A REVIEW : NEURAL CONTROL OF MASTICATION IN HUMANS AS INFLUENCED BY FOOD TEXTURE.

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ABSTRACT: This review summerizes recent approaches to the physiology of the masticatory system in humans that aim to understand how the process is influenced by the material propoerties of foods. the centerpiece is a group of experiments that show that the rate of breakdown of food in human mastification depends principally on the combination of two mechanical properties of foods: toughness(R) and modulus of elasticity (E). Two mechanical indices are constructed from these properties: the square root of their product, $(ER)^{0.5}$, is predicted to explain the rsistance to an incisal bite, while the square root of their ratio, $(R/E)^{0.5}$ is predicted to control the rate of fragmentation during a postcanie bite. Evidence for the latter is reviewed, which also appears to modulate the activity of jaw closing muscles and the extent of lateral mandibular movement during mastication. These studies provide a quantified link between the food stimulus and the physiological response of the mastiatory system for which we know of no parellel. Attempts to extend this analysis have been made by psychophysical investigations of food texture. These support some sensitivity to the mechanical index that we have identified, but are not conclusive. Finally, we provide a chart summarizing physiological responses to food texture that could interest dentists, food scientists and also those interested in the analysis of dentition and diet in mammals.

INTRODUCTION

Chewing (mastication) and swallowing (deglution) of food are vital, but still under investigated, process, particularly in regard to the physical interfacr between teeth and food that is the essence of the process. Chewing is vital for the safe swallowing of solid foods, but when compared to other major motor activites of the body such as locomotion, it is much more variable. This variability probably reflects the complexity of the process, involving coordination of the muscles of the cheeks, tongue, lips and jaws. However, numerous oral and circum-oral receptors relay large quantities of sensory information to the brain. so, rather than regard the body's masticatory motor control as flawed, the variability more likely indicates that management of the intra-oral transport and fracture of an everincreasing number of food particles produced during chewing is a much more difficult tast than walking or running (even when over tough ground). However, there is also another dimension to mastication. In addition to particle breakdown, particle fragments also ususally aggregate towards the end of the chewing process into a cohesive bolus. This aspect is largely due to viscous forces[1] and futher complicates the process.

Here, we review the physics and mechanics of the mouth, concentrating on the definition of the mechanical resistamce of food particles to breaking down in the mouth. the review is centred o work[2] performed at the University of Hong Kong that aims to 'crack' the basic physics involved. However, we attempt to set this work in dental[3], food science[4,5] and industrial contexts[6]. The time seems ripe for this review because there is

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currently considerable interest, both academic and lay, in this subject[7].

GENERAL BACKGROUND

The mastication of many foods is a communication process involving the fracture (cracking) and fragmentation (physical separation of parts) of food particles. Any such process can be subdivided analytically into two functions, termed the selection and breakage (or disribution) functions by researchers working on communication processess in industry[8]. The selection function is defined in terms of the chance that a solid food particle has of being fragmented by the teeth during a chew. The breakage function is the distribution of fragments arising from the breakdown of selected particles. To plot the distribution, the sizes of fragments have to be normalized to the size of the parent particle from which they broke away. If accurate values for these functions can be obtained, then the overall rate of particle size reduction can be predicted from differential equations. Unfortunately, for nearly forty years, no one could solve these equations[9]. so powder scientists in the mineral ore, coal and pharmaceutical industries calculated the overall rate of particle size breakdown in their machines with the aid of number-crunching computer programs (e.g. ref. 10 for an early study).

However, things started to change when the use of these functions began to tricle into oral biology in the 1980's[11,12]. It was quickly established that, for a given food, the selection function appears to depend approximately on the sqare of particle size[11,12]. Thus, large particles are much more likely to be broken than small ones. The brakage function is more difficult to measure but also seems to take a simple from[11,12]. This use of communication analysis attracted fresh attention from theorists and an analytical solution for the commonest behaviour of these functions during communication was eventually provided by F.A. Baragar. This was subsequently verified by a group group based at Utrecht in the Netherlands9 (see also ref. 13). The power of this analysis has not yet been tapped in oral biology because knowledge of it is not widespread and because these functions have yet to be related to the more tangible anatomy and physiology that dentists deal with.

To attempt to add real substance to this analysis and to show how close we now are to writing out mathematical models of the chewing and swallowing process, we focussed in Hong Kong on an explanation of the breakage function in terms of the material properties of foods. To establish the basic physics of this process, it is necessary to look at 'model' foods. Most other publications also report tests on relatively homogenous foods because it was established very early that marked structural heterogeneity, resulting in machanical anisotropy, would make measurement and analysis very difficult[14]. Elastomeric impression materials have also been used instead of foods[15].

Within these limitations, it is possible to define the basic mechanical properties of solid foods that will resist the formation of new surface when they fracture. Arguing from the basics, the mechanical index that governs the elastic (reversible) behaviour of a model food particle at small deformations is its force: displacement gradient. In many foods, small forces produce proportional displacements. Then, the conversion of forces to stresses (by dividing by the area that the force acts over), and that of displacments to strains (by dividing by the linear dimension of the particle that lies in the direction of the force), produces a particle size independent gradient that defines a material property called Young's modulus (E). In many food materials, despite sometimes very marked time dependent behaviour, Young's moduli characaterize deformation almost until fracture.

In contrast to a purely deformational response, where all the energy provided to the food by loading it results in distoration, the process of fracure involves atleast some of the energy entering the food particle to be channelled directly into growth of a crack. The growth of unit area of any such crack is controlled by a property called toughness (which we denote by the symbol R), defined as the energy per unit area of crack required for this growth. Using simple standard mechanical tests differ from mastication in that they purposefully rate is kept constant), their results should apply to food behaviour in the mouth as long as there is no dissoluion in the saliva or melting.

when teeth contact a food particle in the mouth, a force builds up which compresses that particle. At small displacements, the reponse of the particle is largely elastic - i.e. if the particle were removed at this point, it would regain its original shape. However, further movement of the teeth will do permanent damage to the particle by making permanent indentations with the cusps or by cracking it. The actual loadings are complex and will vary accoring to the state of the dentition and to the size and orientation of the food particle.. This does not mean, however, that an analysis is impossible. Some mechanical analysis can be performed without specifying the precise loading geometry[16,17] and, provided that the conditions conditions of loading can be described in general terms, they are capable or predicting the grouping of food properties that are responsible for resisting fracture.

To derive an appropriate food mechanical index, assumptions need tobe made first about the factors that limit the ability to fracture a food particle by, say, an incisal bite or a postcanine chew. In terms of the mechanics, there are two major limits: the displacement or the load. Loads obviously sets limits to stresses, while displacements may not be sufficient to achive the necesary strains. Of these two possiblities, a bite at the front of the mouth by the incisiors is more likely to be limited by stress than by displacement: the food can be pulled (placed in tension) between the teeth and a hand or hands and bent or twisted, all in addition to fractures that might be generated entirely between the incisors. Tension, torison and bending all offer large displacements, only limited by the stresses that can be generated. In contrast, loading of a food particle by the postcanine teeth takes place only in the later part of the jaw-closing phase of a chewing cycle, when there is only a small displacement available before tooth-tooth contact. This is typical of compressive loadings and is very likely to limit the fragmentation of that particle within a chew. Stresses could also be limiting but, for most modern foods, bite forces are very low, and it is much more likely that there is a displacement, than a stress, limitation in mastication. It follows directly from these arguments[18] that, if the displacment is limiting, then the food mechanical index that applies is the square root of(toughness/ Young's modulus) or $(R/E)^{0.5}$. If, instead, stress is limiting, then another food property group, the suare root of (Young's modulus multiplied by toughness), or $(ER)^{0.5}$, applies.

To test these predictions, the modulus and toughness of each food was measured using mechanical testers[19]. Foods can be tested in small and portable machines[20] just so long as these are sufficiently rigid and have discplacement control. In vivo fragmentation tests involve one single bite with the postcanine teeth, conducted as naturally as possible, on a variety of foods with a range of mechanical properties. Unfortunately, there are not enough foods available that are impervious to the actions of saliva without some protective coating intervening between tooth and food. A solution, suggested by Mowlana and Health[21], was to insert food particles inside finger cots and seal cots prior to bites. Subjects made one bite, which they repeated on different samples. The cots were then opened and the fragmentation examined. The change of surface area produced by fracture was recorded by image analysis in a similar manner to van der Bilt et al.[22]. The form of representation of the change in surface area resulting from mechanical fragmentation comes from Bond[23], who worked on the comminution of mineral ores in industry. He showed from an enormous dataset that the change in the reciprocal of the sqare root of typical particle sizes during breakdown was proportional to the energy expended during the process. If we assume similarity of particle shape during chewing, then change in the reciprocal of particle size is dimensionally equivalent to the square root of increase in surface area per unit volume of particles produced during fragmentation. The volume should remain constant of course. Results in powder science since Bond have tended to provide strong support for the use of his 'work index' (e.g. Rose and Sullivan[24]). Results for 38 foods show that change in the square root of food surface area per unit volume due to particle fragmentation is inversely proportional to the value of the displacement-limited food index, (R/E)0.5 described above[2,25]. However, this result still resides in the realm of mechanics. To find out if this food index influences the neuromuscular control of chewing, we needed to study the activity of jaw muscles and jaw movement during normal mastication. Such studies did not require that the food particle be examined after chewing, so finger cots were not neded. However, subselection of foods was still needed to eliminate foods that absorb saliva rapidly and so change their mechanical properties. This study presented other problems: two of the most important muscles, the medial and lateral pterygoid, are too deep to use surface electrodes and much of the temporalis is usually covered by hair. This limits the muscles available to the masseter and anterior temporalis. After a comparison of the surface electromyographic (EMG) response of the masseter and anterior part of the temporalis muscles, the activities of which were synchronized and correlated, the latter was chosen to represent a jaw closing musIce[18]. The level of activity in this muscle was highly correlated with the same food index, $(R/E)^{0.5}$, both when the rectified rms muslce activity was averged for all chews and when data were analyzed chew-by-chew[18]. We concluded that the central nervous system must have been receiving sensory feedback from receptors about the material properties of foods that modulate jaw closing muscle activity.

It is unfortunate that EMG recordings from the medial and lateral pterygoid muscles are difficult to record from because these muscles are solely responsible for lateral movement of the jaw. However, the coordinated activity of all jaw muscles can be studied by monitoring mandibular movements and so modulation of their activity can be judged indirectly. We used a Sirognathograph (Siemens AG, Bensheim, Germany), a three-dimensional magnetic sensing system, and also an ultrasonic system, the Cybermouse (IPC, Freemont, CA, USA; described by Prinz[26]). Details are given in Agarwal[2]. When viewed from in front, the angle that the jaw forms with the verticle component of late closing phase in a chew was highly correlated with displacement-limited food index, $(R/E)^{0.5}$ again[27]. This 'closing angle' seems an important measure of lateral jaw movement and the results show that, whereas verticle movements are much more sensitive to external properties of foods such as food particle size[28], the lateral movements of the mandible are highly influenced by internal mechanical properties.

SENSORY EVALUATION

Interest in the above could be taken beyond oral biology and into food science if it could be shown to have consumer relevance. The psychophysical measurement of food attributes has been given considerable attentionby food scientists for the past halt-century[29,30] and has also attracted recent sporadic interest in dentistry (e.g. Kashket et al.[31]). The perception of the physical properties of foods is called texture and can be sensed by both hand and mouth[32]. It can be investigated by many procedures, but the most common practice is to compare mechanical easurements obtained on universal testing machines with the verbal responses of 'taste panelists', who have often been trained in this work to heightentheir acuity. It is generally claimed that there are strong correlations between sensory attributes and mechanical parameters[2]. There is, however, no standardized methodology, although versions of the General Foods Sensory Texture Profiling Technique are still employed extensively[29,30,33].

Any approach reliant on language is going to be culture-dependent unless linguistic terms have one-to-one translations, a facat that, if true, would reflect some deep-seated (evolved) need in humans to communicate textural evaluations. Such culture-independence has, in fact, been claimed for other senses : e.g. the four basic colour categories, blue, yellow, green and red, which are thought to be universally recognized in human societies. However, such cross-cultural generalizations are extremely unlikely for textural assessment made in the mouth. While our colour vision is thought to have evolved relatively recently,providing an important signal for feeding in diurnal mammals[34], textural perceptions probably have most importance for nocturnal mammals to supplement their foraging, which is primarily by the sense of smell. It has been claimed that the secondary importance of both oral texture and smell in recent human evolution is reflected in a lack of vocabulary to describe responses[2] and that the large body of textural terms present in most languages are culture-dependent devices for the transmission of acquired manual-skills involving tool-making25. The need to train taste panels could be construed as an unwitting attempt to impose these texture terms on an oral context and where such training involves overt manual comparisons, the criticism seems to have obvious substance.

A common test is the comparison test[35,36], which can be of two types : a triangle test or a paired comparison. The objective of both is to determine which of two samples has more of a specific attribute, e.g. in a paired test, to ask jusdges to select the sweeter of two samples or, in a t riangle test, to select the odd one out of three foods offered. Agarwal[2] presented a random series of pairs of four cheeses to 18 untrained panellists, that were matched either for $(R/E)^{0.5}$ or $(ER)^{0.5}$. It is difficult to despense with language altogether, but where science is conducted in cosmopolitan societies, such as Hong Kong, a multi-linguil approach needs to be considered. This study necessitated written instructions in English and Chinese, but visual charts (Fig. 1A) showing intended actions during each test were also used. The data was analyzed by a ranking method and a Chi-square distribution analysis. Details of this analysis were given in Agrawal[2]. It was found that the ranking of the foods produced by judges was identical to that produced by machine testing (e.g. Fig. 1B showing the relationship between estimated ranking of rate of food breakdown and the machine values for the food index, $(R/E)^{0.5}$). Statistical analysis indicates that the overall openion of the judges did not arise by chance ($Z = 25.67$; $p<0.001$ from Chi-square distribution analysis).

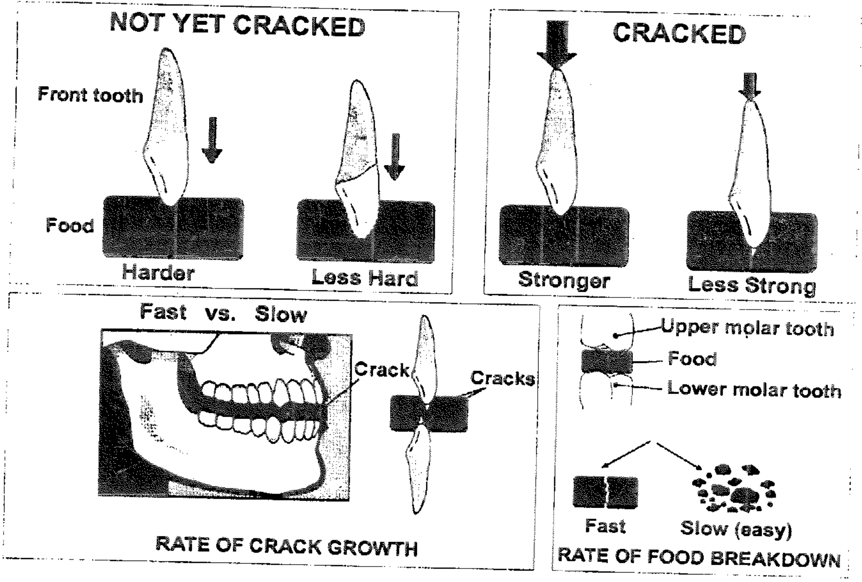
Agrawal[2] also conducted a 'category scaling exercise'[37] on ten subjects using 19 types of cheese. Each untrained panelist was given an evaluation from, in both English and Chinese, containing a scale on which an opinion could be given with a ruler and then converted to a percentage. An analysis was then performed by taking the average score obtained from 10 judges for each question. The pattern of correlations for two such properties, perceived resistance to incision and to the rate of breakdown in mastication, is shown in Fig. 1C. There was a significant relationship between the food index, (R/E)0.5, and the rate of food breakdown percieved by judjes ($r=-0.58$; $p<0.01$) and between resistance to incision and (ER)0.5 ($r=0.79$; $p<0.001$), but not vice versa. These relationships are graphed in Fig. 1D, where the trends are clear, but where there is nevertheless a lot of unexplained variation.

DISCUSSION

Investigation such as the above need to be set in the context of neural control. This is the only way in which fundamental knowledge can be judged - by the ability to predict the responses of subjects to different food inputs. Both chewing and swallowing are rhythmic activites, centrally controlled by pattern generators located in the brain stem[38,39]. Fig. 2 is an attempt to offer an understanding as to how signals from food properties could modulate the activity of the chewing generator. This generator does not start spontaneously, but has to be initiated by a signal. The signal from the cerebral cortex is referred to in Fig. 2 as the "initial command". Feeding must be triggered by internal neural influences such as nutritional state (hunger vs. satiety probably reside in the most appropriate response is probably aided by food texture memory. The location of this memory is unknown.

Fig. 1 Methodology for establishing food factors influencing the perception of the resistance of these foods to fracture and fragmentation. **A** shows several diagrams that have been shown to illustrate their actions and their opinions during trials. The first three deal with incision while the last covers the rate of breakdown during mastication. **B** illustrates the results of paired comparisons tests just for the rate of breakdown during mastication. The overall ranking by subjects, derived from every possible combination of pairs, matches that of (R/E)0.5 values from instrumental tests. **C** shows that the food property index influencing perceived resistance to incision (answers given to diagram at top left in A) is probably not that which is percieved to slow food breakdown (answers given to diagram at bottom right in A). The two relationships which have both theoretical (see text) and statistical support (in C) are graphed in **D**.

A



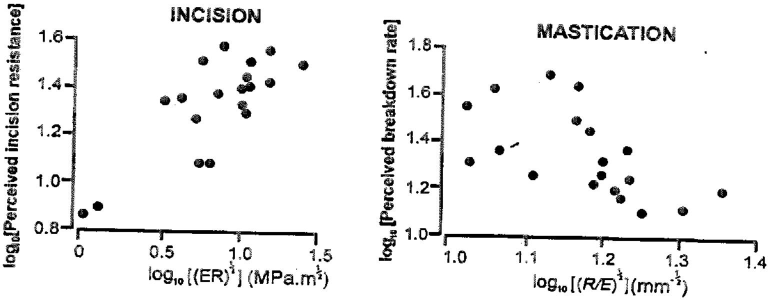
B

Cheese	$(R/E)^{\frac{1}{2}}$ (mm$^{-\frac{1}{2}}$)	Machine vs. Subject ranking	
Danish Feta	13.7	1	1
Jarlsberg	16.7	2	2
Raclette	20.5	3	3
Mozzarella	22.9	4	4

C

	Machine values	
	$\log_{10}[(ER)^{\frac{1}{2}}]$	$\log_{10}[(R/E)^{\frac{1}{2}}]$
Perceived incisal resistance	0.79 ($p < 0.01$)	0.19 ($p > 0.4$)
Perceived breakdown rate	0.38 ($p > 0.1$)	-0.58 ($p < 0.01$)

D



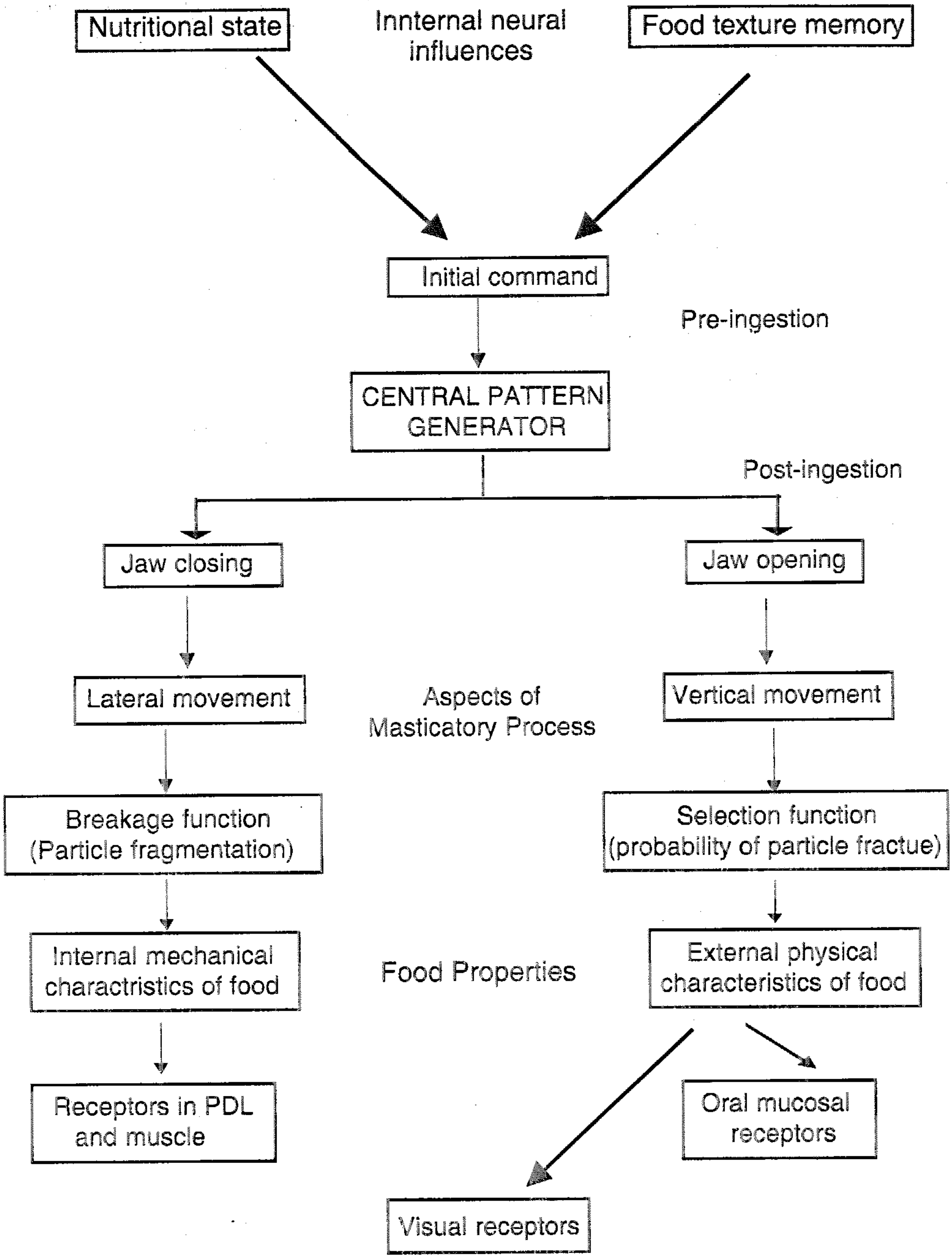


Fig.2 : A model of the influences that food properties may have on jaw activity (see text). The model itself is shown by the solid lines, which indicate logical connections in the model in the manner of a flow chart. Dotted lines indicate connections inside the brain while dashed lines indicate peripheral feedback.

Peripheral signals from the mouth and gut probably relay in the limbic system first of all. This includes the most primitive part of the cortex, that which evolved in early nocturnal mammals, the descendents of which forage using the senses of smell, taste and food texture. The neocortex of higher, diurnal, primates houses an important cisual centre in the occipital lobe and one for hearing in the temporal lobe. These primates, monkeys and apes, live in groups that mostly on the basis of vision (particularly colour vision), but also depend heavily on communication inside their own social group to find food. It seems curious that the senses that are critical for feeding by nocturnal mammals, and those which are important for diurnal mammals are not well associated in human brains. An example comes from smell, which even though it remains a sharp sense in higher primates, has few if any proper 'smell names' in any language. Odours may be distinctive and recognized immediately but can only be communicated verbally by alluding to the names of objects that produce them. Thus, for example, a prominent odour scientist describes a large range of plant smells as "white floral" or "rosy floral", "violet-like floral" or "spiciy floral", none of which could mean anything to anyone without considerable prior experience or training[39]. These difficulties in smell research appear to be paralleled by problems in food texture, the oral evaluation of which also requires training to lift up the shield of 'texture blindness'. Texture work has an advantage in that hand-based terminology can be introduced as an anology, But we nevertheless contend that textural evaluation in the mouth cannot be transmitted directly by language. The reason must be there has never been any need to do so before scientists became interested in it.

Various authors have subdivided food properties into two classes: those expressed at the food surface, such as food particle shape and size, surface roughness and stickiness (called external physical characteristics in Fig.2) versus those properties which are internal to food particles, which we dub internal mechanical properties. The latter include the food indices describes here. These two types of food properties probably have very different influences on the activity on the central pattern generator. As suggested in Fig. 2, we assoicated the general verticality of jaw opening with a need for an efficient gape that clears food particles, variably because of their individual particle sizes, because they stick the teeth together or because the clumping of food particles into an aggregate[28,40]. The influence of food particle size is seen in the value of the selection function, which is a product essentially of tongue and palate action. Neural feedblack is certainly via mucosal receptors, particularly in the highly sensitive areas of the anterior tongue and hard palate. At the base of the right-hand column, we show the importance of visual receptors that, pre-ingestion, can judge the external physical characteristics of foods and trigeer food texture memory.

In contrast in the left column, as shown by data summarized in this review, there seems a clear link between muscles that act in jaw closing and the degree of lateral movement that they produce with the sensing of internal mechanical properties. This must be conducted via receptors in the periodontal ligament and via muscle spindles.

We hope that such models can raise the level of research on chewing from purely empirical studies to something close to physical understanding.

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