An optimization model for mastication and swallowing in mammals

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SUMMARY

Mammalian mastication is a process combining simultaneous food comminution and lubrication. The initiation of swallowing, which is voluntary, has been thought to depend on separate thresholds for food particle size and for particle lubrication. Instead of this duality, we suggest that swallowing is initiated when it is sensed that a batch of food particles is binding together under viscous forces so as to form a bolus. Bolus formation ensures that when the food mass is swallowed, it will pass the pharyngeal region safely without risk of inhaling small particles into the lower respiratory tract. Crucial for bolus formation is food particle size reduction by mastication. This allows the tongue to pack particles together tightly by pressure against the hard palate. A major function of salivation is to fill the gradually reducing spaces between particles, so increasing viscous cohesion and promoting bolus formation. If swallowing is delayed, excessive saliva floods the bolus, separating particles and reducing cohesion. Swallowing then becomes more precarious. Our model suggests that there is an optimum moment for a mammal to swallow, defined in terms of a peak cohesive force between food particles. The model is tested on human mastication with two foods, brazil nut and raw carrot, which have very different particle size breakdown rates. The peak cohesive force is much greater with brazil nuts but both foods are predicted to be swallowed after similar numbers of chews despite the very different food particle size reductions achieved at that stage. The predicted number of chews to swallow is in broad agreement with published data.

1. INTRODUCTION

The most general explanation for why mammals break down, or masticate, food particles in their mouths is because their high metabolic rates demand this. Lower vertebrates, such as reptiles, can ingest and swallow large food particles because their slow rate of digestion of such particles (with small surface areas) is sufficient to meet their needs. Mammals, with higher metabolic rates, could solve their energy requirements by increasing the overall volume that is being digested at any one time. However, the inert bulk contained in a very long gastrointestinal tract would work against one of the major benefits of evolutionary change—an increased locomotor efficiency. A more logical alternative, one that most living mammals adopt, is simply to expose as much surface area of the food particles as possible by fragmenting them before initiating digestion. This increases the rate at which enzymes act, thus providing energy at a higher rate.

In order to achieve rapid particle size reduction rates, there were large anatomical and physiological changes to the oropharyngeal region in early mammals (Smith 1992). However, currently there is no general physiological model of mastication and swallowing. In contrast, models of the abdominal part of the mammalian digestive system have now progressed to the point where its outline can be understood in terms of the general diet of the mammal (Alexander 1991, 1994). These models can predict the need for organs such as stirred tanks (e.g. the stomach), or continuously flowing pipes (such as the small intestine), and the optimal combination of such digestive units. The problem with these models at present is that they do not include much of the physiology of the front end of the process (mastication and swallowing). If the condition in which food is received by the gut cannot be specified, then any model of the digestive system must be deemed incomplete.

The process function of mastication involves not just food comminution but also particle lubrication (Hutchings & Lillford 1988). Simultaneous to particle size reduction, a coat of fluid is added, either from saliva or expressed juice from within some foods, which lubricates it. Hutchings & Lillford (1988) suggest that two thresholds must be satisfied before swallowing can be initiated: a food particle size threshold and a lubrication threshold. Though there are claims that these can be identified (Prinz & Lucas 1995), this 'two threshold' concept appears to have deflected interest from another necessary function

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which is that oral fluid helps food particles to cohere to form a coherent mass—the food bolus. This is important in mammals because when food is swallowed, it must pass rapidly through the pharynx where the foodway crosses the airway. Despite anatomical arrangements unique to mammals that encourage a specified food path (Smith 1992), there is a risk of potentially fatal accidents if food goes the wrong way. The problem is solved to some extent by a very rapid swallowing action but, by forming an adherent food mass, the risk of inhaling food must be greatly reduced. We suggest here that the endpoint of mastication is marked by a peak in the cohesive force that binds food particles together into a bolus. This packaging optimizes transport past the critical pharyngeal region and increases efficiency of the first unit of digestion, the stomach, which acts on food batches.

2. THEORETICAL BACKGROUND

The forces which attract food particles either to each other or to oral surfaces (since food particles can either stick together or to the mouth), derive from oral fluid, and are either viscous forces, which act over very small distances (Cottrell 1964), or surface tension forces. The fluid is basically saliva, but this can be diluted by juice either expressed from the food or ingested with it. Saliva is a complex fluid containing, among other substances, proteins and hyaluronan (Pogrel *et al.* 1996), which increase viscosity (Roberts 1977) and reduce surface tension (Glantz 1970), compared to water. In addition, as is known better for other much thicker mucous secretions (Denny 1980; Zahm *et al.* 1986), saliva appears to set into an elastic solid at very low shear rates (Roberts 1977), acting somewhat like a glue.

We assume, for simplicity, that each particle produced by fracture in the mouth is spherical. As particles break, new surfaces are coated with fluid. This allows them either to cohere or to stick to the walls of the oral cavity. We could model the initial force which sticks particles to the oral cavity as simple adhesion by surface tension; for a spherical particle attracted to the relatively flat wall of the oral cavity, it is

$$F_A = 4\pi r\lambda \qquad (1)$$

where r is the radius of the food particle, and λ is the surface tension of the oral fluid (Bowden & Tabor 1950). F_A does not depend on the thickness of the fluid film and increases with particle size. Once attached to the mucosa, particles may become glued as the saliva sets, but the initial attractive force is surface tension.

Forces between food particles are more complex. Food particles are never stationary in the mouth and are constantly being jostled, both between tongue and hard palate and between the teeth. Thus, we do not implicate surface tension as a potential binding force and also assume that shear rates between particles are too high to allow the saliva to set like a glue. We suspect that it is viscous forces which hold the bolus together.

The sequence of events during a chew have been clarified by videofluoroscopy (Hiiemae & Crompton 1985; Hiiemae *et al.* 1995). In the early part of the opening phase of a chewing cycle, the tongue moves forwards to collect food particles that are deflected towards it after fracture by the postcanine teeth. In so doing, the tongue probably dips its tip, rather in the manner of an intra-oral lap, into the pool of submandibular saliva that accumulates just behind the incisor teeth. The tongue, using the hard palate as a support, then presses the food particles together against the hard palate, mixing these particles with the saliva. Later in the opening phase, the tongue moves backwards, releasing its pressure as it must then throw particles towards one side of the dentition before the jaw turns towards the closing phase. At this point, the particles either stick together or fall apart. This is likely to be sensed by particles falling off the anterior hard palate onto the tongue as the mucosa of both are finely innervated (Ringel & Ewanowski 1965; Laine & Siirilä 1971).

Imagine that the pressure of the tongue in 'early opening' momentarily creates a spherical ball of particles. We can model the forces that tend to hold the bolus together by considering a section through the centre of this ball. This section has two disc-like surfaces on either side of it. The viscous force required to separate these discs is

$$F_V = 3\pi\eta R^4/4d^2t \qquad (2)$$

where η is the viscosity of the saliva filling the spaces between food particles, R is the radius of the disc of food particles, t is the time span over which the separation is made and d is the average distance between particles (Cottrell 1964). The last-named, d, obviously depends on the packing of particles, which is a function of tongue pressure and food particle size.

Particle size distributions produced during mastication can be obtained from an analysis originated by Epstein (1947) and modified by Gardner & Austin (1962). The analysis was developed for understanding industrial comminution processes but has been successfully applied to mastication (Lucas & Luke 1983; Van der Bilt *et al.* 1987). The rate of comminution depends on the following two factors.

(i) The chance that food particles have of being fractured by the teeth during any chew. This is described by the selection function, $S(x)$, where $S(x)\delta x$, for sufficiently small δx, is that the proportion of particles of size range x to $x+\delta x$ that are broken per chew. Experiments carried out in human mastication using test foods or materials show that, for any given mouthful of food, the selection function appears to be related to particle size by a power law: $S(x)=cx^a$ where a is an exponent and c depends on the unit of measurement of particle size (Lucas & Luke 1983; Van der Bilt *et al.* 1987).

(ii) The size distribution of fragments produced by any particle that fractures. This is the breakage function, $B(y,x)$, where $B(y,x)\delta x$ is that proportion of the fragments by volume of size range x to $x+\delta x$ that break to below size y per chew (where $y \leqslant x$). Experiments on humans suggest that the breakage function behaves fairly simply. The relation between parent particle and

its fragmented offspring: $B(y,x)=x^b$ appears valid (Lucas & Luke 1983; Van der Bilt *et al.* 1987; Van der Glas & Van der Bilt 1997) where the value of the exponent b depends on the mechanical properties of the food that is being chewed (Agrawal *et al.* 1997).

From Lucas *et al.* (1986), if the percentage of the total volume of particles of size range x to $x+\delta x$ before the nth chew is $Pn-1(x)\delta x$, then the percentage of particles below size y after the nth chew is

$$Q_n(y) = \int_y^\infty P_{n-1}(x)\, B(y,x) S(x) dx + \int_0^y P_{n-1}(x) dx \qquad (3)$$

where $\int_0^y P_{n-1}(x)dx$ per cent of particles exist below size y before the nth chew. The percentage of particles of size range x to $x+\delta x$ before the $(n+1)$th chew, i.e. $P_n(x)\delta x$, can be obtained from

$$P_n(x) = dQ_n(x)/dx. \qquad (4)$$

3. THE MODEL

Our model is very simple. Particles will agglomerate when $F_V - F_A > 0$. Less trivially, they will cohere best when $F_V - F_A$ is a maximum, which is the point we predict as the best moment to swallow. Our objective is to examine the physiological conditions under which a maximum is observed and to see if this corresponds with the numbers of chews actually taken by subjects in experiments.

An analytic solution for food particle breakdown has now been produced for the first time by Baragar *et al.* (1996). However, our model was numerically solved. We iterated equations (3) and (4) for 150 'chewing cycles', assuming a maximum of one fracture per particle per chew, to generate particle size distributions. These distributions were then used to obtain an estimate of the average distance d between any two particles within the potential bolus. As above, we assume this food mass to be spherical and consider a section cut through its centre. The section resembles a collection of circles of widely varying sizes packed in a plane. It is impossible to pick any simple packing geometry, such as seen in crystals, because of the particle size range. We know of no non-arbitrary method of solving this packing problem, even assuming spherical particle shapes. We therefore ran a simulation. For each chew, a computer program took one particle at random from the computer-produced particle size distributions, placing it in the presumptive centre of the food mass. A further particle was then drawn at random from the distribution. The locus of the centre of this second particle was determined by constructing a line, random in direction, out from the centre of the first particle until a point was reached where the second particle could sit, its circumference just touching but not overlapping the first. This process was then repeated with further particles. In order to fill the plane, for each new particle, the line was rotated by $\pi/50$. The location of the centre of that and all subsequent particles was defined as the first point along this line where the circumference would touch at least one other particle but overlap none. Two examples of particle packing are shown in figure 1.

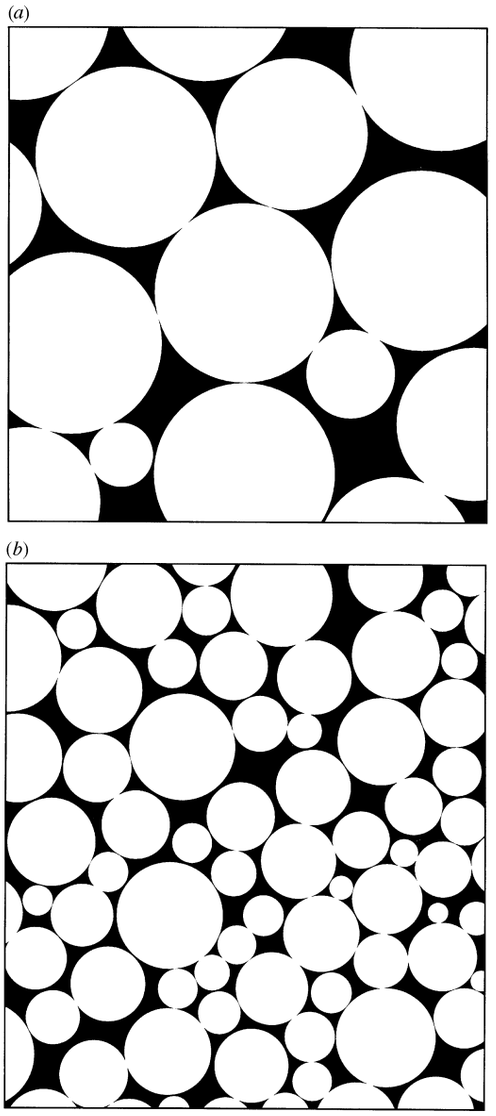

Figure 1. Two examples of spherical packing with particles produced (*a*) early and (*b*) late in the simulated mastication of raw carrot. The packing of particles was not just a function of median particle size; for the same median size, brazil nuts packed tighter than carrot because the great breadth of the distributions with the former included many small fragments which could pack into the interstices.

For each particle size distribution, the average particle separation was found by drawing a series of 100 rays, each again rotated by $\pi/50$, from the centre of each particle outwards. Individual particle separation was the average length of these lines, from the point at which they cut the circumference of the parent circle to that of its nearest neighbour. This was repeated for each particle in the distribution to obtain an overall mean particle separation, s. To this separation was added a layer of saliva, calculated by taking the available pool of saliva at that point in the masticatory sequence as though 'dipping' each particle into the pool such that each particle had an even and equally thick coat, f, of saliva. The average interparticle distance, d, is given by

$$d = s + f \quad (5)$$

Each packing simulation was run up to 20 times for each particle size distribution, the ensuing variation being preserved when analysing overall results.

4. VALUES FOR PARAMETERS

The only good data on food breakdown rates are from studies of human mastication: the measurement of selection and breakage functions require extensive cooperation from subjects. While we claim generality, we can only consider data for humans. We chose two foods which contrast greatly in their breakdown rate in the mouth. Turgid raw carrot (90% moisture, fresh weight basis), breaks down very slowly in the mouth. In this paper, we do not consider release of this moisture by cellular fracture. Brazil nut (5% moisture but with oil) breaks down much more rapidly (Yurkstas & Manly 1950; Agrawal *et al.* 1997). Neither food absorbs saliva during mastication. The value of c in the selection function is taken as 0.0026 when particle size is measured in millimetres, while $a = 2.0$ (Lucas & Luke 1983). This value was also adopted for the simulation with brazil nuts. The value of b, which gives the fragmentation of a single particle, was taken to be 3.0 for carrot (Lucas *et al.* 1986) and 1.2 for brazil nuts ($n = 15$ subjects; Lucas & Luke 1986). Thus, the difference between particle size reduction rates when masticating brazil nuts and raw carrot is assumed here to depend on the breakage function.

The secretion of salivary glands varies in composition with gland structure, the stimulus and length of stimulation (Dawes 1967). The surface tension of mixed saliva (i.e. whole mouth saliva) averages $0.053\,\mathrm{N\,m^{-1}}$ with a fairly narrow range (Glantz 1970). The viscosity of mixed saliva depends on shear rate (Roberts 1977). We performed our own tests, collecting saliva from six human subjects (three males, three females, age range 22–44 yr; median age 35 yr). Within 5 min of collection, the viscosity of a 1 ml sample from each subject was measured at 37 °C with a rheometer (Stresstech, Rheologica Instruments AB, Lund, Sweden), over shear rates of $1–100\,\mathrm{s^{-1}}$. The shear rate relevant to the jostling of food particles on the tongue is probably very low. We chose $4\,\mathrm{s^{-1}}$, close to that suggested by Sherman (1988), for the sensory evaluation of the viscosity of thicker fluids in the oral cavity. The average viscosity of saliva from our experiments at this shear rate is $0.043\,\mathrm{kg\,m^{-1}\,s^{-1}}$.

We assume in the model that the walls of the oral cavity are always lubricated (a residual layer of saliva averaging 0.8 ml remains in the mouth after a swallow; Edgar & O'Mullane 1990), and, therefore, that food particles can stick immediately to the walls of the cavity. However, we also assume that this residual saliva is a film over the oral cavity and is not available immediately to wet food particles. These particles are therefore gradually wetted as food comminution proceeds. The salivary rate was taken as $3\,\mathrm{ml\,min^{-1}}$, which is well within physiological limits (Watanabe & Dawes 1988*a*), and the chewing frequency, 1 Hz. In any chew, food fragments formed were assumed to be coated with saliva immediately, thus making the mouth the equivalent of a 'well-stirred' tank (Alexander 1991).

The model assumes the radius of the particle mass, R, to be constant. In fact, it decreases slightly as particles pack together, but not by as much as d changes. Lastly, the time span, t, over which the bolus can fall apart is suggested as the period of late jaw opening. We assumed 0.25 s for this here.

5. RESULTS

Figure 2 shows how $F_V - F_A$ varies with chew number during masticatory sequences for carrots and brazils. The variation shown in figure 2 is a result of the variation in the variable d produced by repetition of the packing algorithm. Despite scatter deriving from variation in particle packing, it is clear that $F_V - F_A$ is negative initially, showing that food particles easily fall apart and stick to the walls of the cavity. The cohesive force rises rapidly and peaks at about 20–25 chews for both carrots and brazils. Thereafter, this force gradually declines. At peak cohesion, the median carrot particle is about 33% of the size of the original particles; for brazil nuts, it is 20%. This represents about a 9–25-fold increase in surface area respectively over that at ingestion.

The number of chews needed to reach peak cohesion remained relatively insensitive to most changes in the model. Increase in the salivary rate resulted in the bolus getting flooded earlier. If lower values for η are taken, then $F_V - F_A$ is negative for longer, indicating that the large food particles present then are much more likely to stick to the walls of the oral cavity than to each other.

6. DISCUSSION

It is difficult to specify an endpoint for mammalian mastication: particles just get smaller and smaller with increasing numbers of chews. A mammal that is chewing cannot easily ingest more food (Alexander 1994), but this does not suggest a definitive point to stop chewing and commence swallowing. Without any criterion for the optimal release of a comminuted batch of food by swallowing, the rate of food input to the gut cannot be predicted, only empirically modelled. We suggest that the peak cohesive force between food particles is the optimum time to swallow and the turning point in the cohesive force, the moment when cohesion starts to reduce, may be what is actually sensed. The selection in the model of the peak cohesive force as the trigger seems the only simple choice. A threshold value seems more arbitrary without accompanying evidence. The criterion of peak cohesion does not frustrate the presumed metabolic need of mammals to comminute foods—extensive size reduction is necessary to produce a high cohesive force. If swallowing is postponed to permit further breakdown, then there is the risk that the bolus will fall apart as a salivary coat increases particle separation.

Despite substantial differences in the transport of food particles by mammals other than higher primates

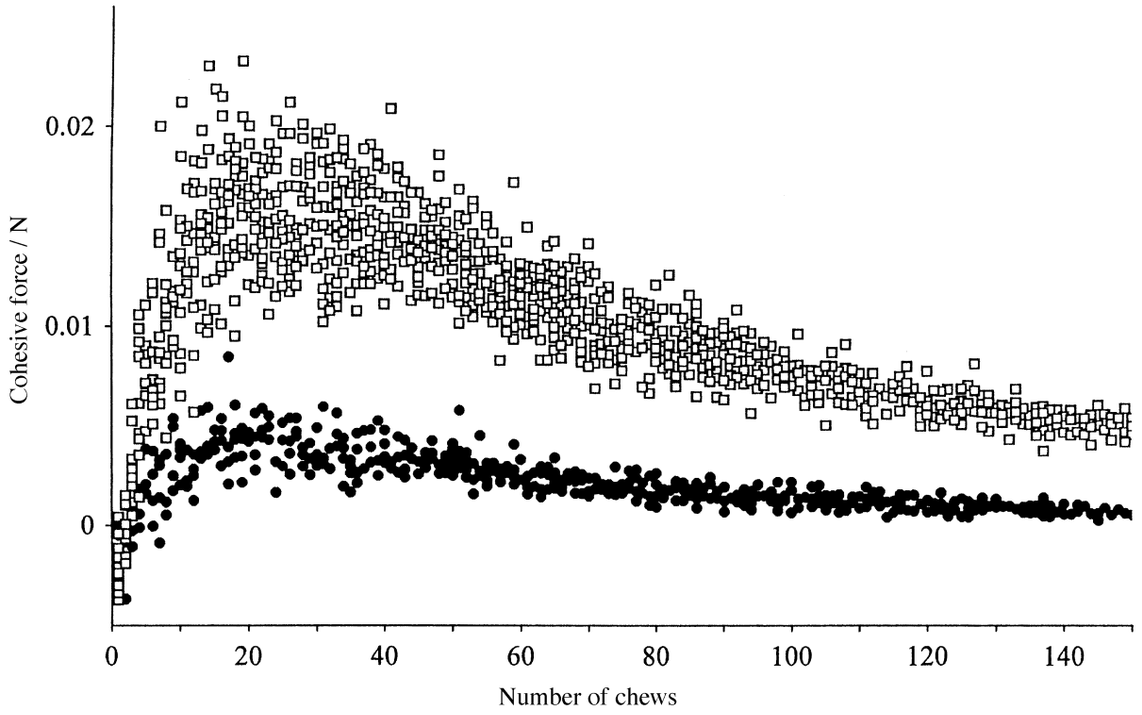

Figure 2. Results of the model. The cohesive force, $F_V - F_A$, plotted against the number of chews taken in the masticatory sequence for raw carrot (closed circles) and brazil nut (open squares). The variability seen derives from iteration of the packing simulation. Despite this, it is clear that the cohesive force peaks at about 20–25 chews.

and man in the oropharyngeal region (Hiiemae & Crompton 1985), we argue that the model is still applicable even if the whole bolus forms in the pharynx. A mammal may pass clumps of food piecemeal back from the oral cavity to the vallecular region of the tongue or the piriform fossa of the pharynx but we predict that the sensory decision to pass food posteriorly would still be based on food actually clumping, i.e. on cohesion. An extra benefit may be that food clumps left to aggregate under zero shear in the pharynx may benefit from the setting of saliva, so glueing food particles together.

In human mastication, the model predicts a number of chews before swallowing that is broadly similar to values reported for dentate subjects in the literature. Lucas & Luke (1986) report a mean of 31 chews to swallow raw carrot ($n=35$ subjects), versus 25 for brazils ($n=15$), but with large ranges. This range could be due to relaxation of selective pressures on the feeding rate in humans and the freedom that some may desire for chewing for extended periods. The results of figure 2 suggest more potential problems with choking may arise from early swallowing, the bolting of food, when the cohesive force is very low than with comminution extended some way beyond the optimum.

The low cohesion predicted for raw carrot corresponds with evidence that carrot particles do not tend to form a bolus (Lucas & Luke 1983, 1986). The model predicts that the most important variable influencing this is the rate of particle size reduction. Raw carrot breaks down slowly and would not tend to form a bolus because the cohesive force with such foods is small.

Our model also explains observations reported by Lillford (1991), who shows photographs of food particles expectorated by a human subject at various stages of a masticatory sequence. At the point of swallowing, food particles cohered into a bolus. However, when the subject was forced to chew on beyond the point where swallowing would normally have been triggered, the bolus began to fall apart. In contrast to the commonly held view of factors that influence the rate of oral emptying (e.g. Storey 1976), we predict a key factor to be the particle size distribution.

Swallowing patterns in humans and higher primates vary from those of other mammals due to the low position of the larynx (Hiiemae & Crompton 1985). However, our model is independent of the location of bolus formation—this could be as far back as the vallecular region of the tongue or the piriform fossa in many mammals. All that would have to be sensed in the mouth is the point at which particles start to cohere. We thus argue that the model has general relevance. Early mammals developed postcanine teeth capable of reducing food particle sizes. In order to control particles, they also developed increased mobility of the tongue and developed muscular cheeks (Smith 1992). In contrast to a stereotypical lower vertebrate which swallows single large particles, small particles are much more likely to get misdirected. Early mammals evolving a masticatory apparatus must, therefore, also

have been under strong selective pressure to evolve a safe anatomical pathway for foods that was separate from the airway. Thus, early during mammalian evolution, a palate developed to seal off the upper respiratory tract and, in the pharyngeal region, a whole set of constrictor muscles were developed which have no homologues in reptiles (Smith 1992). Probably in all mammals, safety in swallowing derives from the elevation of the larynx (Smith 1992). There was, and is, therefore, an active need to detect the state of these particles in the mouth in order to swallow safely. Thus, even though swallowing is known to be controlled by brainstem circuitry producing stereotyped motor behaviour (Jean 1990), peripheral feedback must be extremely important. Most of the experimentation reported is not directly pertinent to our model, but evidence that the activity of muscles in the floor of the mouth depends on the consistency of what is swallowed (Hrycyshyn & Basmajian 1972), and that this is triggered by mucosal stimulation (Mansson & Sandberg 1975) is relevant. Also, salivary inhibition increases difficulty in swallowing (Liedberg & Öwall 1991). Though these observations are consistent with our hypothesis, they do not test it.

We suggest various simple tests of the model. The two key parameters are particle size reduction rate and salivary rate. The smaller the particle separation d, the higher the cohesive peak. More rapid food comminution will also result in a slightly earlier peak. That this is not very obvious in figure 2, where brazil nuts are breaking down much more rapidly than raw carrot, is because the scatter in the density of particle packing obscures it. A faster salivary rate would flood the bolus earlier and cause the developing bolus to break up. The main effects of a higher salivary rate are to produce a smaller peak cohesive force after fewer chews and a more rapid diminution of the cohesive force after the peak is reached. We used foods that do not absorb saliva. The effect of chewing absorbent foods would be to effectively lower the salivary rate.

In humans (but not necessarily other mammals), a key factor in determining salivary rate is the gustatory stimulus (Watanabe & Dawes 1988*b*). Increasing the concentration of tasty chemicals in an otherwise unchanged food should, if salivary rate is increased, promote earlier swallowing. Salivary-thinning agents such as tannins (Prinz & Lucas 1998) or juice expressed from foods should interfere with bolus formation and delay swallowing. In contrast, thickening agents (some food additives) may promote earlier swallowing.

In some respects, the model is oversimplified. The two-dimensional packing algorithm that we invented is only one of many that are possible. Other possibilities should be explored and extended to three dimensions if at all possible. We have also not considered the important problem of the ease of intra-oral transport of the bolus. This can be treated, very crudely, as though food particles are suspended in saliva. Then, at the very low shear rates that we envisage, from the Guth–Einstein equation, the viscosity of the bolus

$$\eta^* = \eta(1 + 2.5C + \alpha C^2) \qquad (6)$$

where C is the concentration of food particles in the bolus by volume. The term αC^2 takes into account the jostling of particles in the high concentrations in a bolus (Guth & Gold 1938). According to Hunter (1987), the determination of the value of the coefficient α, predicted by Guth to be 14.1, demands greater experimental accuracy than is currently available. (For herbivorous mammals that ingest sheet-like particles, a particle shape correction factor can be introduced; Guth 1945.) It can readily be seen from equation (6) that the key factor in bolus formation, the food particle size distribution, plays no role at all in the ease of bolus transport. We suggest, therefore, that bolus formation and bolus transport depend on very different factors and should be separated in the analysis of experimental data, something that is not evident in current descriptions (Thexton 1992). The key factor for bolus transport would appear to be the volume of saliva present.

In the current model, surface properties of foods are assumed constant. However, there are a large number of commercially important human foods that are extremely sticky—melting in the mouth or absorbing saliva (Kashket *et al.* 1991). The problem is important for analysing the masticatory process because the tendency of any food to clump together may well affect the selection function, making it more probable that small particles of brazil nut are broken compared to equivalent particles of raw carrot. The selection function has been measured up to now on foods/materials that do not form a strong bolus (carrot, Lucas & Luke 1983; dental impression material, Olthoff *et al.* 1984). For bolus-forming foods, the general assumption that $S(x)$ is independent of the time that particles have been resident in the mouth may be wrong. Indeed, Baragar *et al.* (1996) find that, in order to fit their theoretical model to actual food breakdown patterns, the expression for the selection function must be modified after a certain number of chews. A tendency towards food agglomeration may be the reason for this. All these factors and the incorporation of finer experimental data, such as the relationship between food properties, salivary rate and even salivary viscosity (as reflected in changes in the composition of saliva over time), herald the possibility of modelling the physiology of the 'front end' of the mammalian digestive system for the first time in terms of bolus mechanics.

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