

## HUMAN JAW MOVEMENT IN MASTICATION AND SPEECH

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**Summary**—The study of jaw movement in humans is a primary source of information about the relationship between voluntary movement and more primitive motor functions. This study focused on the geometric form of the velocity function, as measured by linear voltage displacement transducer. Movement amplitudes, maximum velocities and durations were greater in mastication than in speech. Nevertheless, there were detailed similarities in the shape of the normalized velocity functions. In jaw-closing movements, the normalized functions were similar in form over differences in rate, movement amplitude (speech movements) and the compliance of the bolus (mastication). In opening movements, the functions for mastication and speech were again similar over differences in amplitude and compliance. However, they differed in shape for fast and slow movements. Normalized acceleration and deceleration durations were approximately equal in rapid movements, whereas, for slower movements, deceleration took substantially longer than acceleration.

### INTRODUCTION

The relationship in humans between voluntary movements, such as reaching, grasping and talking, and more primitive motor functions, such as locomotion or mastication, is central to our understanding of motor control. An important aspect is whether elements of basic or primitive movements form a foundation for voluntary behaviour and, if so, the identification of the neural and morphological components that are common to these different classes of behaviour. Evidence to date on the relationship between voluntary movement and primitive motor function has taken the form of parallels between the kinematic and electromyographic patterns of activities such as speech and those of variety of simpler motor tasks.

Such parallels do suggest a common design. The relative timing of the movements of the orofacial articulators in speech and of the limbs in locomotion is preserved over changes in rate in both speech and locomotion (reviewed by Grillner, 1981 and Tuller and Kelso, 1984). Likewise, in speech and locomotion, there are rapid phase-dependent compensations to perturbations during movement (e.g. Abbs and Gracco, 1984; Forssberg, 1979; Kelso *et al.*, 1984). Similar patterns of inter-articulator adjustment have also been reported, for example, in the achievement of spatial targets in physiologically reduced functions, such as the wiping reflex in the 'spinal' frog, and in the complex patterns of grasp and speech in the intact human (Fukson, Berkinblit and Feldman, 1980; Cole and Abbs, 1986; Gracco and Abbs, 1986).

The evidence here is indirect. Because there are physiological and biomechanical differences among the systems in which analogous behavioural patterns have been observed, it is difficult to specify the mechanisms whereby the similarity arises. A preferable alternative is to examine both classes of behaviour in a single multi-function articulator. Jaw

movements in humans are appropriate in this respect. Such movements are involved in wholly reflexive but naturally occurring behaviours such as suckling, swallowing, gagging and vomiting; in voluntary though primitive functions such as biting and mastication; and in the highly complex behaviours of speech, vocalization and oral manipulation. These behaviours share, to varying degrees, a common muscle architecture and histochemistry, as well as sensory, motor and reflex components (reviewed by Abbs and Cole, 1982; Dubner, Sessle and Storey, 1978; Lund, Appenteng and Seguin, 1982).

We have now examined the form of jaw movement through the manipulation of rate, movement amplitude in speech and the compliance of the bolus in mastication. The behaviours were assessed through the geometric form of the velocity function of the jaw. At issue was whether similar velocity functions would be observed in mastication and speech, and if so, the identification of their neural and biomechanical correlates (see Atkeson and Hollerbach, 1985; Flash and Hogan, 1985; Hollerbach and Flash, 1982; Munhall, Ostry and Parush, 1985; Ostry and Munhall, 1985; Ostry, Cooke and Munhall, 1987; Ruitenbeek, 1984; Soechting, 1984, for applications of velocity function analysis in motor behaviour).

### MATERIALS AND METHODS

Measurements of amplitude, duration, and maximum velocity in jaw movement were obtained during mastication and speech; opening and closing movements were both scored, and their onset and termination were identified by points of zero-crossing on the velocity records.

The movements were measured with a linear voltage displacement transducer (Trans-Tek 0243). This transducer consists of a light-weight circular transformer and a metallic core. The transformer

was held fixed relative to the upper skull by means of a modified hockey helmet. One end of the core was inserted into the transformer; the free end was fitted with a 1.5 cm plastic tip and then attached with two-sided adhesive tape to the subject's chin, just posterior to the mental notch. In obtaining measurements of either mastication or speech, the core changes position within the transformer, generating a voltage that varies linearly with its elevation.

The linear voltage displacement transducer was orientated to capture the principal direction of the motion of the jaw and thus to minimize the mechanical contact of the core with the transformer walls. A small-diameter core was used to allow additional freedom of movement. Thus, even though the transducer measured unidimensional movements only, there was little interference with the normal patterns of jaw movement. Subjects did not report loading of the mandible or the obstruction of its path of movement.

Masticatory movements were measured as subjects chewed unilaterally on various rubber tubes (dia. 1 cm). A thick-walled tube had 3 mm walls and a central aperture of 4 mm; a thin-walled tube had a thickness of 2 mm and a central aperture of 6 mm. Two thicknesses of tube were used in order to vary systematically the compliance of the bolus. Each subject was tested at two chewing rates (fast and preferred) and two compliances. For each of the two compliances, five 4-s trials were recorded in the fast condition and seven 4-s trials in the preferred-rate condition. Rubber tubing was used rather than natural food in order to reduce the variability of the masticatory pattern. The pattern observed was thus similar to that obtained after the initial breaking cycles during steady chewing (Luschei and Goldberg, 1981).

Movements of the mandible in speech were measured during repetitions of the syllable *ta* or *te* at two speech rates (fast and preferred). In the production of these syllables the jaw moves from an elevated position for the release of the alveolar consonant to an open or lowered position for the production of the vowel. For each syllable, five 4-s trials were recorded in the fast condition and seven 4-s trials in the preferred-rate condition.

Three subjects were tested in the study; none reported known neurological disorders or speech pathology. They were tested in four blocks of trials: speech, mastication, speech, mastication. In the speech blocks, the order of repetition of the syllables at the two speech rates was randomized. Similarly, in the mastication blocks, the order of trials with the thick- and thin-walled tubes at the two rates was randomized. In total, 48 trials were recorded for each subject.

The recorded jaw movements were low-pass filtered with a cut-off frequency of 30 Hz, then digitally sampled at a 1 kHz rate to 12 bits resolution. The data were then fit with natural cubic spline functions with the knots spaced at 16 ms intervals. Velocities were obtained from the spline-fitting programme.

#### *Computations from past studies*

In order to extend the scope of the findings, it was

decided to compute velocity functions from published records. These were position-time functions from studies whose focus was not the form of the velocity curve; the functions did not appear in the reports from which they were taken. The studies selected for further analysis were ones which involved rate manipulations in conjunction with a greater range of movement amplitudes, different shapes and size of bolus and different speech stimuli. This analysis also enabled a larger group of subjects to be examined. The published records of jaw position over time were photographically enlarged and digitized at 2 mm intervals. This corresponded to temporal sampling at rates ranging from 75 to 150 Hz. After the data had been digitized, they were filtered using a fourth-order, zero phase-lag, Butterworth filter; the cut-off frequency had a signal power of 40 dB below the maximum. The velocity and acceleration functions were calculated using second-order, forward difference equations.

## RESULTS

### *Kinematic comparison of mastication and speech*

The average kinematic measurements are shown in Table 1 for each subject separately; the data are for both opening and closing movements at fast and preferred rates. Overall, amplitudes, durations and maximum velocities were greater in mastication. In both behaviours, acceleration was generally less long than deceleration. However, in fast opening movements this difference was small and often accelerations were longer than decelerations.

The average duration of jaw movement was greater in mastication than speech ( $p < 0.001$ ). At the preferred rate, the average frequencies of mastication were 1.63, 1.42 and 1.42 Hz for subjects CL, KG and KM respectively. The comparable average frequencies for speech were 2.41, 2.23 and 1.93 Hz, again for CL, KG and KM. At the fast rate, average frequencies for mastication were 5.55, 3.72 and 2.67 Hz; the frequencies for speech were 5.92, 4.59 and 3.50 Hz, respectively. Thus, at both fast and preferred rates, jaw movements in speech were faster than those in mastication.

The compliance of the bolus affected the duration of the movement in a similar way for all subjects. It was less with the thick-walled (stiff) rubber tube than with the thin-walled (compliant) tube ( $p < 0.001$ , for KG and KM; CL showed a similar pattern but the difference was not reliable). In contrast, duration of movement varied in a non-systematic manner across subjects as a function of the vowel used in speech.

Movement amplitudes were greater in mastication than in speech ( $p < 0.001$ ). With one exception, such amplitudes were also greater at the preferred rate than at the fast rate ( $p < 0.001$ ; cf. Plesh, Bishop and McCall, 1987). Amplitudes were also assessed as a function of the compliance of the bolus in mastication and the vowel in speech. For all subjects, they were less in mastication of the thick-walled tube ( $p < 0.001$ ), and also less in speech for the syllable *te* ( $p < 0.001$ ).

Average maximum velocities were greater in mastication than in speech ( $p < 0.001$ , for all subjects).

Table 1. Kinematics of the mandible in mastication and speech.  $V_{\max}$  indicates maximum instantaneous velocity; acceleration = acceleration duration; deceleration = deceleration duration, SE are given in parentheses

	Opening		Closing	
	Fast	Normal	Fast	Normal
<i>MASTICATION</i>				
<i>Subject KG</i>				
Amplitude (cm)	0.52 (0.01)	0.63 (0.01)	0.51 (0.01)	0.63 (0.01)
$V_{\max}$ (cm/s)	9.46 (0.14)	7.05 (0.25)	8.00 (0.13)	3.51 (0.14)
Duration (ms)	120 (3.16)	275 (9.31)	149 (2.53)	428 (10.7)
Acceleration (ms)	72 (1.60)	110 (4.93)	46 (0.74)	126 (9.37)
Deceleration (ms)	48 (2.09)	165 (7.22)	103 (2.03)	302 (13.8)
<i>Subject KM</i>				
Amplitude (cm)	0.71 (0.02)	0.73 (0.02)	0.67 (0.02)	0.75 (0.02)
$V_{\max}$ (cm/s)	8.59 (0.24)	6.48 (0.20)	9.55 (0.25)	8.40 (0.49)
Duration (ms)	199 (4.34)	419 (21.0)	176 (2.71)	285 (14.1)
Acceleration (ms)	105 (1.80)	136 (9.40)	59 (1.15)	93 (5.60)
Deceleration (ms)	94 (4.73)	283 (16.4)	118 (2.51)	192 (13.4)
<i>Subject CL</i>				
Amplitude (cm)	0.12 (0.01)	0.53 (0.01)	0.14 (0.01)	0.54 (0.01)
$V_{\max}$ (cm/s)	3.59 (0.15)	6.92 (0.16)	2.74 (0.08)	4.23 (0.10)
Duration (ms)	76 (1.43)	260 (8.65)	104 (1.56)	355 (10.1)
Acceleration (ms)	44 (1.13)	83 (1.78)	40 (0.52)	79 (2.75)
Deceleration (ms)	33 (0.53)	176 (8.14)	65 (1.39)	276 (8.66)
<i>SPEECH</i>				
<i>Subject KG</i>				
Amplitude (cm)	0.20 (0.01)	0.26 (0.01)	0.20 (0.01)	0.26 (0.01)
$V_{\max}$ (cm/s)	3.96 (0.11)	3.15 (0.10)	3.53 (0.12)	2.28 (0.12)
Duration (ms)	104 (1.43)	202 (4.89)	114 (1.16)	246 (5.91)
Acceleration (ms)	46 (0.45)	79 (2.99)	54 (0.81)	120 (5.91)
Deceleration (ms)	58 (1.27)	124 (3.73)	60 (0.85)	126 (4.24)
<i>Subject KM</i>				
Amplitude (cm)	0.39 (0.01)	0.30 (0.02)	0.39 (0.01)	0.29 (0.01)
$V_{\max}$ (cm/s)	5.14 (0.13)	2.87 (0.15)	5.68 (0.14)	2.86 (0.17)
Duration (ms)	148 (1.34)	303 (14.5)	138 (1.73)	216 (7.73)
Acceleration (ms)	58 (0.75)	73 (1.99)	58 (1.08)	84 (5.77)
Deceleration (ms)	90 (1.35)	230 (14.9)	80 (1.09)	132 (5.11)
<i>Subject CL</i>				
Amplitude (cm)	0.13 (0.01)	0.22 (0.01)	0.13 (0.01)	0.22 (0.01)
$V_{\max}$ (cm/s)	3.09 (0.08)	2.78 (0.15)	2.80 (0.07)	3.32 (0.19)
Duration (ms)	79 (1.24)	197 (5.33)	90 (1.41)	218 (12.8)
Acceleration (ms)	44 (0.67)	61 (1.50)	36 (0.60)	78 (2.36)
Deceleration (ms)	35 (0.77)	136 (5.30)	52 (1.21)	140 (11.7)

The compliance of the bolus had systematic effects; higher maximum velocities were obtained for the thin-walled (compliant) tube ( $p < 0.001$  for KG and KM; a similar pattern was obtained for subject CL but the difference was not reliable). Similarly, for all subjects, maximum velocities in speech were greater for the large amplitude *ta* movement than for the smaller amplitude *te* movement ( $p < 0.001$ ).

Average maximum velocities of jaw opening and closing in mastication and in speech varied in a non-systematic manner in relation to the average amplitude of the movement. This finding is well known in studies of speech control (Ostry and Munhall, 1985). However, even though there was no relationship between the mean velocity and amplitude measures, reliable trial-by-trial correlations between movement amplitude and maximum velocity were obtained for opening and closing in both behaviours ( $p < 0.01$ ). A single exception was subject KG whose correlation was not significant for jaw-closing movements in chewing.

#### Velocity curves of mastication and speech

Figures 1 and 2 give ensemble averaged velocity curves normalized on both the horizontal and vertical axes. The normalization was carried out on the individual velocity functions before averaging. Jaw opening and closing movements are shown separately. The normalized curves for opening are presented in order of the duration of increasing relative acceleration (Fig. 1). In both mastication and speech, acceleration was shorter than deceleration at the preferred rate, whereas at the fast rate both had similar durations. Although the curves differ in form as a function of duration they are similar in shape for different movement amplitudes (syllables) in speech and for different compliances in mastication.

Figure 2 shows the averaged curves for the jaw closing, ordered as in Fig. 1. The curves for both mastication and speech tended to be asymmetrical, with deceleration being longer than acceleration. Otherwise, the curves were, at least to a first approximation, similar in form over differences in rate,

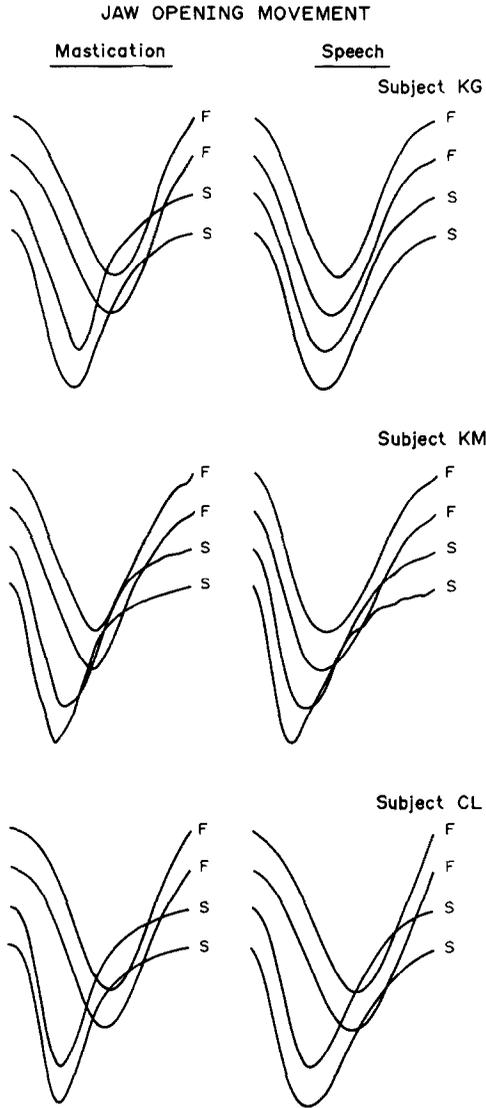


Fig. 1. Normalized, ensemble averaged, velocity functions for jaw-opening movements at two rates. F indicates fast movements; S indicates movements at the subject's preferred rate. There are two curves shown at each rate. In speech, these represent different movement amplitudes; in mastication, the curves are for different bolus compliances.

movement amplitude in speech and compliance in mastication. With the exception of jaw-closing movements in mastication for subject CL, the curves could not be classified on the basis of duration of movement.

The velocity curves were skewed to varying degrees; the skew was assessed by measuring the curves on a trial-by-trial basis to obtain the duration of acceleration and deceleration. The averaged durations and their standard errors are given in Table 1. With the exception of fast opening movements, the average duration of acceleration in both mastication and speech was less than that of deceleration. In fast opening there was no systematic pattern in the duration of movement.

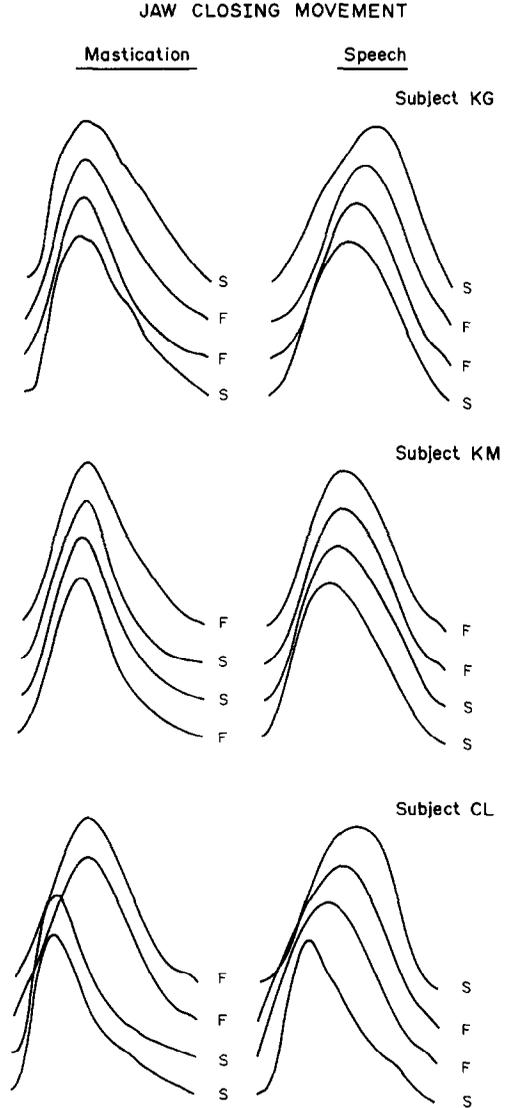


Fig. 2. Normalized, ensemble averaged, velocity functions for jaw-closing movements. F indicates fast movements; S preferred rate movements. Amplitude and bolus compliance were again manipulated.

Thus the velocity functions of mastication and speech were similar. For jaw-opening movements, both behaviours had a similar rate-dependent asymmetry. For jaw closing, the curves for both behaviours had a similar skew that was unrelated to rate of movement.

*Velocity functions computed from published data*

The functions for individual movements were normalized on both the horizontal and vertical axes. These functions were more variable than those of Figs 1 and 2, where ensemble averages are shown.

Jaw movements in humans during unilateral gum chewing were shown at a number of different chewing rates by Morimoto *et al.* (1984, their Fig. 1; see Plesh *et al.*, 1987, Fig. 4, for a similar pattern). The velocity

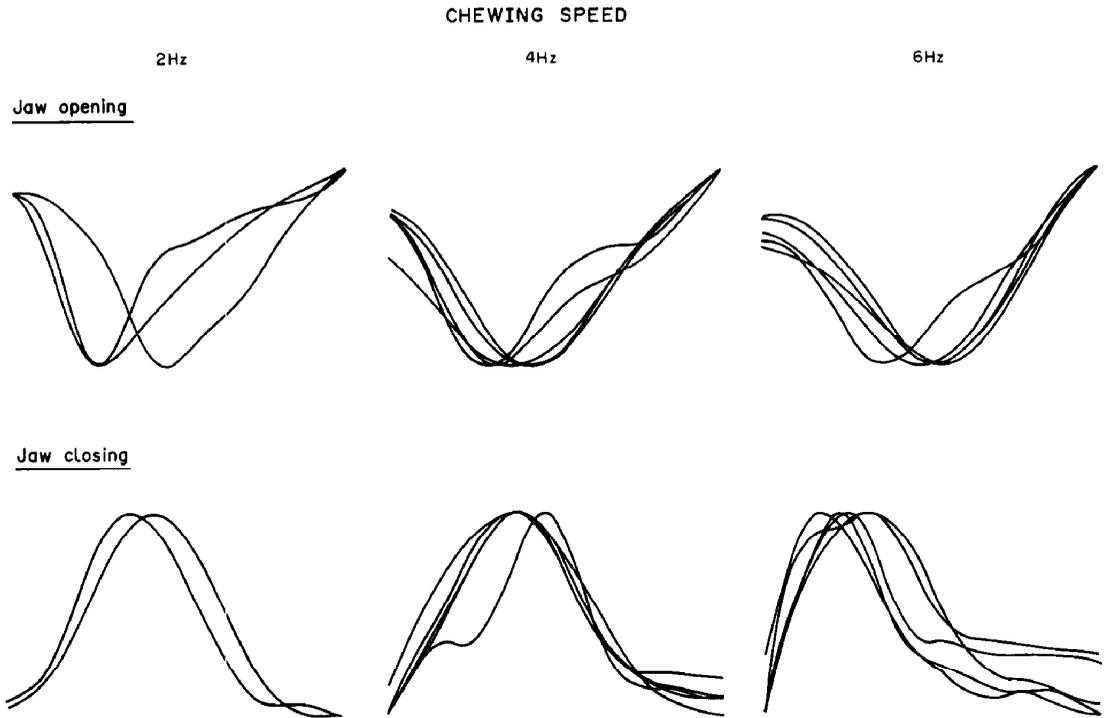


Fig. 3. Normalized, individual velocity functions for cyclic jaw movements during gum chewing at 2, 4 and 6 Hz, computed from data presented by Morimoto *et al.* (1984).

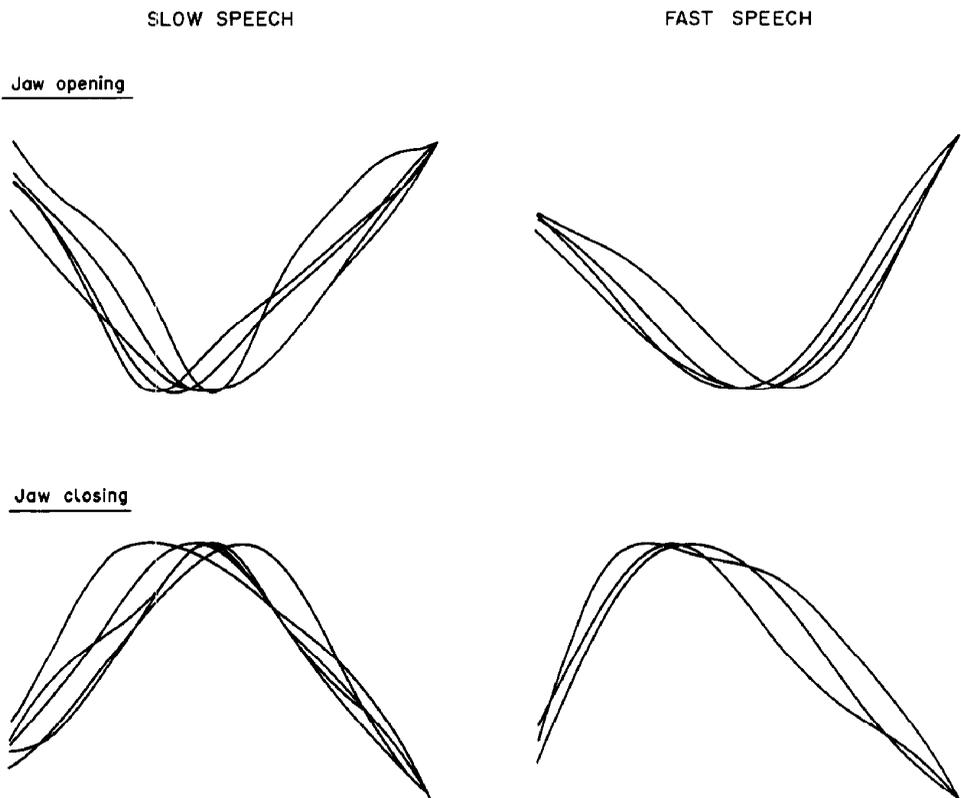


Fig. 4. Normalized, individual velocity functions during increasingly rapid production of the syllable *sa*, calculated from data presented by Nelson *et al.* (1984).

functions for 2, 4 and 6 Hz movements are given in our Fig. 3. Two aspects of the computed curves are of note. As we now observed, there was a rate-dependent asymmetry in the skew of the velocity function of jaw opening. The average proportion of time in the acceleration phase of the movement was 0.34, 0.37 and 0.48 at 2, 4 and 6 Hz, respectively. The velocity functions for jaw closing were likewise skewed. The average proportion in the acceleration phase of the closing movement was 0.39, 0.39 and 0.28 at 2, 4 and 6 Hz, respectively.

Jaw movement amplitudes in data from Morimoto *et al.* (1984) were in the range of 12–14 mm, larger than in Table 1. Indeed, a similar asymmetry was also present in Ahlgren's (1976) study (see below), in which subjects chewed carrots with movement amplitudes in the range of 20 mm. Thus, the skew of the velocity function of jaw-opening movements in mastication occurred over differences in both jaw-movement amplitude and the shape and size of the bolus.

The velocity curves of single utterances in speech have been reported by Nelson, Perkell and Westbury (1984; their Fig. 1) and by Kelso *et al.* (1985; their Fig. 3). In the Nelson study, jaw movements were measured while subjects produced increasingly rapid utterances of the syllable *sa*; our Fig. 4 shows computed velocity functions for selected fast and slow movements; the pattern was similar to that observed by us. In jaw opening, the velocity functions were more skewed in the slow condition than in the fast. The average proportion of time in the acceleration phase was 0.42 for slow movements and 0.52 for fast. In jaw closing, the velocity function was skewed at both rates, with the average proportion of time in the acceleration phase being 0.44 and 0.30 in slow and fast movements, respectively.

A similar pattern was reported by Kelso *et al.* (1985), whose subjects recited a known passage in which they substituted only *ba* or only *ma* for each syllable. This so-called re-iterant speech preserves the metrical (rhythmic) structure of speech but not its other characteristics. In that study the average proportion of time in the acceleration phase of jaw opening was 0.42; in jaw closing, it was 0.36.

Thus the functions for jaw-opening movements in speech have a similar rate-related asymmetry; the functions for closing movements are likewise skewed. Our findings can therefore be extended to a wider range of syllables and to passages that preserve the normal rhythmic structure of speech.

In another example (Ahlgren, 1976), it was not possible to compute directly the velocity functions. However, a quantitative assessment of the duration of acceleration and deceleration in jaw opening and closing during carrot chewing in humans could be made using Ahlgren's Figs 15.1–15.4, which show the movement of the mandible in the frontal and sagittal planes with equal time intervals indicated. The skew of the velocity function was established by determining the number of intervals in the acceleration and deceleration phases of the movement. In the 13 jaw-opening movements measured, acceleration in both planes was shorter than deceleration in all but one case (in 5 cases measurements could not be made in the sagittal plane because of difficulty in following

the curves). In the jaw-closing movements a similar pattern emerged. In all but one case, the jaw-closing movements were shorter in acceleration than deceleration (Ahlgren, Figs 15.1, 15.3, 15.4); the jaw-closing movements shown in the remaining figure have the opposite pattern. Ahlgren's data indicate that the asymmetry of the velocity function of jaw opening was characteristic of jaw movements that differ greatly in amplitude. Moreover, in mastication the asymmetry at normal chewing rates was apparently present in both the lateral and vertical motion of the jaw.

Thus, the computed velocity functions for mastication and speech were similar to ours, suggesting that the findings are characteristic of a larger subject population, a greater range of movement amplitudes, different shapes and size of bolus, and movements that preserve the temporal structure of normal speech.

## DISCUSSION

### *Velocity curves*

For both the opening and closing movements of the mandible, the velocity functions for mastication and speech were similar in shape and varied in similar ways with changes in rate. The similarity was present in spite of large and systematic differences in amplitudes, velocities and movement durations. The compliance of the bolus in mastication and the identity of the vowel in speech did not affect the form of the velocity function in a systematic way. The normalized velocity functions were generally skewed. In opening movements, the extent of the skew varied as a function of rate. Acceleration was shorter than deceleration in slow movements, whereas in fast movements the durations were more nearly equal. In jaw closing, the skew was not rate dependent.

Analysis of published records of mastication and speech gave comparable results. Patterns similar to ours were found for both the opening and closing movements of the mandible over differences in movement amplitude, shape and size of bolus and the nature of the speech movements. The analysis also indicated that our findings are characteristic of the movement patterns of a much larger subject population. In the sections which follow, we explore possible determinants of the similarity of velocity functions of mastication and speech. The discussion focuses on jaw-opening movements that occur primarily along the axis of measurement. A direct comparison of closing movements in mastication and speech was not undertaken because jaw closing in mastication involves lateral movements not adequately measured in our study.

### *Electromyography of jaw muscles*

The muscle activation patterns in mastication are described by Moller (1966, 1976; see Dubner *et al.*, 1978; Luschei and Goldberg, 1981, for summaries). The average activation profiles of all jaw muscles are skewed so that a period of gradually increasing activity is followed by a shorter period of decreasing activity. For jaw openers, Moller (1966) found that activity on the ipsilateral side during unilateral chew-

ing reached a maximum at 60, 54 and 54% of the duration of their total activity for the digastric, lateral pterygoid and mylohyoid muscle respectively. For jaw closers, the same activity reached a maximum at 74, 76, 71 and 63% of the total duration for the anterior and posterior temporalis, masseter and medial pterygoid respectively (Moller, 1966; Hannam *et al.*, 1977; Gay and Picuch, 1986).

The implication here is that in both opening and closing at normal speeds, jaw muscle activity and jaw movement velocity are differently skewed. Whereas muscle activity on average reaches a maximum after the half-way point of the total duration, velocity on average reaches a maximum during the first half of the movement. Thus, it seems unlikely that asymmetry in the velocity curves of jaw movement arises strictly as a consequence of the timing of EMG activity in jaw muscles.

In jaw-closing movements, some of the decoupling of the EMG and velocity patterns results from contact with the bolus, which slows the jaw at the same time as the EMG activity in the jaw closers is increasing in order to break up the food. In the case of jaw opening, Moller (1966) has shown that the activity in the medial pterygoid begins just before the end of the movement. However, the deceleration of jaw opening begins well before the onset of jaw-closer muscle activity and hence cannot be attributed solely to the activity of the antagonistic muscles.

In contrast to studies of mastication, there is some evidence from studies of jaw muscle activity at normal speech rates that the asymmetry in the velocity function arises from a corresponding asymmetry in the EMG activity. Gentil and Gay (1986) showed that there is a general tendency for both opening and closing muscles to be most active early in their representative phases of movement. This was quantified for jaw closers by Folkins (1981), who found that peak activity occurred within 10–100 ms after the beginning of jaw closing for all muscles. There is insufficient evidence at present to determine whether this is also true for the jaw openers in speech.

In spite of some differences in the muscle activation patterns of mastication and speech, there are a number of similarities: the activity in temporalis, masseter and medial pterygoid tends to peak at the same time in mastication and speech, whereas the onset of medial pterygoid activity tends to lead that of masseter and temporalis (Folkins, 1981). However, jaw muscles in speech have a more temporally restricted pattern of activity and hence there is less overlap between opening and closing muscles (Gentil and Gay, 1986).

#### *Afferent input*

During jaw opening in mastication, there is a powerful excitation of the muscle spindle afferents of jaw-closing muscles (Goodwin and Luschei, 1975). Nevertheless, such muscles are electrically silent during the jaw-opening phase. Goldberg and Tal (1978), Goldberg, Chandler and Tal (1982), and Nakamura and Kubo (1978) provide evidence that the silence is the result of post-synaptic inhibition of jaw-closer motoneurons. In their studies, intracellular recordings of trigeminal motoneurons were made during both spontaneous jaw movements and cortically

evoked movements in the guinea pig and cat. In both cases, activation of the digastric muscle coincided with hyperpolarization of jaw-closer motoneurons. The absence of activity in the jaw closers during jaw opening is consistent with the relatively long deceleration phase.

#### *Biomechanical properties of muscles*

Unlike in arm movements, in which the force developed in antagonistic muscles acts to decelerate the limb, in jaw opening in mastication there appears to be little active antagonistic muscle activity for deceleration. Thus, in opening, it seems likely that the deceleration is through the elastic and viscous loads that oppose the movement, that is, loads due to the stretch and rate of stretch of the jaw closers. Some evidence consistent with this possibility has come from human arm movement: positively skewed velocity functions have been obtained in wrist flexion against both viscous and elastic loads (Stein, Cody and Capaday, 1988), but for movements against inertial loads, there were symmetrical functions. The implication is that our skewed velocity functions for preferred-rate jaw-opening movements may be related to the properties of the load-opposing movement.

The jaw can be seen as a linear second-order system in which opening movements are produced by shifting the equilibrium (target) position. The net force that produces opening depends on the difference between the actual and equilibrium position as well as the velocity and acceleration of the movement. The jaw closers are modelled as a viscous spring that resists the opening movement. It can be shown that faster jaw-opening movements can be produced by increasing the stiffness of the openers; the stiffness and viscosity of the closers are assumed to be constant. (The model assumes step or ramp changes in the equilibrium position.) This model can account for the skewed velocity functions observed during preferred-rate opening movements as well as the greater symmetry observed in faster movements.

There are six degrees of freedom for jaw movement in primates, three associated with the opening/closing, protrusion/retrusion and lateral motion of the mandible and three with the motion of the hyoid bone (Otten, 1987). Accordingly, the movement of the hyoid bone may contribute to the asymmetry of the velocity function of the jaw. The hyoid moves in a systematic manner during jaw movements in both mastication and speech. An extensive report of such movement in speech is provided by Perkell (1969; also see Westbury, 1989).

In mastication in humans, the hyoid moves upward and forward during jaw opening and in the opposite direction during closing (Pancherz, Winnberg and Westesson, 1986). The movement during opening is presumably a result of the attachment of the suprahyoid muscles to both the hyoid and the mandible. More complex patterns of hyoid motion in humans have also been reported (Thexton, Wallace and Ebbs, 1976). In speech, the pattern of hyoid movement depends largely on the identity of the vowel. For vowels such as *e* and *a*, as used here, the hyoid moves upward and forward during jaw opening (Perkell, 1969), a pattern similar to that in mastication. How-

ever, for high vowels such as *i* and *u*, it moves in the same direction as the jaw, dropping during the jaw-opening movement for the vowel. For the low vowels, *e* and *a*, the consequence of this hyoid movement is to shorten the vocal tract, thus raising the frequency of the first acoustical energy formant and lowering the frequency of the second (Perkell, 1969).

We have thus identified a number of physiological and biomechanical factors that appear to influence the shape of the velocity functions of mastication and speech. The asymmetry of the function for preferred-rate opening, as well as the more symmetrical curves for faster opening, may result from the elastic, viscous and inertial characteristics of the jaw system. Changes in the form of the velocity function, accompanying increases in movement speed, may result from increasing the stiffness of the jaw openers. For jaw closing, the asymmetry in mastication is due in part to the deceleration imposed by contact with the bolus. In speech there is some indication that the asymmetry is coded directly in the pattern of electromyogram activity in the jaw-closing muscles. A direct comparison of closing movements in mastication and speech was not attempted because in mastication these have substantial lateral components that were not measured.

Issues of interpretation may be raised because of the movement amplitudes in mastication and the nature of the speech task. In mastication, these amplitudes were somewhat less than those previously reported. However, they were appropriate to the size of the bolus, and this was well within the range of normal food particles. Thus, the movement amplitudes were presumed to be normal.

In the speech task, a simple utterance was used. Although it is clear that such utterances lack the lexical, syntactical and metrical structure of natural language they entail a set of co-ordinations and timings that are quite different from those in mastication. Production of these sounds requires, in addition to the movement of the mandible, the co-ordination of the tongue, jaw, lips, velum, hyoid bone, pharyngeal wall, vocal folds and lungs. Although it is fair to refer to this as a reduced task in comparison to natural speech, the reduction does not eliminate the need for temporal and spatial co-ordination that distinguishes it from mastication. The advantage of using these reduced stimuli was that the co-articulation environment could be held constant across successive segments. Thus the changing contextual effects that characterize normal speech were eliminated. This is acceptable in studies whose focus is not the mechanisms of serial order.

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