Effect of Texture of Plastic and Elastic Model Foods on the Parameters of Mastication

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1 Déficience, Incapacité et Désavantage en Sauté Ozole, Dental Faculty, University of Auvergne, Clermont-Ferrand; and 2 Institut National de la Recherche Agronomique, Département Alimentation Humaine, Saint-Genès Champanelle, France

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Foster, K. D., A. Woda, and M. A. Peyron. Effect of texture of plastic and elastic model foods on the parameters of mastication. J Neurophysiol 95: 3469–3479, 2006; doi:10.1152/jn.01003.2005. Mastication is continually modified throughout the chewing sequence in response to the texture of the food. The aim of this work was to compare the effects of an increase in hardness of two model food types, presenting either elastic or plastic rheological properties, on mastication. Each model food type consisted of four products of different hardness. Sensory testing experiments conducted with one group of 14 subjects showed significant perceived differences between products in terms of their increasing hardness. Fifteen other volunteers were asked to chew three replicates of each elastic and plastic product during two sessions. EMGs of masseter and temporalis muscles were recorded simultaneously with jaw movement during chewing. Numerous variables were analyzed from these masticatory recordings. Multiple linear regression analyses were used to assess the respective effects of food hardness and rheological properties on variables characterizing either the whole masticatory sequence or different stages of the sequence. Muscle activities were significantly affected by an increase in hardness regardless of the food type, whereas the shape of the cycles depended on the rheological properties. The masticatory frequency was affected by hardness at the initial stage of the sequence but overall frequency adaptation was better explained by a change in rheological behavior, with plastic products being chewed at a slower frequency. A dual hypothesis was proposed, implicating first a cortical–brain stem preprogrammed mechanism to adapt the shape of the jaw movements to the rheological properties of the food, and second, a brain stem mechanism with mainly sensory feedback from the mouth to adapt muscle force to the food hardness.

INTRODUCTION

Mastication is a rhythmic movement regulated by a central pattern generator (Dellow and Lund 1971), which is sensitive to and dependent on oral sensory feedback (Appenteng et al. 1982; Lund 1991). Mastication is therefore continually modified throughout the chewing sequence in response to the texture of the food bolus (Ahlgren 1966; Horio and Kawamura 1989; Peyron et al. 2002). The effect of food texture on masticatory parameters has, however, not been systematically studied. The main obstacle is that food is a complex stimulus that is difficult to reduce to a single physical dimension as can be done for light or vibration in vision or proprioceptive studies, for example. As a consequence, contrasting results have been obtained concerning the description of the masticatory process. For example, masticatory frequency has been described as increasing (Steiner et al. 1974), decreasing (Huang et al. 1993), or presenting no change (Horio and Kawamura 1989; Yamada and Yamamura 1996) with food hardness. In many cases, authors have used different natural food products to give a scale of hardness when recording mastication (Agrawal et al. 1998; Duizer et al. 1994; Sakamoto et al. 1989; Veyrune and Mioche 2002). This presents a problem because it is not clear whether the masticatory response to a particular product is in response to the hardness of the product and/or to some other textural property (elasticity, plasticity, stickiness, and brittleness to name a few). This challenging problem led to the use of artificial test foods, for example, elastomers (Buschang et al. 1997; Fontijn-Tekamp et al. 2004; Mioche and Peyron 1995; Olthoff et al. 1986; Slagter et al. 1992; Van Der Bilt et al. 1991), which pose a further problem in that they limit the study of natural chewing because they cannot be swallowed. A compromise was the use of gums or chewing gums; however, these natural alimentary gums often offer no more than two hardness levels (Anderson et al. 2002; Bishop et al. 1990; Horio and Kawamura 1989; Plesh et al. 1986; Takada et al. 1994). Lassauzay et al. (2000) and Peyron et al. (2002) helped to clear some contradictions regarding the effect of hardness on mastication by developing visco-elastic (predominantly elastic) gelatin-based model foods of a four point scale of hardness. Shiau et al. (1999) also used model foods (tablets presenting brittle food products of 3 different hardness) to study the effect of test food hardness on muscle activity. From this type of work, differences in masticatory parameters between several model foods can be related directly to the hardness as the other textural properties of the food are constant.

The aim of this study was to compare the effects of two different rheological properties, i.e., elasticity and plasticity, independently of other physical properties such as hardness, on mastication. Two types of model foods presenting different rheological behavior, elastic or plastic, were developed. Each model food consisted of a four-point graded scale of hardness. Variations in the masticatory responses to these products were observed by recording the masseter and temporal muscle activities and simultaneous jaw movements during unilateral mastication in 15 subjects.

METHODS

Subjects

For the sensory tests, a group of 14 subjects consisting of 6 females and 8 males, aged 34.4 ± 8.9 yr, were selected. For the masticatory
experiment, 15 consenting male dental students (aged 24.1 ± 1.9 yr) were selected on the basis of strict dental criteria as described in Lassauzay et al. (2000). This study was approved by the local Ethics Committee, and all subjects gave informed consent after receiving a full explanation of the goals and evolution of the study.

Elastic model foods

Four edible jellied confectionery products having mainly elastic behavior and differing in hardness [very soft (E1), soft (E2), hard (E3), and very hard (E4)] but identical in size and shape (cylindrical, 1 cm height, 2 cm diam) were prepared from four grades of gelatin (Rousselot 100, 150, 200, and 250 blooms, Degussa-Texturants System, Bauppte, France). The procedure for making these products is detailed in Lassauzay et al. (2000).

Plastic model foods

Four edible caramel confectionery products having mainly plastic behavior and differing in hardness [very soft (P1), soft (P2), hard (P3), and very hard (P4)] but identical in size and shape were prepared. The caramels were made from sweetened condensed milk (34 g), 38 DE vegetable fat (18 g). The hardness of the caramels was controlled by heating the caramel mixture until a desired amount of water had evaporated. This was achieved by intermittent weighing of the mixture until the desired water loss of 3, 5, 6, and 7 g for P1, P2, P3, and P4, respectively. The caramels were poured into Plexiglas cylindrical molds (1 cm height, 2 cm diam) oiled with beeswax (Dubois Co., Bouligne, France). When the caramels had cooled, the molds were covered in plastic film and left overnight before turning out.

Rheological measurements

The mechanical characteristics of the four plastic and four elastic products were measured using an Instron Universal Testing Machine (Instron mini 55, High Wycombe, Bucks, UK). The samples underwent two successive uniaxial compression cycles between two piston heads of 5 cm diam. Oil was applied to the piston heads to provide lubrication, avoiding adhesion between the sample and piston heads. Compressions were performed at a constant displacement rate of 50 mm/min and a compression ratio of 50% of the initial sample height. Immediately after the second compression, the sample underwent a relaxation test for 60 s. Data acquisition was performed with a 500-N load-cell at a frequency of 250 points/s.

Sensory tests

The 14 subjects involved in the sensory experiment were asked to assess the hardness of the four plastic and four elastic products using a visual analog scale (VAS) of 10 cm. The VAS was an unstructured line scale with the left end marked “very soft” to the right end marked “very hard.” All hardness assessments were made using the same method. To avoid visual recognition of the sample color and to avoid nonoral indices for texture assessment before chewing, the experimenter placed each sample on the subject’s tongue. Subjects immediately began chewing in a habitual manner and made the hardness assessment just after swallowing and drew a line on the VAS at a place corresponding best to their hardness sensation.

The hardness assessments were done during three sessions. The first session functioned purely as a familiarization session for the subject. The second and third sessions were used to record the mastication of either elastic or plastic model foods. Because the slight stickiness of the plastic products, the subjects were instructed to not use their tongue to clean the food product from their teeth during mastication. Between the mastication of each sample, the subject was given enough time to clean their teeth with his tongue and to take a mouthful of water.

Masticatory recordings and experimental procedure

Jaw movements and muscular activity were recorded simultaneously during chewing of the model foods. Muscle activity was recorded by surface EMG for both left and right temporal and masseter muscles. Jaw movements were recorded in the frontal plane by electromagnetic induction, as previously validated by Peyron et al. (1996). Full details of the experimental set-up are given in Lassauzay et al. (2000). Subjects were seated upright with the head supported. Electrodes were placed over the temporal and masseter muscles, and electromagnetic receiver coils were glued to the central incisors. At the beginning of a trial, the experimenter placed a sample on the subject’s tongue. Before chewing and after swallowing, the subject was instructed to close his mouth and to fit his teeth together to create a reference position for the analysis. On a signal from the experimenter, the subject placed the sample between his teeth and began to chew in a habitual manner. During each session, three samples of each hardness of a given product (3 × 4 elastic or plastic products) were presented in a random order. A further hard sample (E4 or P4) was given to the subject at the beginning of the session so that the subject could determine his preferred side for chewing that was used for chewing all samples. Each subject attended three recording sessions at the same time each day, usually spaced only a few days apart. The first session functioned purely as a familiarization session for the subject. The second and third sessions were used to record the mastication of either elastic or plastic model foods. Because the slight stickiness of the plastic products, the subjects were instructed to not use their tongue to clean the food product from their teeth during mastication.

Data extraction and analysis

The initial steps of the data analysis have been described by Lassauzay et al. (2000). Examples of rectified EMG recordings for the four muscles and simultaneous vertical and lateral jaw movements during chewing of elastic (E1) and plastic (P1) products are given in Fig. 1, A and B. Several parameters were extracted from the jaw movement and muscle activity recordings. Some parameters were taken from an analysis of the complete sequence, e.g., number of chewing strokes, masticatory frequency, EMG activity per sequence (total EMG activity for the 4 muscles during the entire masticatory sequence), and mean vertical and mean lateral amplitudes recorded during the entire sequence. Other parameters were taken from a cycle-by-cycle analysis including the EMG activity per cycle, vertical and lateral amplitudes, opening, closing and occlusal durations, and opening and closing velocities. To obtain EMG activity per cycle, EMG activity per sequence was divided both by the number of cycles and by the four muscles. The EMG activity per cycle corresponds to the EMG activity observed for a single muscle during a single chewing cycle.

Statistical analysis

Statistical analyses were performed with SAS (version 6.12 1998) using General Linear Models for ANOVA. A Student Newmann-Keuls test was carried out between samples for comparison of means (risk at 5%) when the ANOVA indicated there to be a significant difference. A multiple linear regression (MLR) with stepwise forward variable selec-
tion was performed on the average data from the complete sequence to compare the implication of two explicative variables, rheological properties (elastic or plastic) and product hardness, on the modifications of the masticatory parameters. Three other multiple linear regressions with the same kind of variable selection were performed with data from the cycle-by-cycle analysis. Three series consisting of three cycles were chosen to describe the three main stages of the masticatory sequence: the mean of cycles 2 to 4 (series I), the mean of the three cycles in the middle of the sequence (series II), and the mean of the last three cycles (series III). The data from the first cycle were not used in the analysis because the subjects usually used this cycle to place the sample between the teeth and to gather information about the food being chewed (Peyron et al.)

**FIG. 1.** Example of mastication recordings of 2 food products of the same mechanical hardness from 1 subject (A) subject chewing 1 elastic product, E4, and (B) subject chewing 1 plastic product, P2. The 3 traces are, top to bottom, lateral movement, vertical movement, and right masseter activity (ipsilateral side). All cycles from the same complete sequences of mastication are superimposed and displayed in the frontal plane for elastic (C) and plastic (D) products.
R E S U L T S

Rheological measurements of model foods and sensory tests

The rheological properties, either elastic or plastic, of the two groups of products are shown in the curves obtained with an Instron machine (Fig. 2, A and B). Elastic materials deform (strain) instantaneously when a weight (stress) is applied. The strain disappears instantaneously when the stress is removed and the product completely recovers to its original height and shape. Conversely, plastic materials do not return to their original shape when the stress is removed as they exhibit a yield stress which, when exceeded, causes flow and permanent deformation of the product (Borwankar 1992; Bourne 2002). The mechanical hardness, indicated by the maximal stress during the first compression, increased between E1 and E4 and between P1 and P4 (Fig. 2, C and D). The maximal stresses for the elastic products, E1, E2, E3, and E4, were 0.017 ± 0.004, 0.031 ± 0.002, 0.048 ± 0.004, and 0.071 ± 0.003 MPa.
respectively. For the plastic products, the range was larger: 0.017 ± 0.005, 0.074 ± 0.015, 0.287 ± 0.105, and 0.603 ± 0.226 MPa for P1, P2, P3, and P4, respectively. Each product was significantly different from the three others (1-way ANOVA, F = 687, P < 0.001 for elastic products and F = 631, P < 0.001 for plastic products; Student Newman Keuls, α = 0.001). Figure 2, C and D, also shows that, within the two rheological groups, subjects were able to differentiate the hardness of each product (elastic: F = 168, P < 0.001; plastic: F = 360, P < 0.001). Power law relationships were observed between maximal stress values from the first compression and sensory scores for both groups of products, and the data were linearized by taking logarithms (Fig. 2E).

**Effect of hardness on the parameters of mastication**

The mean values of most variables characterizing the sequence were significantly affected by an increase in hardness of both the elastic and plastic model food products (Table 1; Fig. 3). Sequence duration, number of cycles, EMG activity per cycle, and EMG activity per sequence were significantly enhanced with increased hardness whatever the model food type (Fig. 3, A–D, G, and H). The comparison between elastic and plastic foods on the adaptation of the kinetic parameters characterizing the cycles gave some contrasting results. Opening velocity was orderly scaled to increasing hardness while chewing elastic products. This relationship was not evident while chewing plastic products even though statistics showed a difference between the softest product compared with others (data not shown). This relationship was also influenced by the rheological properties of the products but only in the middle and final parts of the masticatory sequence and was slightly influenced by the hardness of the product during the first five cycles only for the plastic foods (data not shown).

**Effect of food rheological properties on the parameters of mastication**

Figure 1 shows examples of electromyographic and mandibular movement recordings from the same subject chewing elastic (E4) and plastic (P2) model foods of similar mechanical hardness as measured by an Instron machine. It can be seen that this subject used approximately the same number of cycles to masticate these two products, 35 cycles for E4 and 38 cycles for P2, but the cycle frequency was lower for the plastic product (1.68 ± 0.13 s⁻¹ for E4 and 1.45 ± 0.21 s⁻¹ for P2). The amplitude and shape of the cycles during mastication differed greatly between the two products in both the vertical and lateral direction (Fig. 1, C and D).

Significantly larger vertical (Fig. 4, A and B) and lateral (Fig. 4, C and D) amplitudes are used when chewing plastic products compared with elastic products. Frequency was lower when chewing plastic products than when chewing elastic products (Fig. 3, A and B), and this could be observed at all stages of the masticatory sequence (Fig. 4, E and F). The closing velocity also was influenced by the rheological properties of the products but only in the middle and final parts of the masticatory sequence and was slightly influenced by the hardness of the product during the first five cycles only for the plastic foods (data not shown).

**Table 1. Effects of hardness on the masticatory parameters characterizing the whole sequence**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Elastic</th>
<th>Plastic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F ratio</td>
<td>Means and Student Newman Keuls groups</td>
</tr>
<tr>
<td>Sequence duration, s</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11*</td>
<td>14.0 ± 5.7*</td>
<td>15.7 ± 6.0*</td>
</tr>
<tr>
<td>Number of cycles</td>
<td>9*</td>
<td>20.3 ± 9.2*</td>
</tr>
<tr>
<td>Mastic. Frequency, s⁻¹</td>
<td>NS</td>
<td>1.43 ± 0.26</td>
</tr>
<tr>
<td>EMG act./sequence (mV.s⁻¹)</td>
<td>35*</td>
<td>8.2 ± 4.2*</td>
</tr>
<tr>
<td>Vertical amplitude (mm)</td>
<td>28*</td>
<td>14.4 ± 4.5*</td>
</tr>
<tr>
<td>Lateral amplitude (mm)</td>
<td>56*</td>
<td>3.6 ± 3.4</td>
</tr>
<tr>
<td>Opening velocity (mm/cycle)</td>
<td>62*</td>
<td>52.4 ± 15.5*</td>
</tr>
<tr>
<td>Closing velocity (mm/cycle)</td>
<td>32*</td>
<td>47.6 ± 13.7*</td>
</tr>
<tr>
<td>Closing duration (s)</td>
<td>NS</td>
<td>0.313 ± 0.107</td>
</tr>
<tr>
<td>Occlusal duration (s)</td>
<td>28*</td>
<td>0.077 ± 0.033*</td>
</tr>
<tr>
<td>Opening duration (s)</td>
<td>3*</td>
<td>0.299 ± 0.109</td>
</tr>
<tr>
<td>Cycle duration (s)</td>
<td>NS</td>
<td>0.67 ± 0.16</td>
</tr>
<tr>
<td>Chew temporal (mV·s⁻¹)</td>
<td>122*</td>
<td>0.10 ± 0.07*</td>
</tr>
<tr>
<td>Non-chew. temporal (mV·s⁻¹)</td>
<td>180*</td>
<td>0.09 ± 0.04*</td>
</tr>
<tr>
<td>Chew. masseter (mV·s⁻¹)</td>
<td>373*</td>
<td>0.11 ± 0.06</td>
</tr>
<tr>
<td>Non-chew. masseter (mV·s⁻¹)</td>
<td>56*</td>
<td>0.10 ± 0.11</td>
</tr>
<tr>
<td>EMG act. per cycle (mV·s⁻¹)</td>
<td>23*</td>
<td>0.105 ± 0.044*</td>
</tr>
</tbody>
</table>

Values are means ± SD. The effects of increased hardness from E1 to E4 (elastic products), or from P1 to P4 (plastic products) is given by F ratio. For each parameter, statistical differences were studied using a Student Newman Keuls test at a risk of 5%. For each parameter and each product, different letters (a, b, c, or d) indicate that statistical difference was observed. The same letter appearing in two or more cases means that no statistical difference was found. *** = P < 0.001; ** = P < 0.01; * = P < 0.1. †EMG activity per cycle for the corresponding muscle; ‡EMG activity per cycle for the four muscles considered together (EMG activity per sequence divided by the number of cycles and by four).
Relative implication of hardness and rheological behavior

MLR performed on the data from the complete sequence is shown in Table 2. As shown in Table 2 and Fig. 4, parameters describing the shape of the masticatory cycles and vertical and lateral amplitudes were more strongly influenced by the rheological properties of the product than by hardness, with as much as 27 and 23% of the total variability of these masticatory parameters explained by the rheological behavior (elastic vs. plastic). The frequency of mastication and closing velocity were also highly dependent on the product type. Table 2 shows that sequence duration, number of cycles, and EMG activity (per sequence or per cycle) were strongly dependent on the hardness of the product and not or only slightly by the product rheological behavior. Opening velocity was less strongly influenced by hardness although this was a more important parameter than product type (elastic or plastic) and explained 10% of the variability.

The MLR performed on the three series of cycles revealed similar results to that performed on the complete sequence (Table 3). The change in rheological properties of the food product (elastic vs. plastic) explained the variations of the lateral and vertical amplitudes of the masticatory cycles during the entire sequence better than hardness. No more than 20% of the variation in the vertical amplitude was explained by the rheological properties for series II (middle 3 cycles of the sequence). Except for occlusal duration, the effect of the product type (elastic vs. plastic) on velocities or durations of the phases of the mandibular movement were more evident during the middle of the masticatory sequence, particularly for closing velocity (12%) and frequency (11%). At the start of the masticatory sequence, the hardness of the product was more important, particularly for describing the frequency of mastication and muscle activities (20–38% of variability explained).
METHODOLOGICAL CONSIDERATIONS

This work further shows the value of using model foods for studying mastication. Similar to the model foods developed by Lassauzay et al. (2000), the plastic model foods developed in this work were both edible and exhibited known and reproducible physical properties. They were also distributed on a hardness range that could be discriminated by both their mechanical and sensory properties. Direct comparisons between elastic and plastic rheological properties were made possible because many factors were controlled. 1) The shape/thickness of the elastic and plastic model food products were the same. This was important because these factors have been shown to influence mastication (Miyawaki et al. 2000; Peyron et al. 1997). 2) The range of hardness of both model food types were known and controlled. It was therefore possible to compare foods of different rheological properties because the variations caused by hardness were accounted for during statistical analyses. In addition, the range of hardness was wider for the plastic products than for the elastic products and therefore the two closest products in terms of mechanical hardness, i.e., E4 and P2, were used preferentially for certain comparisons. 3) The relative purity of the rheological properties within each group of products allowed the identification of the adaptation in masticatory performance as a result of changing rheological behavior. The results obtained in this study were from young, healthy male subjects with good dentition.
Some studies have already shown the adaptation of the masticatory pattern, for example with age, gender, or oral health, to an increase in hardness (Peyron et al. 2004; Veyrune and Mioche 2002). This kind of study could be extended by analyzing the adaptation of mastication to a change in food rheological properties in different physiological conditions.

Descriptors of the adaptation to hardness of model foods

Peyron et al. (2002) showed with elastic model foods that mastication responds to an increased hardness by a strong increase in the number of cycles and the muscular activity of the temporal and masseter muscles. This study confirms these findings for elastic products, extends them to the plastic products, and suggests the following general law: the masticatory apparatus adapts to an increase in food hardness by increasing both the number of cycles and the muscular work. Some of the distinctions between hardness seen in the work of Peyron et al. (2002) and not observed here are likely to be a result of the increased number of observations used in their work: 15 subject with three sessions for the elastic products compared with 15 subjects and only one session per product type in this study because Lassauzay et al. (2000) found subjects to be consistent between sessions. The multiple linear regressions

| Table 2. Effects of food hardness and rheological behaviour on the masticatory parameters of the whole sequence |
|---------------------------------------------------------------|------------------|------------------|------------------|
| Sequence duration, s                                        | Estimated Values | Fisher Ratio     | P                |
| Hardness                                                     | 3.588            | 84               | 0.001            |
| Number of cycles                                            | 4.035            | 55               | <0.0001          |
| Masticatory Frequency, s⁻¹                                   | Hardness         | -0.021           | 0.0438           |
| Vertical amplitude, mm                                       | Hardness         | 0.418            | 0.0229           |
| Rheological behaviour                                        | 3.494            | 39               | <0.0001          |
| Opening velocity, mm.s⁻¹                                    | Hardness         | 1.226            | 0.0008           |
| Closing velocity, mm.s⁻¹                                    | Hardness         | 8.477            | 0.0001           |
| Rheological behaviour                                        | 3.997            | 105              | 0.495            |
| EMG activity per cycle, mV.s                               | Hardness         | 0.078            | <0.0001          |

Values for EMG and movement variables were drawn from the Multiple Linear Regression analyses. The constants were E1 for hardness scale (from E1 to P4) and elastic for rheological behaviour. Only significant results are presented. Shaded cells correspond to a better correlation for hardness and hatched cells correspond to a better correlation for rheology. *EMG activity of the four muscles for the whole sequence †EMG activity per sequence divided by the number of cycles and by the number of muscles i.e. four

Some studies have already shown the adaptation of the masticatory pattern, for example with age, gender, or oral health, to an increase in hardness (Peyron et al. 2004; Veyrune and Mioche 2002). This kind of study could be extended by analyzing the adaptation of mastication to a change in food rheological properties in different physiological conditions.

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| Table 3. Effects of food hardness and rheological behaviour on EMG and movement variables at different stages of the masticatory sequence |
|---------------------------------------------------------------|------------------|------------------|------------------|
| Series I (Cycles 2–4)                                       | Series II (Middle 3 Cycles) | Series III (Last 3 Cycles) |
| Vertical amplitude                                          | 3.7***           | 12.3***          | 0.9*            | 20.9***          | 2.8***           | 5.2***           |
| Lateral amplitude                                           | 2.8***           | 15.4***          | 4.8***          | 17.6***          | 3.7***           | 18***            |
| Opening velocity                                            | 2.7**            | 1.1**            | 1.1**           | 1.1**            | 1.1**            | 1.1**            |
| Closing velocity                                            | 1.4*             | 1.4*             | 1.4*            | 2.4***           | 2.4***           | 2.4***           |
| Occlusal duration                                           | 11.9***          | 1.6*             | 3.1***          | 4.6***           | 3.5***           | 3.5***           |
| Opening duration                                            | 6.9***           | 2.1              | 1.2**           | 5.6***           | 3.3***           | 3.3***           |
| Cycle duration                                              | 18.1***          | 1.3***           | 3.5***          | 8.9***           | 6.3***           | 6.3***           |
| Frequency                                                   | 19.9***          | 4.7***           | 10.6***         | 7.2***           | 7.2***           | 7.2***           |
| EMG activity*                                               | Chew temporalis  | 23.2***          | 9.3***          | 5.6***           | 1.1*             |
| Non-chew. Temporalis                                       | 33.6***          | 13***            | 6.1***          | 7.8***           | 0.8*             |
| Chew. Masseter                                             | 38.2***          | 19.4***          | 7.8***          | 8.8***           |                  |                  |
| Non-chew. Masseter                                         | 36.7***          | 6.4***           |                  |                  |                  |                  |

R² values (%) for EMG and movement variables were drawn from Multiple Linear Regression analyses on series I to III. The degree of significance is indicated by asterisks: ***P < 0.001; **P < 0.01; *P < 0.5. The constants are E1 and elastic. Shaded cells correspond to a good correlation with R² higher than 5%. (−) corresponds to a negative correlation versus constant. Chew and non-chew indicate when considered muscle corresponds to the masticatory or non-masticatory side. Mean EMG activity observed for the cited muscles during the considered cycles.
Descriptors of the adaptation to rheological properties of model foods

Mastication adapted to the two rheological properties tested in this work, elasticity and plasticity, by modifying the shape of the mandibular movements. This was clearly evident from the differences in vertical and lateral amplitudes seen when chewing the two food types. Multiple linear regressions revealed that these parameters were strongly affected by food type when considering both the entire sequence and parts of the sequence, i.e., the start, middle, and end of the sequence. This emphasizes the value of using model foods as pure stimuli for mastication and explains why opposite conclusions were drawn from the observations of mastication adaptation when using various natural foods (Bishop et al. 1990; Gibbs et al. 1981; Horio and Kawamura 1989; Thexton et al. 1980).

It is clear from this study that changes in food hardness must be distinguished from changes in other food textural characteristics which also stimulate mastication. Hardness of food products has been stated to increase (Steiner et al. 1974; Thexton et al. 1980), decrease (Huang et al. 1993), or have no effect on frequency (Horio and Kawamura 1989). This work suggests that this variability depends in part on the rheological properties of the food since there are no (this study) or very little (Peyron et al. 2002) modifications of frequency in response to an increase in hardness with the elastic product, whereas a clear decrease in frequency was observed with increasing hardness for the plastic products. Multiple linear regressions performed in this study showed that the effect of hardness on masticatory frequency was only important during the initial stages of a masticatory sequence and that overall frequency is better described by the food type (i.e., elastic or plastic) than by the hardness. Plastic products were chewed at lower frequencies than elastic products. It is possible that the decrease in frequency was observed during chewing the plastic and not the elastic products simply because the range of hardness for the plastic foods was much greater than for the elastic foods, although this should have been accounted for by the ranking used in the MLR.

The multiple linear regressions performed on the entire sequence or on the three parts of the sequence also showed that rheological behavior was often more important than hardness for explaining the variability of closing or opening velocities and cycle duration. This is probably a direct consequence of the change in the amplitudes of the movements. The shapes of the masticatory cycles were very different when comparing chewing of elastic and plastic foods, notably the vertical and lateral amplitudes of mandibular excursions. Vertical amplitude was influenced by food hardness whereas lateral amplitude was unchanged by an increase in hardness irrespective of the rheological type. Both vertical and lateral amplitudes were the best descriptors to account for rheological changes in chewed food, at all stages of the masticatory sequences.

Finally, when studying the effect of an increase in hardness on the masticatory process, irrespective of the type of product used, EMG activity (per sequence or per cycle) is valuable to describe the changes that occur at any stage of the sequence. On the other hand, kinematic measurements for mandibular movements (frequency, amplitudes, velocities or durations of mandibular displacements) are recommended to better analyze the influence of changes in food rheological behavior on the adaptation of the masticatory function. For all cited kinetic parameters, rheological type was found to be a good descriptor in the middle of the sequence and this was particularly right at all stages of the masticatory sequence for vertical and lateral amplitudes.

This work investigates the different sources of variability of the masticatory process. Some of them, such as interindividual variability, are already known. The impact of food hardness on the masticatory parameters is also well described in the literature, but this new approach with different elastic and plastic model foods shows some important differences. Different adaptations in the masticatory parameters observed in response to changes in food characteristics shows that the adaptation of mastication is highly complex and that the modulation of the masticatory process occurs in response to many textural characteristics of the food and is certainly not limited to food hardness.

The overall masticatory pattern has been described to be the result of a set of command embedding both sensory feedback from the oral cavity relayed by the CPG and neural information from the cortical masticatory area (CMA). This study provides more evidence for the contribution of intraoral sensory feedback on the control of mastication. Our data clearly identified two types of physiological adaptations to the textural properties of foods. A change in the cycle shape had already been shown after mastication of different food types (Hiiemae et al. 1996), and an increased masticatory muscle force had already been observed to counteract an increasing food resistance occurring during the final part of the closing phase (Ottenhoff et al. 1992). These adaptations had never been shown to occur in the same experiment with the same subjects eating the same foods. Such responses to the textural properties of the food are known to be elaborated within the CPG, but different mechanisms have been proposed that all rely on cortical and/or peripheral inputs to the CPG (Lund and Kolta 2006; Thexton and Hiiemae 1997; Yamada et al. 2005).

From our data, it can be suggested that there are two control mechanisms involved, the first mechanism responsible for the adaptation to changes in the food rheological behavior and the second mechanism responsible for the adaptation to food hardness. First mechanism: the changes observed in the kinetic variables, while chewing either elastic or plastic foods, would be sustained by activation of different groups of neurons, located in the CMA, representing different patterns of mastication. There is of course no reason to believe that these different preprogrammed patterns of masticatory cycles would work in an all-or-none fashion. On the contrary, it is likely that an overlapping between them occurs, resulting in a continuum of different types of masticatory cycles, with a cycle-by-cycle adaptation to the continuous information arising from the mouth while the food is being processed (Lund et al. 1998). Grouping of neurons responsible for coordinated jaw, facial, and tongue movements (Yamada et al. 2005) exists in the cerebral cortex as suggested by the result of stimulations of different loci within the CMA that induce different preprogrammed patterns of mastication (Bremer 1923; Westberg et
al. 1998). A direct contribution of neural projections from the cerebral cortex to the CPG is also shown (Lund and Kolta 2006; Yasui et al. 1985). It has been proposed that cortical stimulations activate groups of neurons projecting to functionally similar groups of specialized interneurons in the CPG (Westberg et al. 1998). It has also been suggested that a programming muscle activity occurring during mastication may not be reliant only on the masticatory CPG but also on corticofugal influences (Sessle et al. 1999).

Second mechanism: in our study, an increase in food hardness, whatever the rheological properties, induced an enhanced muscle activity in the jaw closers. This echoes similar results obtained in rabbit where objects of progressive hardness placed between the teeth during experimental mastication induced a progressive increase in the EMG activities of jaw closing muscles, the harder the object, the larger the masseter activity (Lavigne et al. 1987; Liu et al. 1993; Morimoto et al. 1989). Interestingly, in a similar experimental condition, Hidaka et al. (1997) have also shown in rabbit that variables related to jaw closer EMG increased with hardness but kinematic variables did not. This suggests that a fast reaction automatically compensates for the load increase. This load-compensating reaction could depend on both the periodontal receptors and the spindle afferents of the jaw closer muscles which both project to the brain stem main nuclei forming the CPG. In this case, the sensory messages from the periphery would lead to an increased discharge frequency of the concerned group of CPG interneurons. Indeed, the denervation or anesthesia of periodontium and the lesion, in the mesencephalic nucleus, of the spindle afferent cell bodies reduced or nearly abolished the compensation for hardness (Ariyasinghe et al. 2004; Hidaka et al. 1997; Lavigne et al. 1987; Morimoto et al. 1989). The mechanism of the CPG activation by periodontal and spindle afferents is discussed. It may not rely directly on jaw stretch reflex but it appears to allow a positive feedback and feedback control of the jaw closer muscles by which a fast adaptation to hardness could be obtained within the ongoing chewing cycle (Hidaka et al. 1997; Ottenhoff et al. 1992; Peyron et al. 2002).

This elaborated dual hypothesis can be summarized as follows: a cortical and brain stem preprogrammed organization of different groups of neurons shapes the jaw movement to adapt to the rheological behavior of the food and a brain stem mechanism depending on ongoing inputs, triggered by the food being processed, automatically set a load-compensating reaction that adapts the muscle force to the resistance of the food. The first mechanism may mostly depend on the knowledge obtained before the introduction of the food inside the mouth through memory and visual or other sensorial cues. The second mechanism may mostly be a rapid reaction to a previously unplanned food property.

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