in fruit, vegetable, and micronutrient intake, may explain part of the tooth-loss/cardiovascular-disease association [7, 46, 54, 89, 93, 102].

Patients without dementia have 20-fold more teeth in their mouth than age-matched patients with severe Alzheimer dementia. The presence of a large number of teeth in advanced age was identified as a protective factor in respect of Alzheimer dementia. Conversely, edentulous was an independent risk factor for Alzheimer dementia, but not for vascular dementia or ischemic stroke [9]. Tooth loss varies with race, but not with the region of residence; a link between inflammation and the prevalence and incidence rates of stroke was detected [101]. Interestingly, the association between prevalence/incidence rates of stroke is not confounded by inflammation markers such as CRP (C-reactive protein) and WBC (white blood cell count).

Conclusion

Many details are known and investigated on human mastication. Anyhow, further studies are required to clarify special aspects of chewing in individuals. Special focus has to be placed on nutritional aspects related to chewing performance. Intraoral rehabilitations have to be reassessed, whether sufficient masticatory performance is provided by restored occlusions. Furthermore, functional occlusion design may require new concepts and approaches, based on individual chewing pattern.

Conflict of interest

The author declares that there is no conflict of interest.

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