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Influence of age on mastication: effects on eating behaviour

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The present review covers current knowledge about the ageing of oral physiology related to mastication and its effects on eating behaviour. Mastication is the first process undergone by a food during feeding. It has a key role in the maintenance of nutritional status in two respects. First, the perceptions of food's sensory properties elicited during chewing and swallowing are one of the major determinants of the pleasure which drives us to eat; second, the properties of the swallowed bolus are affected by oral conditions and this may modulate the subsequent phases of digestion. Ageing in healthy dentate subjects induces moderate changes in oral physiology. Changes in neuromuscular activity are partly compensated by changes in chewing behaviour. No clear age effect is seen in texture perception, although this does impact on food bolus properties. In contrast, great alterations in both chewing behaviour and food bolus properties are observed when ageing is associated with a compromised dentition, general health alterations and drug intake. Eating behaviour is far more complex than just chewing behaviour and the concerns of the elderly about food cannot be explained solely by oral physiology. Discrepancies are often noticed with older subjects between various objective measurements of oral performance and corresponding measures of self-perception. In addition, although more foods are recognised as hard to chew with increasing age, there is no clear shift in preference towards food that is easy to chew. Food choices and food consumption are also driven by memory, psychology and economic factors. Advances in the understanding of food choice in the elderly need a sustained collaborative research effort between sensory physiologists, nutritionists, and food scientists.

Mastication: Salivation: Elderly: Eating behaviour: Food choice

Introduction

During feeding, mastication is the first transformation process for a food en route to the gut. Basically, it consists of a rhythmic activity of the jaw-opening and -closing muscles, controlled by a central pattern generator (Lund, 1991). This rhythmic activity is modulated by sensory inputs throughout the chewing sequence, allowing adjustment in the masticatory process in response to the bolus texture at any moment. It follows that chewing is a highly complex sensory–motor activity which integrates the various components of the masticatory system, such as teeth and their investing structures, jaw muscles, temporomandibular joints, tongue, lips, cheeks, palate and salivary secretions (Orchardson & Cadden, 1998). During chewing, the food sample is fragmented by compressive and shear bite forces as saliva is incorporated. The resulting small particles form a cohesive mass, the bolus. The point of maximum cohesion may provide the trigger to swallow, thereby minimising the risk of dysphagia (Prinz & Lucas, 1997; Alexander, 1998). Chewing is required to process any kind of solid food but displays a large variability between consumers in terms of duration, mandibular trajectory and levels of muscular activity. However, when comparing the physical properties of the food boli gathered from different subjects similar in dental status, there is insignificant between-subject variability (Mioche *et al*. 2003). This suggests that each consumer has his or her own oral strategy to comminute a piece of food but the properties of the bolus when ready for swallowing vary only slightly between individuals. However, this variability between consumers in terms of chewing behaviour and/or intra-oral food manipulation could also lead to differences in the perception of the sensory qualities of food such as taste, smell and texture.

Chewing behaviour is thought to influence nutritional status in two different ways. On one hand, the perception of food sensory properties elicited during chewing and swallowing is one of the major determinants of the pleasure which drives us to eat. It has therefore a large

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impact on food intake and food choice with a direct consequence on individual nutritional status. On the other hand, the properties of the swallowed bolus can be affected by oral conditions. Very few studies have addressed this topic, but it is possible that the properties of the bolus might affect the release of nutrients during subsequent phases of digestion.

Ageing impacts, to varying degrees, on aspects of oral physiology that play a key role in chewing behaviour. Important changes in demography worldwide are expected over the next 25 years. For example, in Western populations, the 'old elderly' (> 80 years) are the segment of the population with the fastest rate of increase. The food needs for this growing sector of the population have been largely neglected. It is therefore important to clarify the influence of age on chewing behaviour in order to give appropriate recommendations on the specific needs of seniors in terms of food acceptability, to enable them to maintain an adequate nutritional status and high quality of life.

The present review will analyse the effect of age on the various aspects of oral physiology that are involved in chewing. The functional consequences in terms of chewing efficiency and food texture perception are emphasised. Two main influences of age are commonly identified. The first, primary or physiological ageing, is directly related to the effects of the passage of time. 'Healthy ageing' refers to the elderly with good general health and dental status (few or no missing teeth, no removable prosthesis and no oral disease). Secondary ageing is the result of local or systemic diseases, physiological and/or psychological disorders, and physical accidents, and is frequently induced by the side effects of drugs (Busse, 1977). For each point reported in the present review, an attempt is made to analyse the effect of age *per se* from the ageing effects in medicated patients or in patients with specific dental disorders.

Influence of ageing on masticatory apparatus

Teeth

The mechanical role of teeth in food breakdown is conventionally attributed to their shape and position in the mouth; phylogenetic reasons have been advanced to explain the characteristics of the teeth (Kay & Hiiemae, 1974; Muller *et al.* 1995).

In man, primary ageing induces changes in dental arch anatomy. An occlusal abrasion occurs due to repetitive clenching actions during the chewing of hard or tough food. It leads to a flattening of the crown of the tooth that comes into contact with directly opposed food or through interposed food particles (Begg & Kesling, 1977). From the examination of human skulls from ancient populations, a continual eruption of the teeth during ageing produces an unbalanced ratio between the crown and root of the teeth. Occlusal abrasion can be seen as a compensatory process (Begg & Kesling, 1977; Levers & Darling, 1983; Canalda, 1990). Food properties are thought to make a large contribution to tooth abrasion (Smith, 1984). Excessive occlusal abrasion, found in ancient and primitive populations, has become uncommon in developed societies; however insufficient occlusal abrasion is common in populations eating processed foods. Soft foods result in the persistence of occlusal tooth relief and could lead to oro-facial disorders (Planas, 1994). Wear facets develop in young adults but are more frequently encountered in older individuals (Yurkstas, 1949). Contacting surfaces areas are closely related to masticatory performance (Yurkstas, 1965) and the distribution of the wear facets between both dental arches could reflect specific individual chewing patterns (Bourdiol & Mioche, 2000). A positive side effect of this tooth wear on temporomandibular joint disorders has been suggested: the flattening of the cheek teeth could give more freedom to the joint and complaints tend to decrease with increasing age (Gelb & Gelb, 1989).

In primary ageing in the elderly, dental status is characterised by large inter-individual variability, especially in the number of remaining teeth (Hirano *et al.* 1999). Tooth loss is no longer considered to be a consequence of healthy ageing. Caries and periodontal diseases are the major reasons for tooth extraction. Caries is responsible for tooth loss during the first part of the life, but periodontal diseases are the primary cause after the age of 50 years (Hull *et al.* 1997; Chestnutt *et al.* 2000). Osteoporosis can influence oral bone and consequently the state of the dentition (Krall *et al.* 1996). Specific diets for osteoporosis prevention (high intake of Ca and vitamin D) have a beneficial effect on tooth retention (Krall *et al.* 2001). The average number of missing teeth increases gradually with age. A US survey showed that, in the age range 65–69 years, individuals have, on average, eighteen remaining teeth (Carlos & Wolfe, 1989). The average life span of the different groups of teeth shows a postero-anterior gradient, varying from 42 years for the cheek teeth (second molars) to nearly 60 years for the incisors (Nagao, 1992).

The ultimate stage of tooth loss is found in the edentulous population; 40 % of those aged 65–74 years and up to 64 % for those over 75 years (Mersel, 1989; Marcus *et al.* 1994). Of edentulous individuals, 92 % wear dental prostheses (Vargas *et al.* 2001) although 13 % of denture wearers wear them sporadically or never (Osterberg & Steen, 1982). Large differences in the prevalence of edentulism are observed, depending on socio-economic status, as the maintenance of natural teeth becomes increasingly more complex. Treatment can be costly, such as with osteo-integrated implants which contribute to objective oral function improvements (Fontijn-Tekamp *et al.* 2000). In addition to the eating problems described later (p. 49), tooth loss and untreated oral disease (caries and periodontal disease) are associated with the loss of self-esteem, and contribute to a decreasing quality of life in elderly populations. Fortunately, dental epidemiological studies in many countries show a rapid decrease in the incidence of complete tooth loss associated with the constant improvement in dental care and the significant decline in dental caries (Cahen *et al.* 1993).

Muscle activity

Jaw elevator muscles (identified as temporalis, masseter and medial pterygoid muscles), attaching the mandible to the cranium, are known to have a specific organisation (Gaspard *et al.* 1977; Herring & Wineski, 1986; Herring, 1993). The macroscopic anatomy of the masseter muscle suggests they are organised into functionally separate compartments. This would imply regional specialisation within the muscle (Blanksma *et al*. 1992). Different muscle units have a complex pattern of co-contraction depending on the bite force direction (Mao & Osborn, 1994). Due to their fibre type, they are also not as fatigable as other striated muscles (Junge & Clark, 1993). They are, with the exception of the lateral pterygoid, richly supplied with spindles. Jaw depressors (anterior digastric, geniohyoid, and myohiod muscles) link the mandible to the hyoid bone, and are sparsely innervated by spindles. In addition to these muscles, the peri-oral muscles (muscles of facial expression) are also actively involved in mastication, mostly in maintaining the food bolus between the dental arches during closing, so that food particles do not fall into the vestibule (Schieppati *et al*. 1989). Electromyogram signals from surface electrodes provide a good general indication of underlying muscle activity (Yemm, 1977); good correlations are found between surface-recorded electromyographic activity and isometric muscular forces (Hagberg, 1987). Electromyography is therefore often used to obtain biting and chewing measurements, as surface electrodes do not interfere with chewing function.

In senescence, voluntary muscles exhibit age-related changes leading to a decline in the bite force (Bakke et *al*. 1990), as well as macroscopic and microscopic alterations in the anatomy of masticatory muscles (Newton *et al*. 1987). The cross-sectional area and density of both masseter and pterygoid muscles show a significant reduction with increasing age; an impairment is found to be more severe for edentulous individuals (Newton *et al*. 1993). These changes are consistent with a general age-related change of muscle tissue in the body as a whole. However, age changes in oral motor performance are not as marked as in other parts of the body and when age effects are studied using a simple masseteric reflex test, the reflex appears to be maintained until very old age (Kossioni & Karkazis, 1998). Although data on the contractile properties of human motor units are sparse, it is assumed that contractile speed declines with ageing along with a concomitant reduction in the number of motor units (Chan *et al*. 2001). Animal studies have shown that age changes the morphology of the neuromuscular junction in the rat masseter, including a reduction in the terminal nerve area, longitudinal extent, length and fibre diameter. However, these changes do not modify the feeding behaviour of older rats (Elkerdany & Fahim, 1993).

The tongue

The tongue is important during respiration, mastication, swallowing and speech. The muscles of the tongue are striated, and conventionally divided into internal and external lingual muscles. The arrangement of the intrinsic muscles is anatomically unique. These interlace at right angles in three planes, thereby contributing to the very great range of movements the tongue can execute in all directions. The tongue has a rich blood supply, mainly provided by the lingual branch of the external carotid artery.

Little information is available on the effect of age on tongue function. When evaluated using several simple clinical tests, age impairment appears significant in men but not in women (Baum & Bodner, 1983). Speech production is a motor activity in which the tongue plays an important role; it is not affected by physiological ageing to any appreciable extent, suggesting the maintenance of tongue motility with age. However, only a serious impairment would alter speech (Sonies *et al*. 1984). The blood supply to the tongue appears to remain constant, irrespective of age (Price & Darvell, 1981). Tongue strength decreases with age in dentate subjects (Koshino *et al*. 1997). However, the enforced use of the tongue in paramasticatory function in the edentulous elderly wearing dentures leads to an increase in tongue strength, to even greater than in young dentate subjects (Price & Darvell, 1981).

Oral sensitivity

Sensory inputs from the oral cavity arise from the oral mucosa, periodontal receptors, muscle spindles and temporo-mandibular joint receptors (De Laat, 1987). The outputs of these receptors control the bite force, mandibular trajectory, soft tissue behaviour and the initiation of swallowing. Oral sensitivity has been extensively investigated by psychophysical methods (Crum & Loiselle, 1972). The most sensitive receptors are in the front of the mouth. The edibility of any material contacting the front teeth is immediately analysed in two ways: if edible, the sample is transferred to the post-canine teeth, accurately positioned onto the occlusal surfaces and processed or, if assessed as inedible, it is spat out. Among the mechanoreceptors participating in chewing control, the periodontal receptors are primarily free nerve endings tangled in the periodontal ligament that maintains the tooth in the alveolar bone. Each tooth root is surrounded by many such receptors which encode the direction and velocity of a force applied to the tooth crown. These receptors play a key role in bite force regulation (Türker *et al*. 1994) and represent a very sensitive load detection system (Trulsson & Johansson, 1994; Mioche & Peyron, 1995) and are involved in many tactile functions (Jacobs & Van Steenberghe, 1994). In contrast, very little is known about the role of the temporo-mandibular joint receptors during chewing; some control the direction of displacements and others its velocity (Osborn, 1985).

Tactile thresholds are significantly higher in elderly than in young subjects, irrespective of disease or medication (Thornbury & Mistretta, 1981). A steady increase in tactile threshold of about 1 % per annum between 20 and 80 years has been reported (Stevens, 1995). An age effect is also found in in-mouth shape recognition (stereognosis); the elderly require 80 % more time and make more errors than young subjects (Landt & Fransson, 1975). Tooth extraction damages the surrounding periodontal ligament, destroying the periodontal receptors. Therefore, the consequences of edentulousness on oral proprioception are severe. In denture wearers, high oral perception, assessed by stereognosis, was first thought to contribute to poor denture adaptation (Berry & Mahood, 1966) but this has not been confirmed elsewhere (Muller *et al*. 1995). In contrast, during chewing, dentures can increase sensitivity to stickiness and particles such as tomato pips and nut fragments which slip beneath the denture.

Salivary secretions

Saliva is important for mastication, taste, deglutition, digestion, the maintenance of oral hard and soft tissues, the control of oral microbial populations, and voice and speech articulation. In healthy individuals, the daily secretion of saliva normally ranges from 0·5 to 1·5 litres. Saliva is composed of more than 99 % water and less than 1 % solids, mostly proteins and salts. It is secreted from the three paired major salivary glands: the parotid, submandibular and sublingual glands (together accounting for about 90 % of the fluid production), as well as from the minor salivary glands in the oral mucosa (10 % of saliva production). Saliva from the different glands differs in composition (Schenkels *et al*. 1995). The serous parotid glands produce a thin, watery, amylase-rich fluid which accounts for up to one half of the mouth volume of saliva during chewing. Resting saliva secretion is produced predominantly by the submandibular glands which have both serous and mucous acinar cell types. The sublingual glands, which contribute 1–2 % of the unstimulated volume of whole saliva, mainly consist of mucous acinar cells. Both submandibular and sub-lingual saliva are more viscous and mucin-rich than parotid saliva (Pedersen *et al*. 2002). The minor glands, distributed throughout the oral mucosa, play an important role in the lubrication of the epithelial surfaces in the mouth.

Various stimuli affect salivary secretion. Stimulation can be extra-oral, such as expectations or visual cues (Epstein *et al*. 1996) or odours (Christensen & Navazesh, 1984), although there is no olfactory–salivary reflex in man (Lee & Linden, 1992). The rate of flow is also modulated by intra-oral stimulation such as taste or mastication; flow rates are higher with hard and/or dry foods and with large boli (Pangborn & Lundgren, 1977). During mastication, parotid saliva is secreted preferentially on the chewing side, directly onto the bolus being chewed, with a 10-fold increase from resting flow. This ipsilateral increase in output starts within less than 1 s and is effected mainly by periodontal receptors (Hector & Linden, 1987). The most obvious action of saliva is to provide lubrication during chewing. Further, saliva is essential in the formation of the food bolus. Fragmented food particles are progressively bound into a matrix of released food fluids and dissolved components of the food (Prinz & Lucas, 1997).

Saliva and sensory perception. Saliva is involved in the perception of the taste, flavour and texture of foods. The taste system may be thought of as fulfilling two separate roles in feeding behaviour. On one hand, it allows the identification of essential nutrients such as minerals (salts), carbohydrates, proteins (amino acids) and fats. The other, equally important, role is to identify harmful and potentially toxic compounds (bitter and sour) before they are ingested (Gilbertson, 1998).

To be perceived, taste compounds have to be first dissolved in saliva, and carried to the site of interaction. The taste receptor cells are found in the tongue and also on the soft palate, and in different parts of the oral mucosae. In addition to the primary salivary glands, minor lingual serous salivary glands (von Ebner glands) are located close to the tongue taste buds (foliate and circumvallate papillae). Saliva secreted by these glands provides the immediate environment of the taste buds, and recent evidence suggests it could modulate taste perception (Spielman *et al*. 1993; Gilbertson, 1998). In addition, saliva may act as a buffer, affecting the extent to which we perceive sourness (Christensen *et al*. 1987). After a reduction of salivary flow rates, lower sourness recognition thresholds are observed (Norris *et al*. 1984). Saliva flow rate is also believed to affect the assessment of some food-texture and mouthfeel attributes. For example, the action of the enzyme α-amylase present in saliva, which initiates the digestion of starch, could decrease the perceived thickness of the food (Guinard *et al*. 1997).

Saliva and physiological ageing. There is abundant literature describing age-related alterations in salivary function. Secretion appears to be stable with age, particularly parotid salivary flow stimulated during artificial bolus chewing (Canalda, 1990; Osterberg *et al*. 1992; Wu *et al*. 1993) or food chewing (Bourdiol *et al*. 2004). Results are less clear concerning the sub-mandibular, sub-lingual saliva secretions, which decrease with age (Yeh *et al*. 1998). In edentulous patients, who have no periodontal receptors, a masticatory–parotid salivary reflex is observed. In this case, the afferent nerve endings in the mucosa under dentures could take over the sensory role to maintain reflex control (Scott *et al*. 1999).

In addition to these objective observations on salivary flow, complaints of dry mouth are reported by up to 25 % of the institutionalised elderly, and self-assessment of dry mouth is more often than not correlated with salivary flow (Osterberg *et al*. 1992).

Detection and recognition thresholds increase with age for all tastants (Schiffman, 1993). The elderly complain about taste disturbance, reporting either a diminution of taste or the presence of an unpleasant taste sensation. At the peripheral level, old age seems also to be associated with a reduction in the number of circumvallate (and, to a lesser extent, the foliate) papillae due to a slowing down of the turnover and renewal of taste buds. There is no evidence that taste impairment is related to dysfunction in saliva secretion.

Xerostomic patients. Xerostomia (dry mouth) requires specific attention; it is a very common side effect of medication, in particular antidepressants, antihypertensives, antipsychotics, which are all more commonly consumed by the elderly than by any other age group (Sreebny & Schwartz, 1986). Severe xerostomia is also encountered after radiotherapy of the neck or head region and in autoimmune diseases such as Sjögren's syndrome. Dry mouth is rarely associated with systematic dehydration and the increased consumption of water does not overcome the oral dryness.

A proper salivary flow is known to maintain oral health by preventing caries and tooth loss. There could be an interaction between xerostomia and tooth loss. Indeed, xerostomia is often associated with tooth loss, particularly with Sjögren's syndrome patients, but surprisingly tooth loss is observed several years before the first symptoms of xerostomia (Baudet-Pommel *et al*. 1994).

The lack of salivary flow from the major glands in xerostomic patients does not *a priori* preclude secretions from minor salivary glands, such as the von Ebner glands, associated with cirucumvallate and foliate papillae. Therefore, it is possible that a proportion of xerostomic patients have sufficient saliva secretion from von Ebner's glands, and thus, relatively unimpaired taste perception. However, complaints about taste and chewing impairments are common in these patients. Irrespective of these aspects, dry mouth creates further impairment for denture wearers as it decreases the ability to wear dentures.

Deglutition

Swallowing (the movement of a bolus from the oropharynx to the oesophagus) involves the coordination of more than twenty-five muscles. The pharyngeal stage of swallowing is a complex, sequential series of rapid events (Hiiemae & Palmer, 1999).

The impairment of swallowing is common in the elderly and causes significant morbidity and mortality (Palmer & DuChane, 1994). In contrast to speech, part of the swallowing mechanism appears to have a limited capability to compensate successfully for age-related changes in muscular tissue and sensory functions. Older subjects often make multiple movements of the tongue and hyoid bone before swallowing (Sonies *et al*. 1989). Temporal changes in swallowing are observed with age (Robbins *et al*. 1992); recent ultrasonic investigations showed that the elderly spent less time in pre-swallow bolus manipulation, although a lengthening of the post-ingestive phase was observed (Chi-Fishman & Sonies, 2002).

The incidence of swallowing disorders may reach 30 to 40 % in the institutionalised elderly (Siebens *et al*. 1986). However, according to Sonies (1992), oropharyngeal dysphagia in the elderly is the specific result of a pathological condition or illness that may occur more commonly with age. A decrease in salivary flow rate among the elderly does not modify swallow duration (Sonies *et al*. 1989) but it does increase the number of complaints about swallowing difficulties (Logemann *et al*. 2001).

Eating function

Chewing pattern and texture

The concept of texture is confusing, since texture is a sensory property that refers to food structure (Hutchings & Lillford, 1988). According to the classical definition of Szczesniak (1963), texture is the sensory manifestation of the structure and the manner in which this structure reacts to the applied forces; the specific senses involved being sight, kinesthesia and hearing. The importance of texture in the overall acceptability of food varies widely, depending upon the type of food. More complete and up-to-date information related to food texture can be found in Bourne (2002).

Food structure is known to influence various aspects of the chewing process from the characteristics of a single chew to the temporal organisation of the chewing sequence. The load applied onto the food during the closing phase of a chewing cycle is closely related to food hardness (Fig. 1) (Horio & Kawamura, 1989; Mathevon *et al*. 1995; Hiiemae *et al*. 1996; Agrawal *et al*. 1998; Mioche *et al*. 1999; Mathonière *et al*. 2000; Peyron *et al*. 2002). Muscular activity developed to overcome food resistance is modulated within a single bite in approximately 20 ms after tooth-food-tooth contact (Van Der Bilt *et al*. 1995). In consequence, during chewing, muscle activity is found to respond to food texture as early as the first chew (Mioche *et al*. 2003). Several kinetic parameters of a chewing cycle also depend on the food properties such as its shape (Gibbs *et al*. 1981), vertical dimension (Diaz-tay *et al*. 1991; Peyron *et al*. 1997) and jaw closing angle (Agrawal *et al*. 2000). These variations in the general shape of the chewing cycle are believed to reflect some aspects of the intra-oral events of tongue activity which enable, with cohesive food such as meat, the placement of new food surfaces onto dental arches from one cycle to another (Fig. 2) (Mioche *et al*. 2002*c*). This pattern also relates to the so-called selection function defined for brittle food (Lucas & Luke, 1983; Prinz & Lucas, 1995).

Besides these variations within a single chew, the overall chewing sequence is also affected by the food's structure. The masticatory sequence is defined as all jaw movements from the introduction of food into the mouth until swallowing. Both the duration of the chewing sequence and the number of chews increase with food hardness and bolus size. They represent the simplest indicators of the difficulty in processing a specific food. In contrast, the chewing rate, presumably under automatic control, does not appear to be affected by texture (Kohyama *et al*. 2002), age (Karlsson & Carlsson, 1990; Kohyama *et al*. 2002) or dental status (Nakamura e*t al*. 1988; Slagter e*t al*. 1993). The amount of saliva released also varies with food properties. It increases with dry or crispy foods (Kapur & Collister, 1970; Pangborn & Lundgren, 1977) and food hardness (Bourdiol

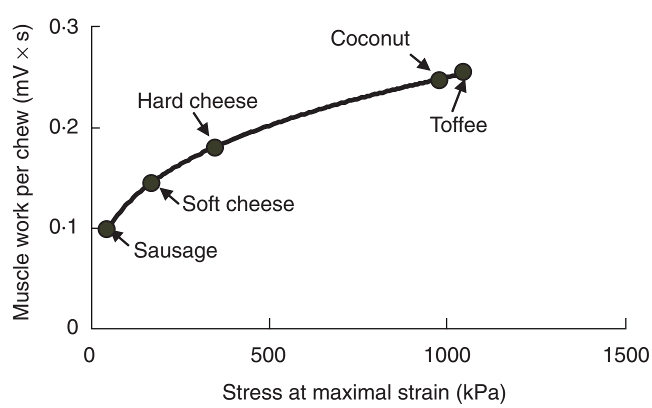

Fig. 1. Relationship between mean muscle work per chew recorded by electromyelography during chewing and the stress at maximal strain measured by compression test in an Instron machine from five different products ($y = 0{\cdot}0298x^{0{\cdot}3077}$; R^2 0·999). Values are means from thirty-six subjects. (From Mioche *et al*. 1999.)

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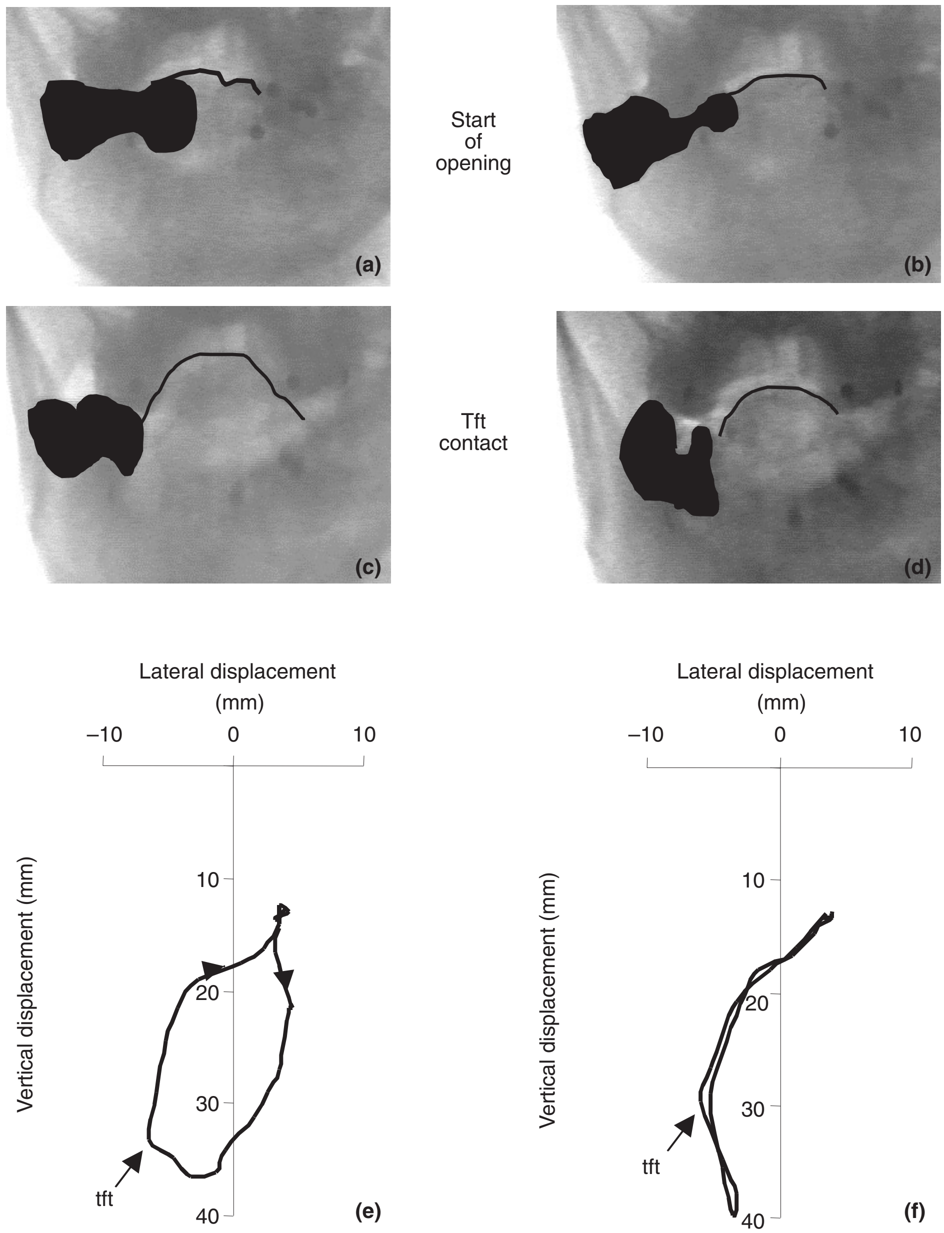

Fig. 2. Examples of tongue pushing (cycle 1; (a), (c) and (e)) and cheek pushing (cycle 3; (b), (d) and (f)) obtained by videofluorography in frontal view, from a sequence in which the subject was chewing meat. The upper images, (a) and (b), show the position and shape of the meat at the start of jaw opening; the lower, (c) and (d), its position at the next tooth-food-tooth (tft) contact. The lower plots, (e) and (f), show the movement path of the lower right canine marker in those cycles. They are very different. The 'open' loop for tongue pushing can be interpreted as facilitating free tongue movement, whereas the 'closed' but lateral loop for cheek pushing suggests jaw movement linked with and facilitating cheek activity on the active side. (From Mioche *et al.* 2002*c*.)

et al. 2004) but this effect is thought to be related to the bite force (Hector & Linden, 1987). Finally, swallows and clearance duration are overall parameters which could also be modulated by food properties.

The adaptation of mastication to the food structure appears to be protective, since high forces could damage the teeth or the joint; it could also optimise the rate at which mammals break down their food. The capacity to process various types of food is believed to play a major role in evolution (Rybczynski & Reisz, 2001; Lucas *et al*. 2002). In man, the pleasure from the sensory qualities of food (taste, smell and texture) elicited during chewing is one of the major determinants which drives us to eat. Most of these perceptions depend on the degradation process during chewing and swallowing. Jaw muscle activity is highly correlated with perceived hardness, suggesting that such motor activity could be a sensory cue for hardness perception (Mathevon *et al*. 1995; Mathonière *et al*. 2000). It is, however, noteworthy that chewing behaviour displays large variability between subjects although, for a given individual, it is relatively consistent in terms of unilateral *v.* bilateral chewing, preferred chewing side or tongue activity. Differences between individuals in terms of food acceptability could originate, to some extent, from variability in their chewing behaviour and/or intra-oral food manipulation (de Wijk *et al*. 2003). Motor strategies developed to chew a food are believed to modulate the range of perception. An illustration is found in wine tasters, who develop particular in-mouth manipulation to elicit specific perceptions. Shama & Sherman (1973) found that, when evaluating the viscosity of a product, subjects manage to analyse the shear rate whilst applying an approximately constant shear stress between tongue and palate with liquid foods, whereas for more viscous foods the sensory clue is given by the shear stress developed at an approximately constant shear rate. Psychophysical studies conducted on solid models suggest that the sensory clues responsible for hardness perception can be either the amplitude of the deformation (compliance) for soft material or can shift towards the bite forces to obtain a given deformation with harder products (Mioche & Peyron, 1995). Finally, human chewing behaviour can be better seen as an individualised balance between optimisation of the chewing efficiency and perception that each of us wants to have elicited, consciously or not, during chewing.

Effects of age on chewing behaviour

For the healthy elderly, various alterations of the chewing pattern have been found in both individual chews and in the overall organisation of the chewing sequence. Jaw muscle activity is significantly depressed by age. This affects foods such as dry bread or meat that are hard to chew (Kohyama *et al*. 2002; Mioche *et al*. 2002*b*) but not foods that are easy to chew, such as gelatine gels (Hatae *et al*. 2001). Bite forces appear to be more slowly and loosely adapted to food texture in the elderly than in younger individuals (Mioche *et al*. 2002*a*). A reduction of vertical mandibular displacement and velocity has been observed in elderly individuals, probably associated with muscular impairment (Karlsson & Carlsson, 1990). The conjunction of lower shear and compression bite forces associated with a slower tooth penetration into the food sample could reduce the tooth-food-tooth forces and consequently food breakdown. Whatever the type of food, a lengthening of the chewing sequence has been observed (Feldman *et al*. 1984; Kohyama *et al*. 2002); this can be seen as an adaptive behaviour developed to overcome a small but consistent muscular weakness. However, from routine observations, it appears that lengthening in chewing duration occurs to a point where the mastication duration stays compatible with an average or 'social' time course for meal consumption. Despite this lengthening, meat boli, gathered just before swallowing, are slightly but significantly less comminuted in elderly than in young subjects with comparable dental status (Mioche *et al*. 2002*b*).

Chewing efficiency defines the ability to prepare a swallowable bolus from a piece of food. Sieving methods are classically used to quantify the level of comminution of a brittle material after a certain number of chewing strokes. Chewing efficiency is dramatically affected by the number of teeth (Feldman *et al*. 1980; Heath, 1982) although this is not the only factor. In denture wearers, masticatory efficiency is about one-sixth of that achieved by young adults with natural dentition, and chewing duration is twice as long (Heath, 1982). An interesting model, developed by Hatch *et al*. (2001), summarises this point. Various parameters believed to participate in chewing efficiency (age, sex, functional unit, maximal bite force, etc) are pooled to build a multivariate model of masticatory performance. This shows a non-significant direct impact of age on masticatory performance. A rheological model of the chewing process, based on such observations, would be interesting to develop to understand what the elderly actually swallow. The consequences of ageing on the chewing process are summarised in a flow chart (Fig. 3).

The prevalence of reported impairment of chewing ability increases from 2 % in young adults (16–34 years old) to 44 % in individuals aged over 85 years (Osterberg *et al*. 1996). It is associated with a general physical decay (Hirano *et al*. 1999) and/or related to a reduction of daily physical activity (Osterberg *et al*. 1996; Miura *et al*. 1997). Self-assessment surveys suggest that a significant impairment of masticatory ability occurs when fewer than twenty well-distributed teeth are present (Agerberg & Carlsson, 1981; Steele *et al*. 1997; Budtz-Jorgensen *et al*. 2000). However, such self-assessments are poorly correlated with objective indicators of chewing efficiency (Agerberg & Carlsson, 1981; N'gom & Woda, 2002). For example, 75–80 % of edentulous individuals up to the age of 74 years did not report any impairment of masticatory ability (Osterberg *et al*. 1996).

There is little information on the consequences of age on the perception of food texture. Chewing behaviour appears to be adapted to moderate alterations of oral physiology in dentate healthy elderly individuals and consequently no clear age effect on texture perception is observed. Sensory assessment of texture conducted using two sets of products (cookies and meats) fails to show any specific age impairment on texture perception (Mioche *et al*. 2002*a*). However, it has been shown that for elderly subjects retronasal flavour perception can be more impaired by age than orthonasal odour perception (Duffy *et al*. 1999). This could suggest a change in intra-oral food manipulation and/or transformation.

When age is associated with dental decay, chewing behaviour cannot compensate for oral physiological impairment, so severe consequences for texture perception are to be expected. From texture assessments obtained using a large range of meat products, we found that denture wearers chewed tough but juicy meat more easily rather than more tender but drier meat, as did dentate subjects, and their tenderness assessment was accordingly modified (Veyrune & Mioche, 2000). It was hypothesised that for denture wearers, juiciness may be more important than tenderness for meat acceptability.

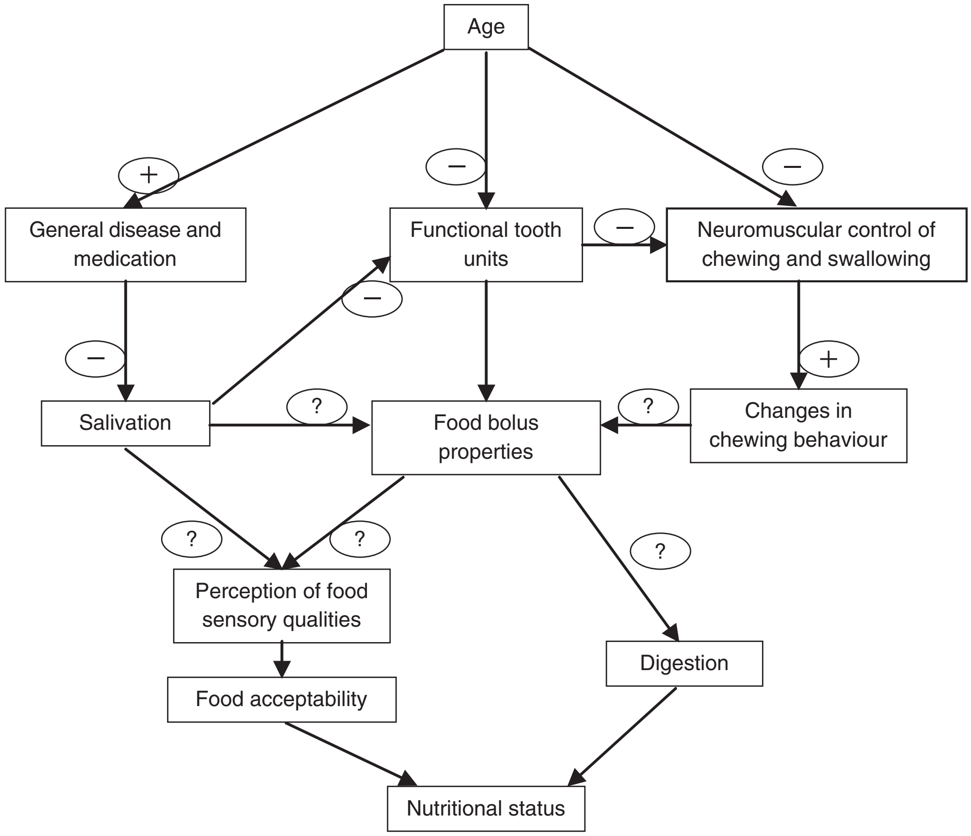

Fig. 3. Flow chart summarising the main ageing changes induced by age in the eating process. (+), Positive tendency of the relationship; (–), negative tendency of the relationship; (?), partially known or unknown consequences.

Among the healthy elderly population, the age effect is found to be more severe for odour perception than for taste perception (Schiffman, 1997). By contrast, texture perception appears to be relatively stable with age. It can therefore be hypothesised that texture plays a more important role among the food sensory properties (texture, odour, taste) that contribute to food enjoyment in healthy elderly, even if, as for taste, no clear relationship can be established between an increasing threshold of perception and the ability to enjoy food (Schiffman, 1993).

The respective weight of each sensory attribute in food acceptability is deeply affected by dental status. During ageing, changes in odour or taste perception are not clearly identified as a cause of food rejection, unlike texture; 30 % of elderly subjects report avoiding food they find difficult to chew. Foods are considered to be difficult to eat when they need a long chewing time, and/or they are tough, crunchy, hard, brittle, dry, rough or sharp; such foods include meat, vegetables, and breads. But, as for flavour, there is no clear relationship between ease of chewing and preference. Young adults like more challenging textures than do the elderly; however the easiest to chew textures such as purée are not liked by either age group (Roininen *et al*. 2003).

Relationship between mastication, digestion and nutrition

Very few studies have considered the impact of oral function on the subsequent processes of digestion. The pioneer work of Farell (1956) emphasised that the impact of chewing on digestion depended on food properties. He defined three categories of food depending upon undigested residues found after ingestion with or without prior chewing. The first group (fish, egg, rice, bread, cheese) is completely absorbed, whether chewed or not. A second group (various kinds of meat and vegetables) leaves a large residue without chewing and some residue after chewing. A third group (chicken and lamb) leaves no residue if chewed, but some residue when not chewed. Recently, chewing efficiency has been shown to have a significant effect on gastric emptying (Pera *et al*. 2002). Chewed foods are more easily cleared from the oesophagus (Pouderoux *et al*. 1999) and Marciani *et al*. (2000*a*,*b*) showed that the consistency of an ingested meal also modulated the emptying of the stomach. In addition to this direct relationship between mastication and digestion, poor chewing efficiency is related to various gastrointestinal disorders (Mercier & Poitras, 1992; Brodeur *et al*. 1993).

The decline in chewing efficiency associated with tooth loss is often considered a factor which contributes to inappropriate food choices by the elderly (Wayler *et al*. 1982; Chauncey *et al*. 1984; Garcia *et al*. 1989). However, if there is a net influence of dental status on food choice (Osterberg & Steen, 1982; Hutton *et al*. 2002), this trend is weaker when considering nutrient intake (Fontijn-Tekamp *et al*. 1996); a significant effect has only been described for vegetables (Osterberg *et al*. 2002; Chen & Huang, 2003). Haematological studies suggest that dental status does not significantly affect nutrient intake (Sheiham *et al*. 2001). Studies are currently in progress to elucidate the role of mastication on the kinetics of amino acid release after meat consumption in the elderly, which is of interest to limit the effect of muscle loss during ageing (Arnal *et al*. 2002).

Conclusion

Healthy ageing induces only moderate changes in oral physiology. Changes in neuromuscular activity such as decreased bite force may be partly compensated by changes in chewing behaviour such as lengthening of the duration of chewing. Texture perception is maintained relatively consistently with ageing, but modification of the chewing sequence leads to some changes in the properties of the food bolus.

By contrast, substantial alterations in both chewing behaviour and food bolus properties are observed when ageing is associated with compromised dentition, impaired health and medication. The consequences of these effects on the later stages of digestion remain to be determined. Surprising discrepancies are noticed between objective measurements of oral performance and the corresponding self-perception, as for example, between salivary flow and oral dryness perception or between chewing performance index and satisfaction with chewing.

The consequences of healthy ageing on food acceptability are complex. Although some foods are recognised as hard to chew, there is no clear shift in preference towards foods that are easy to chew. Sensory-specific satiety is a decrease in the desire to eat a specific food during the time course of its consumption; its decline with age has been clearly demonstrated (Rolls & McDermott, 1991). Therefore, older individuals tend to eat a more monotonous diet, which is a possible cause of an unbalanced or inadequate diet. Modifications in the chemosensory system have been proposed to explain such changes, but a more general decline in appetite may also be important. As texture perception appears to be better preserved during healthy ageing than odour and taste perception, it is assumed that the importance of texture in the overall acceptability of food increases. Chemosensory losses in the elderly could be compensated in part by adding pleasant texture sensations such as crunchiness or chewiness.

Finally, eating behaviour is obviously far more complex than chewing behaviour, and changes or complaints due to age cannot be explained by limiting the observations to oral physiology. Food choices and food consumption are also driven by memory, psychology and economic factors. Advances in the understanding of food choice in the elderly need a sustained collaborative research effort between sensory physiologists, nutritionists, and food scientists.

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