Human oral function: a review

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Abstract
Chewing is the first step in the process of digestion and is meant to prepare the food for swallowing and further processing in the digestive system. During chewing, the food bolus or food particles are reduced in size, saliva is produced to moisten the food and flavors are released. Taste and texture of the food are perceived and have their influence on the chewing process. There are several factors determining the chewing result. The teeth are important in the masticatory system. They form the occlusal area where the food particles are fragmented. This fragmentation depends on the total occlusal area and thus on the number of teeth. Another important factor in mastication is the bite force. The bite force depends on muscle volume, jaw muscle activity, and the coordination between the various chewing muscles. Also the movement of the jaw, and thus the neuromuscular control of chewing, plays an important role in the fragmentation of the food. Another aspect of chewing is how well the tongue and cheeks manipulate the food particles between the teeth. Finally, the production of sufficient saliva is indispensable for good chewing.

Large differences in oral function exist among various groups of subjects, such as dentate subjects, partial and complete denture wearers, and subjects with implant-retained overdentures. Both maximum bite force and masticatory performance are significantly reduced, when dentures replace natural teeth. Oral function also is impaired in orthognathic patients, both before and after surgery, and in patients with a neuromuscular disease, myasthenia gravis. The muscle activity, needed to overcome the resistance of the food during mastication, consists of two contributions: an anticipating and a sensory-induced component. The anticipating muscle activity is generated only if food resistance is expected. The sensory-induced muscle activity immediately starts after food contact. About 85% of the muscle activity needed to crush the food is sensory induced, which indicates that jaw muscle activity is mainly of sensory origin.

Key Words:
Mastication, chewing efficiency, food comminution, particle size distribution, saliva, swallowing, neuromuscular control

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Introduction
Chewing, talking, laughing, smiling, and yawning are important functions of the masticatory system. Often, patients are confronted with problems in performing these functions. This may be due to a malfunction of the jaw muscles, jaws and/or jaw joints or the neural system. The research on the masticatory system deals with the general question of how (neuro-)physiological and mechanical properties of the jaw muscles, jaws, and jaw joints affect the development of normal and abnormal form and function of the masticatory system. In this way a better insight can be obtained into the etiological factors involved in the development of disorders of the masticatory system and an improvement can be gained in the diagnostics and the treatment modalities. Masticatory function has been extensively investigated in both animal and human. In this review, the focus will be on human oral function.

Masticatory Function
Subjective masticatory function (defined as masticatory ability) has been studied by interviewing subjects as to their own assessment of that function, e.g.\(^1,6\). Masticatory ability appeared to be closely related to the number of teeth. Impairment of chewing ability occurs when less than 20 well-distributed teeth are present\(^1\).

Objective masticatory function (defined as masticatory performance) has often been measured by determining an individual’s capacity to grind or pulverize a test food. Several studies have shown that masticatory function is reduced in people who have lost postcanine teeth, e.g.\(^15,16-20\) and in those who wear removable dentures, e.g.\(^15,17\). Implant-supported prostheses improve the oral function and satisfaction in edentulous patients, e.g.\(^19,20\).

Methods to Determine Masticatory Function
The rate of breakdown of food depends on many anatomical and physiological variables. Study of the comminution of solid food is of interest in revealing the relative importance of these variables to masticatory performance. A wide variety of methods has been used to analyze chewing performance: for example, measuring sugar loss from chewing gum\(^21\), measuring color change in chewing gum\(^22,23\), a colorimetric method to determine the release of dye when chewing raw carrots\(^24\), photometric methods to quantify changes in color\(^25,27\), and optical scanning of chewed particles\(^28,29\).

However, in the majority of the studies the degree of breakdown of the food has been determined by sieving, e.g.\(^11,19,30-33\). Both natural foods, such as peanuts, almonds, carrots and synthetic materials have been used as test materials in experiments determining the masticatory performance. A natural test food has the advantage that it is normally consumed, so that subjects are accustomed to it. However, the consistency of the food may vary due to seasonal and geographical influences. To avoid these variations in consistency, artificial food is a good alternative, which has often been used, e.g.\(^15,19,31,33\).

Sieving and analysis methods
A wide variety of sieving methods has been applied in studies on chewing. Some authors have used test sieving with only one sieve, e.g.,\(^19,20\). In these studies the masticatory performance was defined by the weight percentage of masticated food that would pass a sieve with a fixed aperture. Sieving methods, which use more than one sieve, give more detailed information on the distribution of particle sizes in the chewed food, e.g.\(^7,12,15,19,30-33\). Recently, the single and multiple sieve methods were compared\(^35\). It was concluded, that the multiple sieve method yields better results than the single sieve method. Thus, the multiple sieve method should be preferred. However, the larger amount of data obtained with the multiple sieve method complicates the description of the particle size distribution. Several mathematical equations have been proposed, which express the masticatory efficiency in terms of the weights retained on the various sieves, e.g.\(^7,31\). In other studies, the cumulative weight of the comminuted food particles was represented in a plot showing the cumulative weight percentage undersize as a function of the sieve aperture or particle size, e.g.\(^30,32,33\). The cumulative weight percentage undersize for a certain sieve aperture is defined as the percentage of the particles by weight that can pass that sieve. An example of data points plotted in this way can be seen in Fig. 1.

The figure shows the results of a chewing experiment in which a dentate subject with an average masticatory function chewed 10, 20, and 55 times, respectively on an artificial test food. The data points are curve-fitted with a distribution function\(^39\). A logarithmic scale was chosen for the sieve apertures, because of the wide range in sieve apertures (0.25-8.0 mm), thus avoiding congestion of data points in the region of small sieve apertures. As may be expected, the data points of the experiments with different number of chewing cycles shift towards smaller particle size upon an increasing number of chewing.
cycles. The test food consisted of 8 cubes with an edge size of 8 mm of a dental impression material (Optosil®, www.bayer.com)\textsuperscript{35}. The cumulative weight distribution of particle sizes may be characterized by the median particle size, \(X\), which can be obtained from the graph by determining the theoretical sieve aperture through which 50\% of the weight can pass. The number of chewing cycles needed to halve the initial particle size, denoted as \(N_{50}\), is a good measure of chewing efficiency\textsuperscript{40}. The median particle size decreases as a function of the number of chewing strokes, \(N\), according to the relation \(X = c N^{-d}\). This relation describes the rate of food breakdown and therefore the variables \(c\) and \(d\) characterize the masticatory efficiency of the subjects\textsuperscript{40}.

Models Describing Comminution

Matrix method for calculating particle size distributions

An approach in which the breakdown of a material is considered as the composite result of two processes, selection and breakage\textsuperscript{35}, has been successfully applied to the analysis of food comminution\textsuperscript{12, 41, 42, 43}. Selection was defined as the chance that a food particle is placed between the teeth and comminuted or at least damaged during a chewing cycle. Factors related to selection are for instance movement of jaw, tongue and cheeks, the total occlusal area of the molar teeth, tooth shape, particle shape, particle size and the total amount of food in the mouth. If a food particle has been selected, it will be fractured between the teeth into fragments of variable number and size. This is called the breakage process. Breakage depends on factors such as tooth shape, fracture characteristics of the food and the intensity and coordination of jaw-muscle activity, which is generating the bite force. Experiments on comminution of natural food\textsuperscript{42} and artificial food\textsuperscript{43} showed that the selection and breakage processes could be adequately described by rather simple functions. The selection chance was found to increase as a power function of the particle size, whereas the weight fractions of the fragments of a selected particle could be adequately described by a cumulative distribution function\textsuperscript{44, 45}. Due to the repeated selection and breakage of particles in each chewing cycle, the size distribution of the particles of the test food will change. Relatively large particles will gradually disappear, while small particles will become more abundant. The way in which selection and breakage influence the process of food comminution can be determined by means of a mathematical model based on matrix algebra\textsuperscript{40}. This model enables description of the changes in particle size distribution during comminution. The matrix also describes how particles of different sizes are comminuted. To calculate this matrix, the particle size distributions in various phases of chewing must be known and the breakage of particles must be determined in a calibration experiment. The results from the matrix model were verified experimentally by a double-labeling method\textsuperscript{43}.

An analytic probability density for particle size in mastication

In the beginning of the chewing process, when many unbroken food particles are still present in the mixture, empirical functions, describing the distribution of particle sizes, fail to give a good description. To solve this problem, mathematical formulae were derived to characterize the distribution of chewed food particles by size as a function of the number of chewing cycles\textsuperscript{46, 47}. The reduction of food particle sizes was again considered to be the composite result of a selection and a breakage process. The probability density \(P_{n+1}(x)\) of finding a particle of size \(x\) after \(n+1\) chewing cycles was computed from \(P_n(x)\) by selecting a proportion of particles of size \(y\) from \(P_n\) to be converted to particles of size \(x < y\) by a breakage function. Measures of central tendency, average, median, and most probable size were obtained as a function of the number of chewing cycles\textsuperscript{47}. The measures of central tendency characterize the degree of food comminution during the chewing process and can be used to quantify chewing performance. The comminution of food is described in terms of the selection and breakage functions in a convenient, efficient analytic way, valid for all phases of the chewing process.
A selection model to estimate the interaction between food particles and molar teeth

In the selection process, every food particle has a chance of being placed between the antagonistic post-canine teeth and being subjected to subsequent breakage. The selection chance, being the ratio between the number of selected and offered particles, has been mathematically described as a function of the number of particles offered, in terms of the number of breakage sites available on the teeth and particle affinity, i.e. the fraction of breakage sites occupied by one particle. It was demonstrated that the number of selected food particles of a single size asymptotically approaches the total number of breakage sites available for that size, when the number of particles offered increases. From this relationship the critical particle number can be determined. The critical particle number indicates the number of particles by which the breakage sites become saturated.

Factors Influencing Masticatory Function

Many factors are known to influence masticatory performance, such as loss and restoration of postcanine teeth, bite force, age and gender, sensory feedback, occlusal contact area, and oral motor function. Only one factor at a time was studied in the majority of these studies. The main factors influencing masticatory performance were determined in only a few of these studies. Number of functional tooth units and bite force were confirmed as the key determinants of masticatory performance.

Occlusal factors

Many people have deficiencies in masticatory performance because of loss of teeth, malocclusion, or periodontal disease. However, in spite of their handicap, most people manage to eat successfully even though they are unable to comminute their food perfectly before swallowing. In order to improve the masticatory function, missing teeth are often replaced by fixed or removable prosthodontic appliances. Indeed, a clear relationship exists between dental state and masticatory performance as determined with a chewing test. A considerable variation in the masticatory performance is found, which may be related to many different factors such as the total occlusal surface, the occlusal contact area, the number of teeth present, the number of occluding pairs of teeth, tooth shape, the preferred side and the action of the soft tissues. In a study on the influence of occlusal factors on the masticatory performance in 32 young dentate subjects, it was found that the rate of comminution was most highly correlated with the occlusal area of the postcanine teeth. An even more important factor controlling the masticatory performance of people with natural teeth proved to be the amount of occlusal contact area of molar and premolar teeth, which is on average one fifth of the total occlusal surface. A multiple regression analysis was used to predict the masticatory performance from occlusal factors. Their findings revealed a significant correlation between masticatory performance and the state of occlusion. However, the multiple regression analysis showed that only 48% of the masticatory performance score could be predicted from the occlusal factors, which indicates that other factors may also affect masticatory performance. The number of postcanine teeth appeared to be less important than the number of occlusal contacts of these teeth. In these studies, the number of occluding posterior teeth was expressed in occlusal units. An occluding molar pair was counted as two occlusal units, whereas a premolar pair was counted as one occlusal unit. The number of occlusal units per side was also determined as the distribution of occlusal units is known to influence chewing performance, e.g. for chewing performance.

Maximum bite force

Significant correlations are reported between masticatory performance and maximum bite force for subjects with natural dentition, shortened arch as well as complete arch. This indicates that a higher bite force leads to a better fragmentation of the food. However, in some groups of edentate subjects, such a correlation did not exist. In a group of subjects with implant-retained overdentures maximum bite force and masticatory performance were not related. This was caused by large variations in both maximum bite force and masticatory efficiency.

Sensory feedback and manipulation of food

The selection process of human mastication is normally treated as a mechanico-statistical function rather than a specific motor response driven by sensory input. However, the selection of food depends on the manipulation of the food by the tongue and cheeks to sort
out coarse particles and bring them on to the occlusal surfaces of the teeth for further reduction\textsuperscript{53}. A chewing stroke will be ineffective for particle reduction when there is an insufficient quantity of large particles between the occlusal surfaces. It has been shown, on a quantitative basis, that local anesthesia impairs chewing efficiency\textsuperscript{53}. Ten persons with intact dentitions chewed on standard quantities of peanuts on their preferred chewing side. An average of 40 chewing strokes was required after unilateral anesthesia to achieve almost the same performance achieved with 20 strokes before anesthesia. Thus, peripheral sensory impairment affects masticatory performance in dentate persons. Also tongue motor skill may play an important role in the manipulation of the food. Tongue motor skill was examined by a ultrasound system in 3 groups of subjects: 30 healthy adult dentates, 10 elderly dentates, and 20 complete denture wearers\textsuperscript{56, 59}. The tongue motor skill of the elderly dentates and complete denture wearers were statistically lower than those of the adult dentates. Furthermore, the tongue motor skill and masticatory performance were significantly correlated. In a recent study, an index of oral manipulative skill was introduced by measuring the fastest possible movement to bite on a small rubber ball (diameter of 8mm) repetitively between the right and left posterior teeth\textsuperscript{60}. The cycle time of the movement was significantly correlated with the masticatory performance as obtained from chewing peanuts. Masticatory performance appeared not to be correlated with oral stereognostic ability in a group of 71 dentate subjects and 64 denture wearers\textsuperscript{62}. Apparently, the ability to recognize the edible test forms (made from raw carrots) in the mouth is not related with the chewing result in both dentate subjects and denture wearers. 

**Age**

In a comprehensive study of oral function in humans\textsuperscript{72} the masticatory performance was determined for a group of 814 subjects between 25 and 75 years of age. The investigation was limited to persons with natural dentition or with missing dentition replaced by a fixed prosthesis. According to this study, masticatory performance does not alter significantly with age in persons who have a complete or almost complete dentition. However, in these persons, there is a significant increase with age in the number of strokes used to prepare the test food for swallowing. Although maximum bite force appeared to be significantly larger in a group of young dentate subjects as compared to old dentate subjects, no significant differences in masticatory efficiency were observed\textsuperscript{73}. Apparently, the lower maximum bite force of the older subjects was still high enough for chewing the test food. 

**Saliva**

Saliva participates in digestive functions by contributing to food breakdown, by dissolving and releasing food taste and odor chemicals, and by lubricating the food bolus for swallowing\textsuperscript{61}. Reduction of particle size, reduction of resistance against food deformation and the formation of a coherent bolus that can be swallowed are the main goals of the chewing process. Saliva moistens the fragmented food particles during chewing, so that the food can be swallowed\textsuperscript{62, 63}. However, in a group of 177 dentate subjects only a low, but significant correlation \((r = 0.19)\) was found between the flow rate of saliva and masticatory performance as obtained with an artificial food (unpublished observations). Salivary glands and the saliva they produce also play a major role in the health of the oral cavity and the proximal portion of the gastrointestinal tract\textsuperscript{64}. 

**Food texture and taste**

Food texture has a large influence on the chewing process, e.g.\textsuperscript{61, 65, 66}. A clear relationship between muscular activity and food properties has been reported\textsuperscript{67, 68}. The number of chewing cycles preceding the first swallow depends on the texture of the food\textsuperscript{62, 67}. A firm and dry food, as for instance nuts, requires many chewing cycles to fragment the particles and to wet them with saliva before they can be swallowed\textsuperscript{69}. Although it may be expected that the taste of food also has much influence on the chewing process, it is disappointing to notice that experiments and thus data on this question are scarce\textsuperscript{69}. It is suggested that an influence of taste on the chewing process runs via its relation with saliva flow rate. Flavor release from food may be related to the surface of the fragmented food particles and thus it will be related to masticatory performance\textsuperscript{70}. 

**Swallowing threshold**

The swallowing threshold is influenced by the masticatory performance. Subjects with a reduced chewing performance, due to an inadequate dentition,
needed more chewing cycles to prepare the food for swallowing than those with a good performance. Furthermore, they swallowed larger food particles than those with good performance. Thus, subjects with an inadequate dentition compensate for their reduced chewing performance by chewing for a longer period of time and by swallowing larger food particles. The initiation of swallowing, which is voluntary, has been thought to depend on separate thresholds for food particle size and for particle lubrication. However, instead of this duality, it has also been suggested that swallowing is initiated when it is sensed that a batch of food particles is binding together under viscous forces so as to form a bolus. The swallowing process has been studied directly with videofluorography. Food movements during complete feeding sequences on soft and hard foods, coated with barium sulfate, were investigated with this technique. The movements of tongue, jaw, hyoid, and food were recorded, so that the various stages of intra-oral transport, including swallowing, could be quantified.

Oral function in various groups of individuals

Dentate subjects

In most studies on the relation between dental state and masticatory function, subjects with a poor dental state were compared with subjects who have a complete dentition. However, there have been few studies that directly determine the influence on masticatory function of prosthodontic treatment. The objective masticatory function improved immediately after prosthodontic treatment. Thereafter, a further gradual increase in masticatory efficiency occurred until after a month the masticatory function was optimal. The masticatory performance of partially edentulous patients has been studied before and after completion of prosthetic restoration. The results of the patient group were compared with data obtained for a control group of subjects having a full dentition. In this way it was quantified to what extent the masticatory function could be restored to normal levels. The total number of occluding postcanine teeth increased as a result of the prosthodontic treatment, yielding a significantly improved objective masticatory function. The average masticatory performance was found to approach the level of a control group of subjects with a complete dentition, if all occlusal units of the longest posterior side were replaced. Subjects with an incomplete dentition tended to chew predominantly at the side of the longest posterior arch. Rehabilitation of post-canine teeth restores some of the objective masticatory function and leads to an increased appreciation of the masticatory function, although no correlation between the change in objective and subjective masticatory function was found.

Complete denture wearers

The ability of denture wearers to break down test food is very poor as compared with that of young adults with natural dentitions. Food pulverization experiments have shown that complete denture wearers have a much lower chewing efficiency than persons with natural dentitions. Complete denture wearers needed on average 4 times, 6 times, and even 8 times the number of chewing strokes of dentate persons to achieve the same degree of pulverization. It was found that the difference in chewing efficiency between dentates and denture wearers depends on the consistency of the food. The denture wearers needed on average 3 to 5 times the number of chewing cycles for a soft, respectively hard food. One of the factors leading to the decrease in chewing performance is the reduced bite force that denture wearers can develop due to a lack of retention and stability of the denture. The bite force of these subjects obtained with maximum clenching (unilateral) ranges from 77 to 135 N, whereas the average maximum bite force (unilateral) for dentate persons varies from 330 to 522 N. The maximum bite forces of denture wearers may be even lower than the forces needed to penetrate natural foods, such as boiled meat (80 N), raw carrot (118 N), and rye bread (167 N). Thus, denture wearers might have difficulties in biting and incising such foods. As a consequence, full denture wearers select only a few food particles at a time, so the total force needed to crush the food is limited. We may conclude that edentulous persons are handicapped in masticatory function and even clinically satisfactory complete dentures are poor substitutes for natural teeth.

Implant-retained overdentures

The objective oral function significantly improves when the mandibular denture is supported by oral implants. The maximum bite force of subjects with a mandibular denture supported by implants is 60 to 200% higher than that of subjects with a conventional denture.
However, the average bite force after treatment was still only two thirds of the value obtained for dentate subjects\(^{20}\). The masticatory performance also significantly improved after implant treatment\(^{46, 77}\). The number of chewing cycles needed to halve the initial size of the food decreased from 51 to 28\(^{77}\). The improvement of oral function after implant treatment does not seem to depend on the degree of implant support\(^{16, 87}\). In these studies, it was shown that bite force and masticatory performance did not differ among subjects with mainly implant-borne overdentures on a transmandibular implant and subjects with mucosa-borne overdentures on two implants.

The attachment type of implant-retained mandibular overdentures may influence the retention and the stability of the denture, and thus the oral function. In a within-subject crossover clinical trial the influence of retention and stability of the denture on the maximum bite force and the corresponding EMG, and on the masticatory performance was studied\(^{20, 77}\). Eighteen subjects received two permucosal implants and three suprastructure modalities: magnet, bar-clip, or ball attachment. The 3 suprastructures were worn successively by all 18 subjects, so a within-subject comparison of the oral function obtained with the 3 attachment types could be made. No significant differences in maximum bite force, muscle activity, and masticatory performance were found among the 3 attachment types\(^{20, 77}\).

The subjective oral function of subjects with an implant-retained overdenture has been recently reviewed\(^{88}\). Both chewing ability and satisfaction improved as a result of implant treatment\(^{89, 90}\).

**Orthognathic patients**

A reduced chewing performance has been reported for patients with a mandibular prognathism, who were scheduled for orthognathic surgery\(^{95, 95}\). After surgical correction, chewing performance improved significantly in three out of five of these studies\(^{91, 93, 95}\). Patients with a hypoplastic mandible also showed a reduced chewing performance before treatment\(^{96}\). In this study the patients needed about twice the number of chewing cycles as the controls to halve the initial size of the food particles. The chance to select a food particle for breakage as well as the degree of breakage was significantly smaller for the patients than for the controls. These findings suggest that the reduced chewing performance of pre-orthognathic surgery patients is due to an impairment of both selection and breakage of food particles.

**Neuromuscular disease: Myasthenia Gravis**

Fluctuating weakness of voluntary muscles and abnormal fatigability on exertion are the most prominent characteristics of *myasthenia gravis*, a neuromuscular disease in which the neuromuscular transmission is impaired by an autoimmune reaction to the postsynaptic acetylcholine receptors. All skeletal muscles may be involved. *Bulbar myasthenia gravis* refers to weakness in jaw muscles. Myasthenia gravis patients with bulbar involvement may suffer from difficulties in swallowing and chewing, changed facial expression, and dysarthria.

A group of 20 bulbar myasthenia gravis patients has been compared with a group of 20 healthy controls, matched for age, gender, and dental status\(^{97}\). Masticatory muscle strength, chewing performance, and tongue force were quantified in patients with bulbar myasthenia gravis and compared with that of the healthy subjects. The maximum bite force was significantly lower for the myasthenia gravis patients than for the controls: 264 ± 40 N versus 487 ± 48 N\(^{98}\). The chewing performance was impaired in the patient group\(^{99}\). The median particle size after 15 chewing cycles was 5.6 ± 2.0 and 3.2 ± 1.4 mm for the patients and controls, respectively. The force of the tongue, which plays an important role in the swallowing process, was measured with the use of a tongue force transducer\(^{100}\). The results indicated that maximum tongue force in the patient group was significantly lower in all directions than the tongue force of the controls\(^{101}\).

**Neuromuscular control of chewing**

The movement of the jaw, and thus the neuromuscular control of chewing, also plays an important role in the comminution of the food. Chewing requires muscle activity to make the movements of the jaw and to exert forces in order to cut or grind the food. A relatively low level of muscle activity is observed in the surface EMG of the closing muscles of subjects making pseudo-chewing movements without food. More muscle activity is generated if the closing movement is counteracted by food resistance\(^{96, 102}\). Apparently, a small part of the muscle activity observed during chewing is needed just for the basic rhythmic movements of the jaw, and additional
muscle activity is required to overcome the resistance of the food. The total amount of EMG activity has been shown to depend on the texture of the food: more EMG activity is observed for harder foods.

Central pattern generator
The brain stem has been shown to be an essential part of the central nervous system that is necessary for mastication, because decerebrate animals and animals without a cerebellum or spinal cord can still chew. The basic rhythmic activity of the jaw-opening and jaw-closing muscles is probably evoked by a central pattern generator located in the brain stem. Cortically evoked rhythmic trigeminal activity remained present in animals after elimination of sensory feedback from peripheral receptors. This shows that neither muscle spindle afferents nor periodontal afferents are essential to the basic rhythmic activity patterns of mastication. Cortical stimulation of the anaesthetized rabbit induced rhythmic mandibular movements in the awake animal. The central pattern generator may be switched on by activity of higher centers or by intraoral stimuli.

Peripheral feedback
Comparison of the movements and the activity patterns in the motor nerves evoked by cortical stimulation of the paralyzed animal with those of natural chewing before paralysis, has demonstrated the important role of sensory feedback in mastication. During cortical stimulation, the central pattern generator produces stereotyped open-close cycles, whereas during natural chewing the movement trajectories of the consecutive chewing cycles vary considerably. Moreover, the activity of the jaw-closer-motoneurons is much smaller in fictive mastication than during natural chewing. This suggests that to adequately fulfil the motor tasks of the mandible during chewing, the central nervous system requires information about the position and velocity of the mandible, about the forces acting on the mandible and on the teeth, and about the length and contraction velocity of the muscles involved. An increase of the amplitude and the duration of the activity of the jaw closing muscles of the rabbit was observed, when cortically induced rhythmic open-close movements were obstructed by a steel ball or a foam strip between antagonistic teeth. This effect was reduced after elimination of feedback from the periodontal pressoreceptors by deafferentiation. It was concluded that periodontal pressoreceptors, and muscle spindles, provide positive feedback to the jaw-closing muscles during mastication.

Simulated chewing experiments
The neuromuscular control of chewing in humans has been studied in our laboratory, e.g. In these studies food resistance was simulated by a computer controlled external load, acting on the mandible in a downward direction during closing (Fig. 2).

Fig. 2 - Schematic drawing of the experimental setup. In the experiment, an external force simulates food resistance.

Sequences of cycles with a load were unexpectedly alternated with sequences of cycles without a load. Jaw movement, and EMG of the masseter, temporalis, and digastic muscles were recorded. It was demonstrated that the additional muscle activity, needed to counteract the external load, consists of two components: an anticipating component starting before the onset of the food simulating load and a peripherally induced component starting after the onset of the load. The anticipating component is generated only if a counteracting load is expected. The onset of the anticipating muscle activity occurs immediately after the moment that the jaw starts closing. Peripherally induced muscle activity is generated on average 23 ms after the onset of the load. About 85% of the muscle activity needed to overcome the external load is peripherally induced, which indicates that the muscle activity is mainly of sensory origin. However, when the movement rate of chewing was doubled (fast chewing with 120 cycles per minute), the contribution of peripherally induced muscle...
activity decreased to only 40%. Therefore, as jaw movement speed increased, emphasis in the control of the muscle activity shifted from sensory induced (closed-loop) to feed forward (open-loop) control\(^1\). Muscles spindles are primarily responsible for the peripherally induced muscle activity as was demonstrated in an experiment on anesthetized rabbits\(^1\). The masticatory system is mainly closed-loop controlled. A reason for this may be the fact that the relatively large forces needed for food fragmentation must be controlled under uncertain conditions. First, no optical feedback is available in the chewing process. Furthermore, food resistance may vary largely from cycle to cycle. Thus, immediate muscle response is necessary to maintain a constant chewing rhythm. Force-velocity properties of the jaw-closing muscles play a major role in the situation that the food resistance suddenly disappears\(^1\). In that case reflex activity is too slow to limit the jaw velocity at impact. The force-velocity properties of the muscles provide a quick mechanism for dealing with unexpected closing movements and so avoid damage to the dental elements. An experiment with rhythmic arm movements, comparable to the rhythmic jaw movements described above, showed that arm and jaw muscles respond differently to loading\(^1\). In the arm muscles, there was little reflex activity, but a large anticipatory response. This indicates that reflexes do not play an important role in these rhythmic arm movements. This emphasizes that the mainly reflexly induced control of the jaw closing muscles is a unique phenomenon.

Acknowledgements

This work was supported by the University Medical Center Utrecht and the Netherlands Institute for Dental Sciences. I am grateful to Dr. F.A. Fontijn-Tekamp for critical reading of the manuscript.

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