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Oral physiology and mastication

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Abstract

Mastication is a sensory-motor activity aimed at the preparation of food for swallowing. It is a complex process involving activities of the facial, the elevator and suprahyoidal muscles, and the tongue. These activities result in patterns of rhythmic mandibular movements, food manipulation and the crushing of food between the teeth. Saliva facilitates mastication, moistens the food particles, makes a bolus, and assists swallowing. The movement of the jaw, and thus the neuromuscular control of chewing, plays an important role in the comminution of the food. Characteristics of the food, e.g. water and fat percentage and hardness, are known to influence the masticatory process. Food hardness is sensed during mastication and affects masticatory force, jaw muscle activity, and mandibular jaw movements. When we chew for instance a crispy food, the jaw decelerates and accelerates as a result of resistance and breakage of food particles. The characteristic breakage behaviour of food is essential for the sensory sensation. This study presents a short review of the influence of oral physiology characteristics and food characteristics on the masticatory process.

Keywords: Mastication; Swallow; Saliva; Food; Perception

1. Introduction

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. The water in the saliva moistens the food particles, whereas the salivary mucins bind masticated food into a coherent and slippery bolus that can be easily swallowed [1]. The initiation of swallowing, which is voluntary, has been thought to depend on separate thresholds for food particle size and for particle lubrication [2]. 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 bound together under viscous forces so as to form a bolus [3]. 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. While saliva and food have been shown to influence the chewing process, the relationship between amount of saliva and mastication has not been extensively studied [4]. Taste and texture of the food are perceived and have their influence on the chewing process. The time until swallowing was shorter and fewer chews were observed as palatability of the food increased [5]. The effects of sensory factors were most evident at the beginning of meals and decreased until the end of meals [6].

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2. Influence of oral physiology on chewing

All ingested solid foods, regardless of bite size and initial texture, are processed in a stereotyped way by humans [7–9]. After ingestion the food is transported from the front of the mouth to the occlusal surfaces of the post-canine teeth (Stage I transport). Then the food is processed by a series of masticatory cycles needed to comminute and soften the food (food processing stage). The number of processing cycles increases as foods become more difficult to chew. When food is ready to be swallowed it is propelled posteriorly into the oropharynx (Stage II transport). Food accumulates in the oropharynx until it is finally swallowed.

Characteristics of the oral system, like, e.g., bite force, chewing performance, and salivary flow rate will influence the masticatory process, e.g., size reduction of food particles, salivation and mixing of food particles into a food bolus that can be swallowed. The number of chewing cycles needed to prepare food for swallowing (stage I transport until swallowing), defined here as swallowing threshold or moment of swallowing, is rather constant within a subject for one type of food, whereas large variations in the number of chewing cycles until swallowing were observed among subjects [10,11]. For instance, the number of chewing cycles needed to swallow 9.1 cm^3 of peanuts varied between 17 and 110 in a group of 87 dentate subjects [12]. Furthermore, the moment of swallowing appeared to be strongly correlated among various natural foods [11,12]. This means that subjects who used a small number of chewing cycles for one food consistently also used small numbers for all types of food. This implies that there are "slow" and "fast" swallowers (subjects who swallow any food after a relative low or high number of cycles, respectively). This is partly the result of the individual's physiology, but possibly also of the social context.

Chewing performance can be determined by quantifying the degree of fragmentation of an artificial test food (Optosil, a silicon rubber) after a fixed number of chewing cycles [13]. Subjects chew on cubes of Optosil with an edge size of 5.6 mm for 15 chewing strokes. The degree of fragmentation of the chewed food is determined by sieving the food through a stack of sieves. The amount of test food on each sieve is weighed and the median particle size of the chewed food particles is determined from the weight distribution of particle sizes. The degree of fragmentation of the chewed food is well described by the median particle size. Large differences in median particle size after 15 chewing cycles on 5.6 mm cubes of Optosil were obtained in a group of 87 healthy dentate subjects, ranging from 1.60 to 5.27 mm [11].

The moment of swallowing was shown to be only weakly correlated with the chewing performance [11,12]. Thus, a subject with a high masticatory performance does not necessarily swallow food after a smaller number of chewing strokes than a subject with a less high masticatory performance. As a consequence subjects with a high masticatory performance will, on average, swallow finer food particles (median particle size of about 1 mm) than subjects with a less high performance (median particle size of about 3 mm; see Fig. 3 of [11]). It could well be that this will influence the perception of the food. If so, chewers with a high performance would on average perceive food in a different way than subjects with a less high chewing performance.

Mechanically stimulated salivary flow rate can be determined from chewing on a piece of tasteless Parafilm. Over a period of 5 min a subject expectorates saliva at 30-s intervals into a pre-weighed container and flow rate (ml/min) is calculated. In a group of 266 healthy subjects salivary flow rates ranged from 0.16 to 3.8 ml/min [12]. In this study it was shown that the moment of swallowing was only weakly correlated ($r=-0.13$; $p=0.04$) with the salivary flow rate of a subject. Salivary flow rate only explains 2% of the variance in the swallowing threshold. This means that a subject with a relatively high salivary flow rate does not necessarily swallow food after fewer chewing cycles than a subject with less saliva. As a consequence subjects with relative high salivary flow rates are used to swallow better moistened food than subjects with less saliva. Again this may influence the perception of the food. However, previous work in our laboratory has shown that there was no relationship between a subject's salivary flow rate and sensory ratings [14]. Thus, a subject with a larger salivary flow rate during eating did not rate food differently from a subject with less salivary flow. However, an artificial increase of 0.5 ml of saliva significantly influenced the sensory ratings of semisolids [15]. The addition of a fluid affected the mouth-feel attributes of thickness and melting of vanilla custard dessert. The fact that the perceived effect was equally strong for water as for α-amylase solution and saliva, and that a larger fluid volume increased the effect is evidence that the decreased sensation was mainly due to dilution.

The effect on the sensory ratings of adding fluid to a solid food is unknown. Food properties may be modified by the additional fluid, which may lead to changes in chewing force, mandibular jaw movements, and number of chewing cycles to prepare the food for swallowing. It can be hypothesized that an artificial increase in the amount of saliva mixing with food could also influence the perception of the food. Preliminary results of a study in our lab in which various fluids (water, solution of α-amylase, or artificial saliva containing mucins) were added to solid food showed a significant influence of these fluids on oral physiology parameters as well as on textural and sound attributes [16]. For dry foods like melba toast and cake the addition of 5 ml of water to the food significantly reduced the muscle activity and the number of chewing cycles until swallowing. Several texture and sound attributes [17] were also significantly lower after water had been added. The effect of the mucins and α-amylase in the solutions was rather limited. Doubling the volume of tap water had a larger effect. Adding a fluid to solid food clearly facilitates the chewing of dry foods, like melba toast and cake. However, no significant influences on oral physiology and perception of the additional water were observed for carrot (90% water) and cheese (35% water and 31% fat).

3. Influence of food properties on chewing

Characteristics of the food, like, e.g., water and fat percentage and hardness are known to influence the masticatory process. Food hardness is sensed during mastication and affects masticatory force [18], jaw muscle activity [19–23], and mandibular jaw movements [24–27]. The masticatory force during chewing samples of silicon rubber was shown to increase from 100 to 150 N, when the hardness of the samples increased by a factor of 2 [18].

Food characteristics also have a large influence on the number of chewing cycles needed to prepare the food for swallowing [11,12,26,28]. In a group of 87 dentate subjects the number of chewing cycles varied from on average 17 cycles for a portion of 9 cm^3 of cake up to 63 cycles for an equal portion of carrots [12]. Also the volume of the food largely influences oral physiology. For larger portion sizes, subjects needed more time and chewing strokes before they swallowed the food [11,29] The number of chewing strokes needed to prepare the food for swallowing linearly increased as a function of the food volume ($P<0.001$) [11].

Dry and hard products required more chewing cycles before swallowing. Evidently, more time is needed to break the food down and to add enough saliva to form a cohesive bolus suitable for swallowing [30]. Thus, a dry product needs a longer time in the mouth to allow for enough secretion of saliva. Confirming this, buttering dry foods (cake, Melba toast and toast) significantly reduced the number of chewing cycles of these foods [12]. The reason for this is probably that butter enhances lubrication and bolus formation of dry products, decreasing the time needed in the mouth to form a coherent bolus. Similar results were observed in a study in which lubrication of the food bolus had been experimentally varied [31].

4. 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 [32,33]. 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 [20–23].

4.1. 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 [34–38]. 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 [33]. Cortically evoked rhythmic trigeminal activity remained present in animals after elimination of sensory feedback from peripheral receptors [34,39]. 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 rhythmical mandibular movements in the awake animal [40]. The central pattern generator may be switched on by activity of higher centers or by intra-oral stimuli [35,41].

4.2. 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 [38]. 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 [38]. Moreover, the activity of the jaw-closer α-motoneurons is much smaller in fictive mastication than during natural chewing. This suggests that to adequately fulfill 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 [40,42,43]. This effect was reduced after elimination of feedback from the periodontal pressoreceptors by deafferentation. It was concluded that periodontal pressoreceptors, and muscle spindles, provide positive feedback to the jaw-closing muscles during mastication.

4.3. Simulated chewing experiments

The neuromuscular control of chewing in humans has been studied in our laboratory, e.g., Refs. [44–46]. In these studies food resistance was simulated by a computer controlled external load, acting on the mandible in a downward direction during closing (Fig. 1). 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 digastric 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

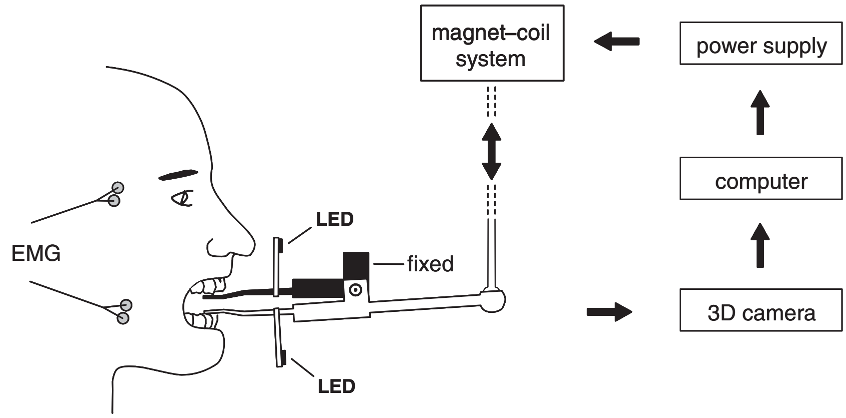

Fig. 1. Experimental setup for external loading of jaw muscles.

(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 [47]. Muscle spindles are primarily responsible for the peripherally induced muscle activity as was demonstrated in an experiment on anesthetized rabbits [43].

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 [48]. 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 [49]. 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.

5. Neuromuscular control of chewing crispy food

The crispy/crunchy nature of food products is an important sensory characteristic on which consumers base their appreciation. When we chew crispy food, the jaw decelerates and accelerates as a result of resistance and breakage of food particles. The characteristic breakage behaviour of a crispy food is essential for the sensory sensation. Our chewing muscles will generate the chewing force needed to break the food. The electrical activity of the chewing muscles will abruptly decrease when the food breaks, thus preventing too fast jaw closing and damage of the teeth. The breakage behaviour of a crispy food

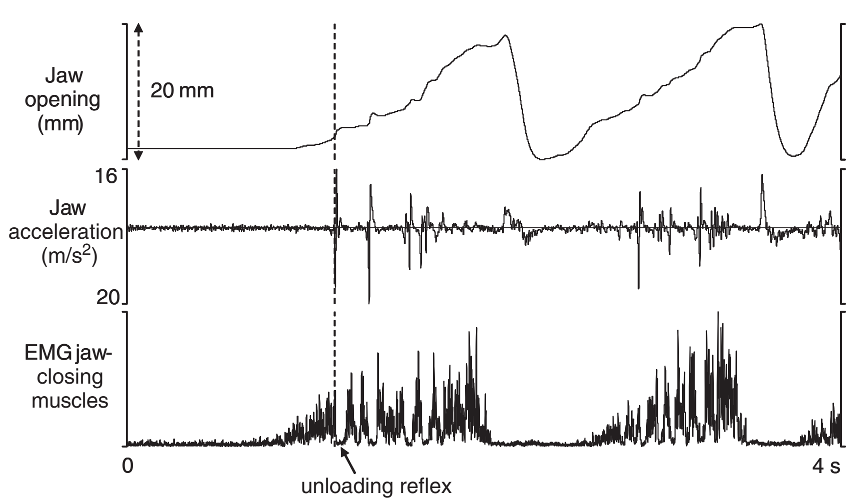

Fig. 2. Jaw movement, jaw acceleration, and rectified jaw muscle activity of a subject who starts chewing on a Brazil nut. The dashed line indicates the first breakage of the nut. The breakage is followed by an unloading reflex in the jaw closing muscles.

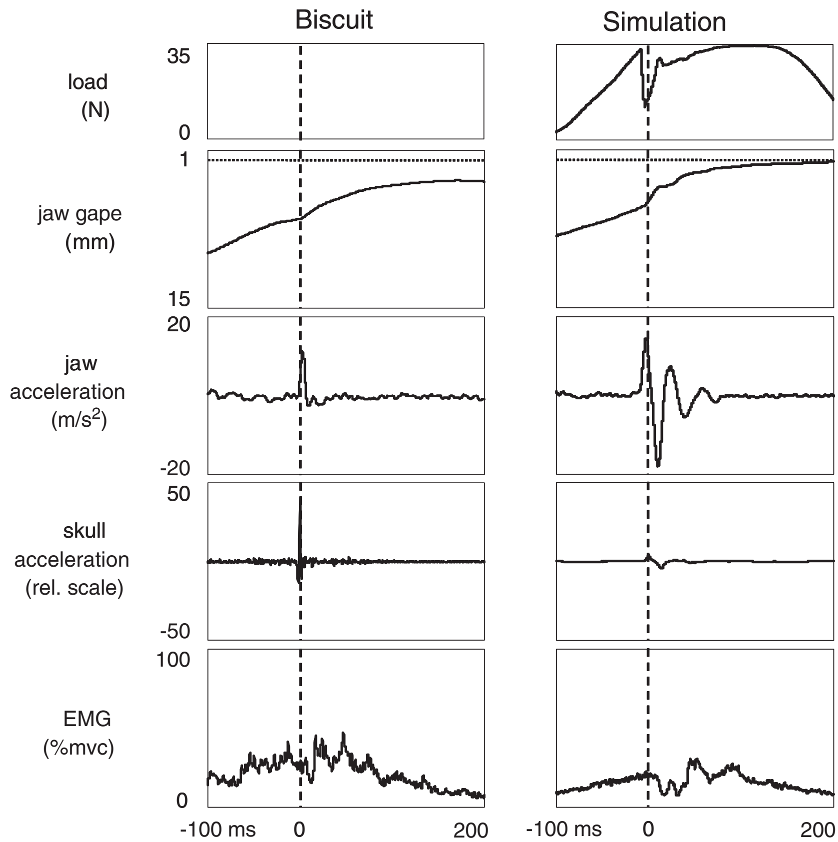

Fig. 3. Jaw gape, jaw acceleration, skull acceleration, and rectified muscle activity for chewing biscuit and simulated chewing.

during chewing could be quantified by studying the neuromuscular control of the jaw movement during chewing of crispy foods. Such a study was recently performed on crispy foods [50]. The electromyogram (EMG) of the jaw closer muscles, the jaw movement, and the vibrations of the skull were measured while a subject chewed Brazil nuts, carrots and biscuits. Several distinct peaks in the acceleration of the jaw and of the skull were detected in the first cycles while chewing on nuts and carrots (Fig. 2). Furthermore, unloading reflexes in the corresponding EMG signals were observed. More, but less pronounced peaks in the acceleration of the jaw were observed when the subject chewed biscuits.

Another approach to study the chewing of crispy foods is to simulate the mechanical resistance of a crispy food [50]. In that way the breakage behaviour of a food during chewing can be manipulated in a reproducible way. Instead of the food resistance present while chewing on a food, an external load was generated by a magnet-coil system (Fig. 1). The external load thus mimics the load that would be present while chewing a crispy food. The force-deformation characteristics, as obtained from chewing a crispy food, were used to program the load for simulated chewing. The simulated crispy food resistance should thus show similar muscle activity and jaw movement as with the natural food. Indeed, the muscle activity evoked while chewing on a natural food was very similar to the muscle activity observed during simulated chewing with a corresponding load profile (Fig. 3). The skull vibrations occurred in synchronization with acceleration of the jaw, which occurs when the food breaks or after a dip in the load profile. Significant differences in texture attributes were observed for load profiles that simulate different breakage behaviour of a food. We may conclude that simulated chewing is a promising tool for studying neuromuscular and sensory aspects of chewing crispy foods in a controlled and reproducible way.

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