

**EVIDENCE THAT THE HUMAN JAW STRETCH REFLEX  
INCREASES THE RESISTANCE OF THE MANDIBLE TO  
SMALL DISPLACEMENTS**

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SUMMARY

1. Small 'step' or sinusoidal displacements were imposed on the mandible while human subjects maintained an average biting force of 10 N. Phase-related changes in the force resisting sinusoidal displacement were used to determine the mechanical stiffness of the human mandibular system as a function of the frequency of stretching.

2. Jaw-muscle electromyographic (e.m.g.) responses to 'step' stretches were of 8 msec latency and generated a very substantial force response. Jaw-muscle e.m.g. responses having longer latency were not observed.

3. The mechanical stiffness of the human mandible was relatively constant as a function of the frequency of stretching, having a typical magnitude of about 15 N/mm ( $\pm 200 \mu\text{m}$  stretch) or 10 N/mm ( $\pm 1500 \mu\text{m}$  stretch) at mean biting forces of 10 N. The force resisting displacement was phase-advanced at all frequencies.

4. Modulation of jaw muscle electrical activity evoked by sinusoidal stretches increased in amplitude as a function of increasing stretch frequency. E.m.g. modulation was 60–100 degrees advanced at frequencies of 1–10 Hz, but the phase decreased at higher frequencies, becoming negative (lagging stretch) at frequencies of 30 Hz and above. These characteristics are consistent with the idea that the jaw stretch reflex is dependent on jaw muscle spindle afferent fibres exciting jaw-closing motoneurons by relatively direct (but not necessarily monosynaptic) connexions.

5. The relationship between jaw-muscle activity and voluntary fluctuations of isometric biting force suggests that human jaw muscles can be modelled as a second-order linear 'filter'. The corner frequency for human jaw muscle is about 3 Hz; thus it would appear to be considerably slower than jaw muscle of monkeys.

6. The *reflex* stiffness of the human mandible, estimated quantitatively on the assumption that human jaw *muscle* stiffness is similar to the intrinsic stiffness of the gastrocnemius of the cat, ranges between 5 and 9 N/mm at frequencies between 1 and 8 Hz. Since this reflex stiffness is about the same as muscle stiffness in this frequency range, we conclude that the stretch reflex of the human mandible contributes functionally to its postural stability.

7. Reflex stiffness appears to be greater in the monkey mandible relative to muscle stiffness than in the human mandible. The difference is argued to be a manifestation of the difference in jaw muscle contraction speed between the two species.

8. The fact that the mandibular stretch reflex appears to be stronger than the stretch reflex of the limbs of intact animals and humans is discussed in terms of the special anatomical and functional features of the mandible.

#### INTRODUCTION

Not many years ago, it seemed reasonable to conclude that relatively direct synaptic connexions of afferents from muscle spindles play a major role in maintaining postural stability in the face of disturbing influences. The view was based originally on the pioneering observations of Liddell & Sherrington (1924) on the stretch reflex of the decerebrate cat. The anatomical and neurophysiological features of this system, described over several decades of investigation, tended to support the concept at least circumstantially since the system included all of the elements essential for reflex regulation of muscle length.

More recently, however, the concept has been considerably weakened. In studies of the reflex responses to limb displacements in intact animals and humans, investigators have found that long-latency responses, perhaps involving cortical circuitry, are far more effective in generating significant forces to restore the limb position than the initial monosynaptic response (Crago, Houk & Hasan, 1976; Marsden, Merton & Morton, 1976; Melvill Jones & Watt, 1971; for general review, see Desmedt, 1978). Responses elicited in human leg muscles by disturbances of posture have a latency of about 100 msec and can be suppressed within a few trials if inappropriate; that is, if they would tend to destabilize the subject further (Nashner, Woollacott & Tuma, 1979).

While the demise of the simple muscle-length-servo interpretation of the spinal stretch reflex has had the desirable effect of focusing attention on new studies and several new interpretations of the function of these reflex connexions (Allum, 1975; Binder & Stuart, 1980; Botterman, Binder & Stuart, 1978; Houk, 1979), it is probably as yet unwarranted to suggest that the stretch reflexes mediated by direct spinal connexions have *no* function in resisting displacements of the limbs. In at least one neuromuscular system, that controlling the mandible, it appears that the direct connexions of muscle spindle afferent fibres are capable of producing very significant resistance to displacement. Lamarre & Lund (1975) found that merely loading the mandible of human subjects during a closing movement, without actually stretching the jaw-closing muscles, elicited a vigorous, short-latency electromyographic (e.m.g.) response in these muscles. The response had the same latency as the response to a rapid phasic stretch, and since the afferents of jaw muscle are known to make monosynaptic connexions to the motoneurons (Hugelin & Bonvallet, 1957; Kidokoro, Kuboto, Shuto & Sumino, 1968; Appenteng, O'Donovan, Somjen, Stephens & Taylor, 1978), it is reasonable to conclude that the loading response was monosynaptic. Lamarre & Lund (1975) did not observe any longer-latency responses after the initial, presumably monosynaptic, response. Goodwin, Hoffman & Luschei (1978) measured the resistance of the monkey's jaw to imposed sinusoidal displacements during a controlled isometric bite and concluded from data obtained before and after destruction of the muscle spindle afferent fibres that resistance to displacement from reflex modulation of muscle activity was much larger than that due to muscle stiffness at stretch frequencies between 3 and 10 Hz.

In the present investigation we used sinusoidal displacements of the human jaw during an isometric bite to determine whether humans, like monkeys, have a reasonably strong stretch reflex. That this is so is suggested by the vigorous e.m.g. responses to loading or stretch of jaw-closing muscles (Lamarre & Lund, 1975); however, the actual contribution of reflex-modulated muscle activity to resistance of the jaw to displacement can only be evaluated with respect to the stiffness contributed by the contracting muscle. With the monkey, it was possible to determine directly the inherent muscle stiffness by abolishing the reflex (Goodwin *et al.* 1978). Since this could not be done with human subjects, we used, instead, the results of an experiment on the stretch reflex of the hindlimb muscles of the decerebrate cat (Rosenthal, McKean, Roberts & Terzuolo, 1970) to estimate the intrinsic stiffness of the human jaw muscles. The stretch reflex of the human jaw appears to contribute significantly to the stability of the mandible, particularly at low frequencies of displacement, but its contribution relative to that provided by muscle stiffness is smaller than that found in the monkey. The basis for this difference and a comparison with the results obtained in studies of displacements of human limbs are our main points of discussion.

#### METHODS

*Subjects.* Five males, ages 29–48, with healthy natural teeth and Class I (normal) occlusion served as subjects. Three of the subjects were the authors, and two of them were tested on repeated occasions. Additionally, limited testing, which produced results very similar to those reported, was conducted on a male of 10 and a female of 22.

*Apparatus.* The subjects produced incisal biting forces across a pair of stainless-steel beams. The upper beam was short and was rigidly attached to an immobile framework. The longer, lower beam was hinged at a point 24 cm distal to the end where biting force was applied. It was attached to a powerful electromagnetic linear actuator (LTV Ling Altec Ltd, Model 408) at its midpoint by a precision rotational bearing. Forces applied to the lower beam were sensed by resistance-wire strain gauges bonded to the beam between the attachment of the actuator and the incisal biting point. The position of the lower beam was sensed at a point 6 cm from the biting point by a small tungsten light bulb and an optical position sensor (United Detector Technology, PIN SC/10). We used the signals from the position sensor to control the power amplifier supplying current to the actuator and to record the movements of the lower beam. This mechanical servo system produced constant-amplitude sinusoidal displacements against the loads used in this experiment at frequencies up to 80 Hz for  $\pm 200 \mu\text{m}$  displacements, and up to 50 Hz for 1500  $\mu\text{m}$  displacements. Its stiffness was 50 N/mm. Most of the compliance was in the actuator and the control system rather than in the beam between the position sensor and the biting point, however, so changes in the position signal, which were used for calculation of the jaw stiffness, were a good representation of the actual displacements applied to the mandible.

Surface e.m.g. potentials were detected from the right and left masseter muscles of each subject by Ag-AgCl disk electrodes attached to the skin with adhesive collars. They were amplified by isolated differential amplifiers having bandpass characteristics of 20 Hz–5 kHz. All data were recorded on an FM instrumentation tape recorder (DC to 2.5 kHz) and were subsequently displayed and analysed with conventional devices and a Raytheon minicomputer.

*Procedure.* The subject was seated in a dental chair with height and tilt adjusted to enable him to produce a comfortable incisal bite (interincisal distance of 13 mm) across the beams of the jaw-displacement servo. An impression of the incisors was made in dental acrylic attached to the biting surface of the beams. It enabled the subject to reproduce the biting position and also distributed the mechanical forces on the teeth. The biting force was displayed on an oscilloscope placed in front of the subject. When displacements were applied to the mandible, the subject adjusted biting 'effort' to keep the force fluctuations produced by the displacements centred about a line on the oscilloscope representing the desired biting force. Masking the oscilloscope after the subject had produced the appropriate force and asking him to keep 'effort' constant

did not affect the results. One might suspect that the subjects could voluntarily 'track' the force response at low frequencies of displacement and thereby control jaw stiffness. At frequencies of 2 Hz and above such tracking was reported by the subjects to be totally impossible, but at displacement frequencies of 1 and 2 Hz, the subjects could affect the results by pacing their voluntary bites to the displacements. Attempts to increase or decrease jaw stiffness by such pacing, however, produced extremely variable results. In contrast, asking the subject to keep his 'effort' constant, to make only the periodic adjustments necessary to keep the force fluctuations centred about the desired biting force, produced very consistent measures of stiffness for any particular subject. We cannot prove the point, but we believe that our measures of stiffness at low frequencies of displacement (1 and 2 Hz) were not affected by 'voluntary' responses of the subjects.

Sinusoidal jaw displacements ranging in amplitude (half peak-to-peak) from 50 to 1500  $\mu\text{m}$  at frequencies of 1, 2, 3, 5, 8, 10, 12, 15, 17.5, 20 and 30 Hz, and 50–200  $\mu\text{m}$  additionally at frequencies of 40 and 50 Hz, were applied at biting forces of 2–30 N. After pilot experiments, we elected to use amplitudes of 200 and 1500  $\mu\text{m}$  at a biting force of 10 N as our standard test for all subjects. Step (square-wave) displacements at amplitudes of 100 and 200  $\mu\text{m}$  and a frequency of 1 Hz were also used with all subjects. At frequencies above 3 Hz 150 continuous cycles were applied, and at frequencies of 1, 2, and 3 Hz 100 cycles were applied. The subject was allowed to rest between tests of frequencies.

In an additional experiment, two subjects were asked to modulate their biting force, in the absence of jaw displacement, in rhythm with an audio oscillator, the output of which was sinusoidally modulated at low frequencies (0.1–4 Hz). They kept the mean force at approximately 10 N and produced a modulation of about 3 N, which was approximately the force change produced by 200  $\mu\text{m}$  displacements. The purpose of this experiment was to determine the transfer function between the e.m.g. and force modulation in the absence of stretch. Voluntary force modulation at frequencies above 4 Hz proved to be very difficult, so the relationship between e.m.g. and force fluctuations for frequencies of 5–16 Hz was determined from the normal tremor that occurred when the subjects maintained a steady (not purposely modulated) isometric biting force of 10 N. The isometric force tremor of the human jaw, like that of the monkey jaw (Goodwin *et al.* 1978), is composed of a relatively broad spectrum of frequencies.

*Data processing.* We used a computer program to determine the average force, position, and rectified (but unfiltered) e.m.g. of each of the masseter muscles across two-cycle intervals (5 Hz and above) or a one-cycle interval (3 Hz and below). The computer program was triggered by a timing pulse from the wave form generator used to drive the jaw-displacement servo. Typical examples of these averages are illustrated in Fig. 1B; each average is for fifty cycles. Examination of records produced on a direct writing oscillograph did not reveal any obvious serial dependency of consecutive cycles; thus, basing the average on two out of every three cycles or on alternate cycles was not deemed to make any significant difference. We used a Fourier Transform algorithm to compute the fundamental sinusoid at the displacement frequency for each of the average variables, together with the zero-order harmonic, or mean value. We then used the amplitude and phase of the calculated sinusoids and their mean values to compute the stiffness of the jaw (the amplitude of the force modulation divided by the amplitude of the displacement), the relative modulation of the e.m.g. (amplitude of the e.m.g. modulation divided by its mean value), and the phase of the force and e.m.g. modulation with respect to the displacement. At frequencies of less than about 15 Hz e.m.g. modulation was reasonably sinusoidal (see Fig. 1B), but of course contained far more harmonic distortion than the force or position records. Above 15 Hz it often decreased to zero for a portion of the cycle. Therefore, fitting the e.m.g. response with a sinusoid, by the Fourier Transform algorithm, resulted in unreliable estimates of the amplitude of e.m.g. modulation (since the sinusoid could take negative values). The peak of the calculated sinusoid generally corresponded well with the peak of the e.m.g. response in these instances of non-linearity, however, so we believe that this procedure still produced a reasonable estimate of the phase, or timing, of the reflex response to displacement.

We analysed the data obtained by having the subject voluntarily modulate his biting force at various frequencies to determine the gain and phase relationship between e.m.g. and force modulation in the absence of stretch by sampling a single cycle on the averager at an interval corresponding to the tracking frequency. If, for example, the subject was 'pacing' a 1 Hz

modulation, the computer was set for a sweep interval of 1 sec, and then the sweep was randomly triggered by the experimenter. The fundamental sinusoids of the force and rectified e.m.g. were calculated and noted, and then another cycle was sampled. Ten cycles were analysed at each frequency. It was not critical that the force modulation be sinusoidal or at exactly the desired frequency; the point was to have a large fundamental. To analyse frequencies above 4 Hz, we sampled 1 sec intervals of the force 'noise' produced by the subjects and computed the 5th through 16th harmonic of the force and e.m.g. records. The magnitude and phase of the force/e.m.g. relationship obtained on the ten samples at each frequency were averaged and plotted on log-log co-ordinates. This procedure yielded a result (the transfer characteristic of a critically damped second-order linear system) that is very similar to the results of experiments in which other techniques were used for obtaining the transfer characteristic of muscle (Mannard & Stein, 1973; Rosenthal *et al.* 1970).

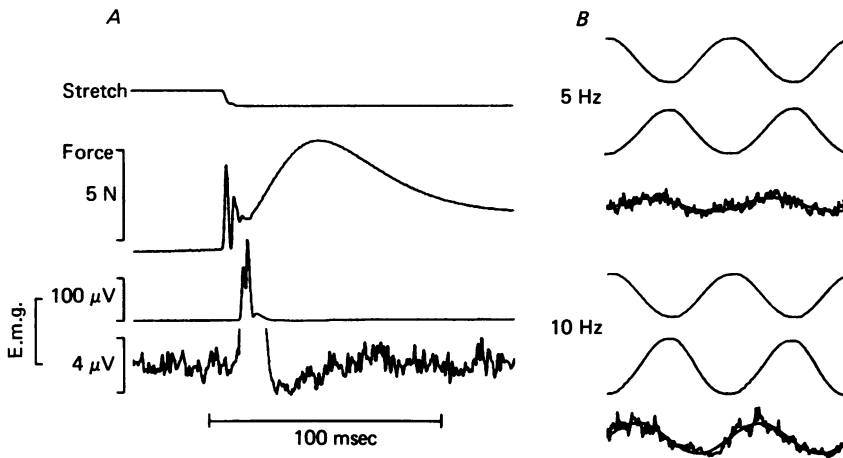


Fig. 1. Averaged records of position, force, and rectified e.m.g. of the right masseter muscle of a human subject during  $200\ \mu\text{m}$  'step' jaw displacements (A) and  $\pm 200\ \mu\text{m}$  sinusoidal displacements at 5 and 10 Hz (B). Downward displacement of the position signal represents an increase in the interincisal distance (note that position signal is top trace of each set in B). Upward displacement of the force trace represents an increase in biting force. A and B have the same force calibration and were obtained with a mean biting force of about 10 N. E.m.g. response in A is displayed at two gains, the main response to displacement being truncated in the lower record. The smooth line drawn through the e.m.g. responses in B is the calculated fundamental at the displacement frequency. The e.m.g. modulation in these records is approximately  $\pm 25$  and  $\pm 50\%$  of the mean e.m.g. level at 5 and 10 Hz, respectively. Averages are based on 50 sweeps.

## RESULTS

### Responses to 'step' displacements

A record of the force and e.m.g. response to a  $100\ \mu\text{m}$  downward displacement of the mandible that is typical of all but one of the subjects is shown in Fig. 1 A. An initial transient force response, with zero latency, was produced by the short-range stiffness of the muscle and the mass of the mandible. A large transient e.m.g. response, which produced a very substantial force response having the general appearance of a muscle twitch, occurred about 8 msec after the beginning of stretch. The

force then decayed to a level somewhat higher than that preceding the stretch. Usually there was some depression of the e.m.g. immediately after the initial response, which could have been produced by a variety of mechanisms, such as late inhibition or motoneuron synchronization, but there were never any consistent or significant late peaks of activity.

In one subject the e.m.g. and force responses produced by 'step' stretches were quite small compared with those for the other subjects. We repeatedly tested this subject, using a variety of biting positions and even totally anaesthetizing the upper and lower incisors and lip, but the response to 'step' stretches remained small.

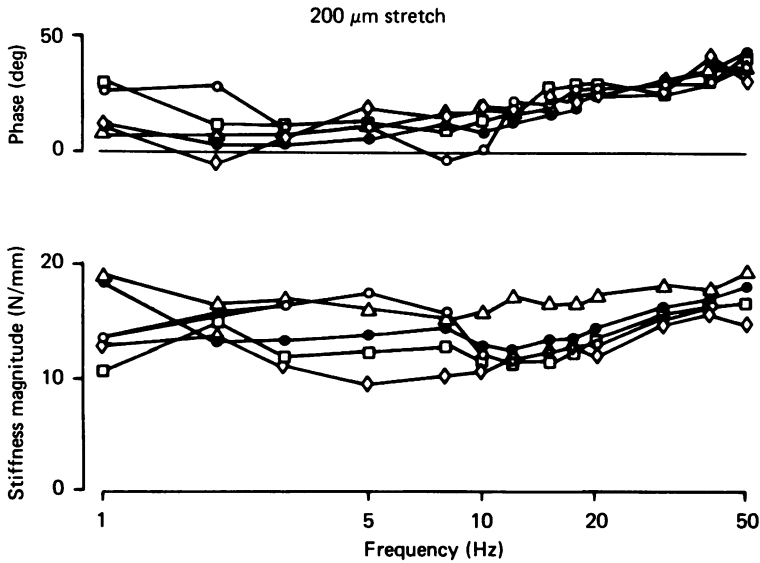


Fig. 2. Magnitude and phase of jaw stiffness of five human subjects as a function of the frequency of sinusoidal stretching. Stretch amplitude was approximately  $\pm 200 \mu\text{m}$  and mean biting force was 10 N at all frequencies. The characteristics of jaw muscle e.m.g. modulation occurring during the determination of these data are shown in Fig. 3.

#### *Jaw stiffness measured with sinusoidal displacements*

The forces and e.m.g. responses observed during sinusoidal displacements were temporally locked to the movements at all frequencies and amplitudes for all subjects. We never observed the phenomenon of surface e.m.g. responses on alternate cycles reported for human calf muscles by Rack, Ross & Walters (1979), or sustained oscillations after the servo was turned off as observed in the human ankle by Agarwal & Gottlieb (1977).

The stiffness of the jaw as a function of the frequency of sinusoidal stretching at small amplitudes (approximately  $200 \mu\text{m}$ ) is illustrated in Fig. 2 for each of the five main subjects. The magnitude of stiffness was relatively constant for all subjects, the values ranging between 10 and 20 N/mm. There was intersubject variation between

1 and 10 Hz but considerable consistency among four of the subjects at higher frequencies. Two of the subjects, data for which are represented in Fig. 2 by open triangles and filled circles, were tested on repeated occasions and the differences between them illustrated in Fig. 2 were always present. The open triangles represent data from the subject who produced only weak responses to 'step' displacements of the mandible. The phase of stiffness was almost always positive; i.e. the force response reached a peak somewhat before the maximum downward displacement of the

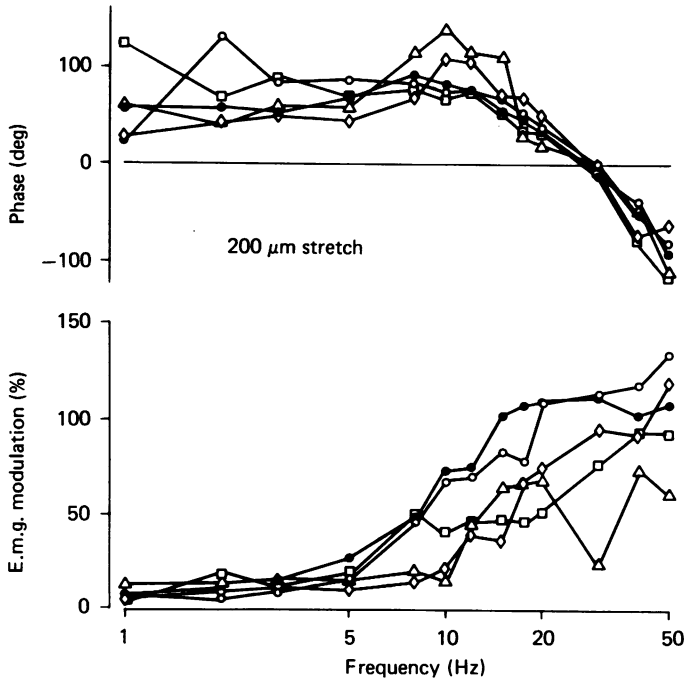


Fig. 3. Magnitude and phase of modulation of the e.m.g. activity of the right masseter muscle of five human subjects as a function of the frequency of sinusoidal stretching (magnitude expressed as percentage of mean level). Stretch amplitude was approximately  $\pm 200 \mu\text{m}$  and mean biting force was 10 N at all frequencies.

jaw. Intersubject variation was apparent, but the general trend was for a gradual decrease and then an increase in the phase of stiffness from the lowest to the highest frequencies.

The characteristics of e.m.g. modulation during sinusoidal jaw displacement are illustrated in Fig. 3. The great intersubject variation at high frequencies was probably not due to random measurement error since consistent differences were seen between the two subjects tested repeatedly (open triangles and filled circles). A comparison of Figs. 3 and 5 will also show that differences between subjects were generally ordered the same for different amplitudes of stretch. The phase of the e.m.g. modulation was positive up to frequencies of 30 Hz for all subjects but tended to 'roll-off' at higher frequencies, a characteristic that would be expected from a reflex having a short fixed delay. We would stress that the phase was reasonably

consistent between subjects, did not have any marked discontinuities, and was substantially advanced on jaw position for frequencies below 20 Hz.

In Figs. 4 and 5 are illustrated the stiffnesses and e.m.g. modulations for the five subjects during high-amplitude (approximately  $1500\ \mu\text{m}$ ) stretches. The main features are similar to those shown in Figs. 2 and 3, but the magnitude of stiffness is more consistent across the subjects and is lower than that seen with small stretches.

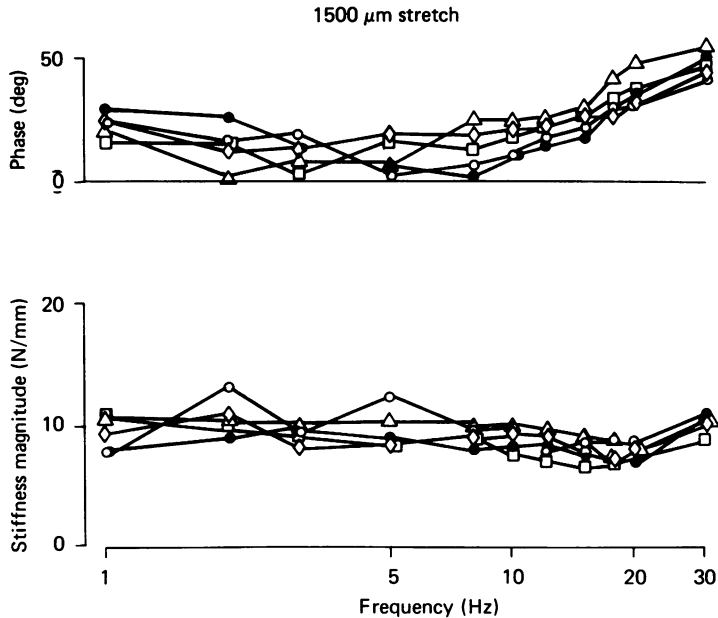


Fig. 4. Magnitude and phase of jaw stiffness of five human subjects as a function of the frequency of sinusoidal stretching. Stretch amplitude was approximately  $\pm 1500\ \mu\text{m}$  and mean biting force was 10 N at all frequencies. The characteristics of jaw muscle e.m.g. modulation occurring during the determination of these data are shown in Fig. 5.

Except for a small decrease in stiffness between 10 and 30 Hz, the magnitude of stiffness of the jaw was about 10 N/mm at all frequencies. Also, the modulation of the e.m.g. at low-frequency, large-amplitude stretches was very substantial. With low-frequency, small-amplitude stretches, e.m.g. modulation could only be detected by averaging; but with large stretches, it could readily be seen on raw records at all frequencies of stretching.

#### *Transfer characteristic of human jaw muscles*

Estimates of jaw muscle 'speed' based on the contraction times of average motor unit twitch responses of humans (Goldberg & Derfler, 1977; Yemm, 1977) and monkeys (Clark, Luschei & Hoffman, 1978) suggest that the jaw muscle of humans is considerably slower than that of monkeys. The difference could account for the major differences in the characteristics of jaw stiffness between these two species (see Discussion). To obtain an estimate of the transfer characteristic of the muscle



actually used by the subjects to produce the bite response at the levels of force we had been using, we compared the gain and phase of the force and e.m.g. modulation associated with voluntary bite force modulation in the absence of stretch (see Methods).

Fig. 6 illustrates the results of our analysis compared with the transfer characteristic of a critically damped second-order linear system having a corner frequency

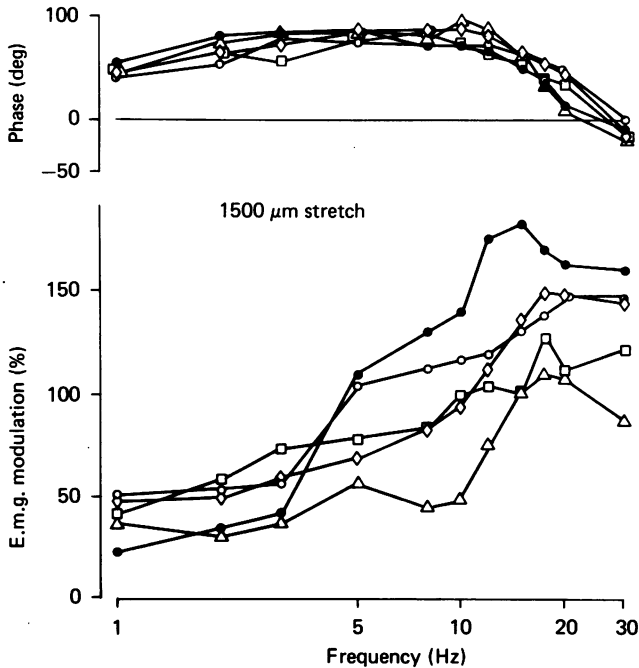


Fig. 5. Magnitude and phase of modulation of the activity of the right masseter muscle of five human subjects as a function of the frequency of sinusoidal stretching. Stretch amplitude was approximately  $\pm 1500 \mu\text{m}$  and mean biting force was 10 N at all frequencies.

of 3 Hz. The fit to the data, particularly for those frequencies for which we had large fundamental harmonics for both the e.m.g. and force modulation (5 Hz and below), seems quite reasonable. A similar analysis for the monkey, with natural tremor as input 'noise' (Goodwin *et al.* 1978), yields a second-order transfer characteristic but with a corner frequency of about 10 Hz. These observations support the contention that the jaw muscle of humans is considerably slower than that of monkeys.

#### DISCUSSION

##### *Estimates of the relative contributions of reflex stiffness and muscle stiffness*

The stiffness of a neuromuscular system, treated as a vector, can be defined to be equal to the sum of two other vectors, muscle stiffness and reflex stiffness (Rosenthal

*et al.* 1970). In our experiment the magnitude and phase of stiffness of the intact jaw were determined. If either the reflex or muscular stiffness were known, the other, unknown stiffness could be calculated by vector arithmetic. In the study by Goodwin *et al.* (1978) the stretch reflex could be eliminated and the muscle stiffness directly measured (the stiffness observed in active but unmodulated muscle). We do not have direct information on the muscle stiffness of human jaw muscles, but it seems possible at least to estimate its magnitude and phase, as a function of frequency, from other experiments.

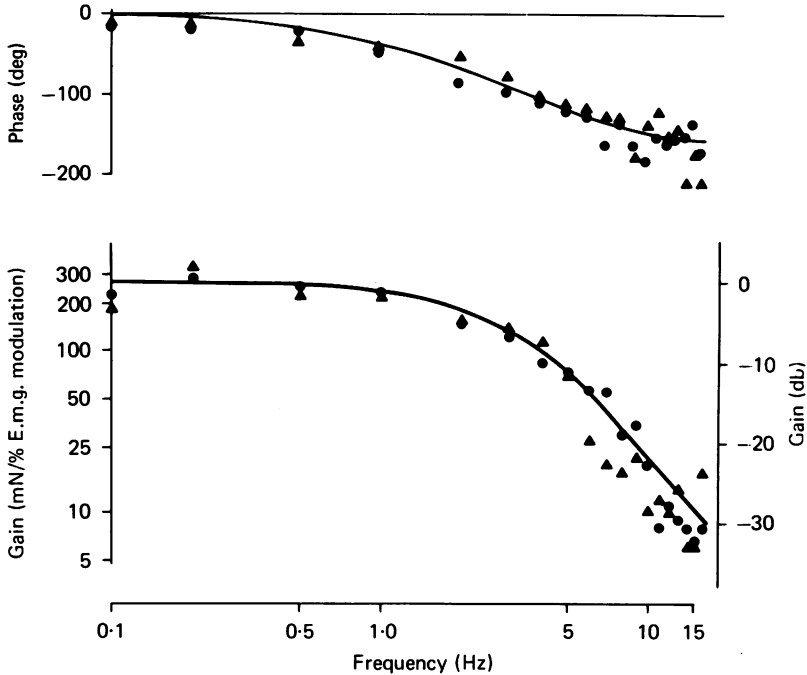


Fig. 6. Gain and phase relationship of fluctuations of isometric biting force and jaw muscle e.m.g. at frequencies between 0.1 and 16 Hz for two human subjects. Continuous line through the data points is the transfer characteristic of a critically damped second-order linear system with a corner frequency of 3 Hz. The mean biting force was approximately 10 N. At the higher frequencies force lags behind and is markedly attenuated relative to the modulation of jaw muscle activity; i.e. the jaw muscle 'filters' its neural input.

The short-range stiffness of muscle is very likely to be due to distortion of the cross-bridges formed between the thin and thick filaments of muscle (see discussion in Rack & Westbury, 1974). If we assume the mechanical properties of cross-bridges in different species to be similar, then the muscles in different animals ought to exhibit the same short-range stiffness if they are producing the same force and are subjected to the same amplitude and frequency of stretch. The dependence of stiffness on the frequency of stretch may be related to the contraction speed of the muscle, however. The stiffness of the monkey jaw muscle changes much more as a

function of the frequency of small sinusoidal stretches (Goodwin *et al.* 1978) than the stiffness of cat hindlimb muscle does (Rosenthal *et al.* 1970). For this reason, and because the human jaw muscle appears to be considerably slower than that of monkeys, we used data derived from the study of the gastrocnemius of the cat (Rosenthal *et al.* 1970) to estimate human jaw muscle stiffness. The gastrocnemius of the cat has a transfer characteristic very similar to that of human jaw muscle (compare Fig. 6 with Fig. 23 from Rosenthal *et al.*).

Using the data from Fig. 6 of Rosenthal *et al.* (1970), we estimate that the magnitude of muscle stiffness of the human jaw decreases at a rate of 5.5 db/decade and its phase is positive and constant in the frequency range from 1 to 30 Hz. Nearly constant phase of muscle stiffness has been observed in both the cat gastrocnemius (Rosenthal *et al.* 1970) and in the monkey jaw muscles (Goodwin *et al.* 1978). The data do not preclude some frequency-dependence of the phase, but it appears to be relatively small, and for simplicity, we have assumed it to be negligible. Fitting the data for the cat gastrocnemius to those for the human jaw requires one assumption: at a sufficiently high frequency the 'filtering' property of muscle attenuates the reflex stiffness to negligible values even though the e.m.g. modulation is large. Certainly in the monkey, the reflex stiffness of the jaw was negligible at frequencies well above the corner frequency of the muscles. We therefore assume that in the human the jaw stiffness at 30 Hz and above is entirely due to muscle. Thirty Hz is a decade above the corner frequency of the human jaw muscles (Fig. 6), so even if the e.m.g. had increased by 20 db, the response of the muscle would still be attenuated by about 20 db, given the transfer characteristic of our Fig. 6. Given these assumptions and the data from Rosenthal *et al.* (1970), we estimate the phase of human jaw muscle stiffness for frequencies below 30 Hz to be the same as that observed at 30 Hz, and its magnitude to be the same as that observed at 30 Hz, but decreasing for lower frequencies at a rate of 5.5 db/decade. Using these estimates, one can calculate reflex stiffness by subtraction. The results of this calculation are shown in Fig. 7, along with the observed total muscle stiffness.

The properties of the reflex stiffness illustrated in Fig. 7 were derived without reference to measures of the e.m.g. other than its use in estimating the transfer characteristic of the human jaw muscles. Given a reflex stiffness and the transfer characteristic of the muscles involved, one may ask what the magnitude and phase of the input to the muscles would have to be to produce this reflex stiffness. If the properties of the reflex stiffness we have derived are reasonable, there should be some correspondence between the theoretically necessary input to the muscle and e.m.g. responses evoked by the stretch stimuli.

The results of such a comparison are shown in Fig. 8. For small amplitudes of stretch, there is generally a good fit between the magnitude and phase of the e.m.g. modulation and the theoretical input to the muscle necessary to produce the derived reflex stiffness. For large stretches, the phases are reasonably close, but the magnitude of the measured e.m.g. modulation would not appear to increase with frequency nearly as fast as would be necessary to overcome the attenuating properties of the muscle. There are several possible reasons for this discrepancy, the most parsimonious being that our measure of e.m.g. modulation, when it is large (as it is with large stretches), fails to reflect accurately the input to the muscles.

Despite the discrepancy of the magnitude of the e.m.g. modulation for large stretches, we interpret the results of this analysis to indicate generally that our estimate of reflex stiffness is consistent with the observed e.m.g. modulation. Clearly, a reflex with an output that is significantly phase-advanced on muscle length and with a gain that increases with increasing frequency of stretch (a reflex driven by a

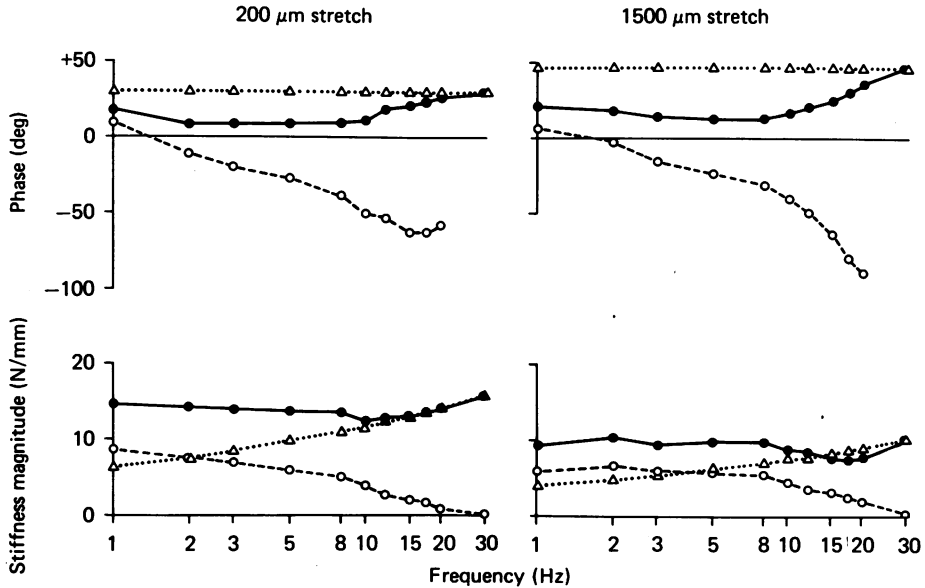


Fig. 7. The magnitude and phase of measured jaw stiffness (average of five subjects) is shown as a continuous line (average,  $n = 5$ ). The estimated muscle stiffness is the dotted line, and the calculated reflex stiffness is the dashed line. Amplitude:  $\pm 200 \mu\text{m}$  (left) and  $\pm 1500 \mu\text{m}$  (right). Assumptions involved in using the data from Rosenthal *et al.* (1970) on the muscle stiffness of the gastrocnemius muscle of the cat to estimate the stiffness of human jaw muscle are discussed in the text. Reflex stiffnesses were obtained by vectorial subtraction of the estimated muscle stiffness from the measured stiffness of the jaw for each frequency. The mean biting force used in determining the jaw stiffness was 10 N. The phase of calculated reflex stiffness at 30 Hz is undefined since the magnitude of reflex stiffness at 30 Hz is, by assumption, zero.

receptor having a sensitivity to velocity) could compensate for the 'filtering' properties of muscle and extend the range of frequencies over which the stretch reflex can generate a significant resistance to stretch. Of course, such a point has been made previously by Poppele & Terzuolo (1968).

#### *Differences between the jaw stretch reflexes of humans and monkeys*

The curve describing the stiffness of the jaw of the intact monkey as a function of the frequency of stretching is quantitatively quite different from that of the human jaw. The magnitude of stiffness of the monkey jaw is greatest at frequencies between 5 and 10 Hz. It falls to small values for lower frequencies. The curve has a large and consistent 'dip' at frequencies between 10 and 30 Hz. The magnitude of stiffness of

the human jaw is quite constant down to frequencies of 1 Hz, and the curve has only the mere suggestion of a 'dip' between 10 and 20 Hz. The phase of monkey jaw stiffness is similar to that of human jaw stiffness when tested with large stretches, but it becomes negative over a range of frequencies when tested with small stretches. That is, the force resisting displacement lags behind displacement. As originally noted by Joyce, Rack & Ross (1974), a force response that lags behind stretch

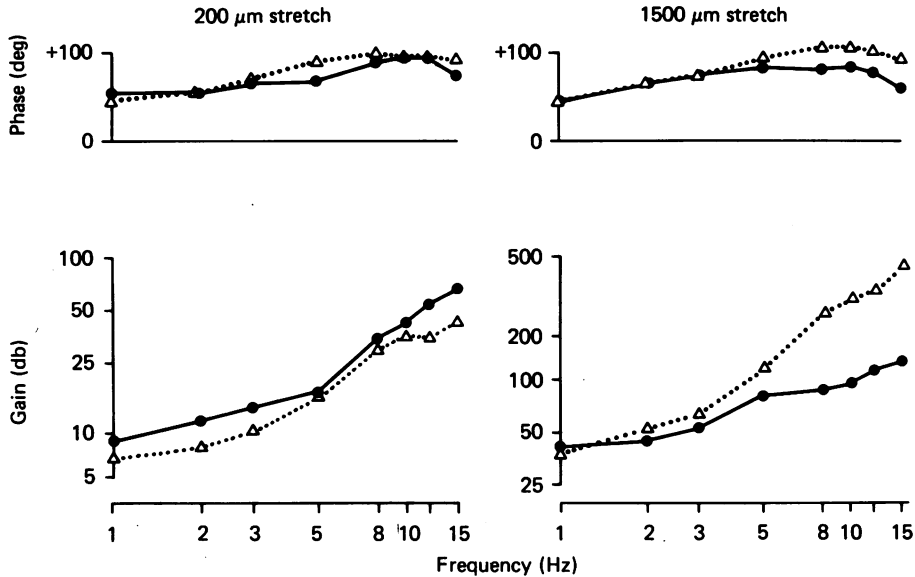


Fig. 8. Magnitude and phase of the measured e.m.g. modulation (●—●) (average,  $n = 5$ ) as a function of the frequency of stretching compared with the input to human jaw muscle ( $\Delta \cdots \Delta$ ) theoretically necessary to produce the calculated reflex stiffness ( $\circ \cdots \circ$  of Fig. 7). It is assumed in this analysis that the human jaw muscle has the transfer characteristic of the critically damped second-order linear system shown in Fig. 6 and that reflex stiffness is a manifestation of modulation of muscle activity 'passed' through this 'filter'. It is also assumed that the transfer characteristic of muscle, determined under isometric conditions, is not changed when muscle is stretched at small amplitudes.

represents work being done on the stretcher by the limb and therefore must necessarily be due to a strong reflex response of the muscles. A negative phase of stiffness is due to a large reflex response that is delayed by conduction time in the afferent and efferent pathways and the 'filtering' properties of muscle. To produce a negative phase of jaw stiffness, however, the lagging reflex response must be large relative to that produced by muscle stiffness at a given frequency. If, in the human, the reflex stiffness, relative to muscle stiffness, is as great as it is in the monkey, there should have been a frequency at which a negative phase of jaw stiffness could have been produced. Since we could not produce a significant negative phase of jaw stiffness in the human with any combination of mean biting force, frequency, and amplitude of stretching, we conclude that the reflex stiffness of the human jaw compared with its muscle stiffness, is significantly lower than in the monkey.

If our estimates of the relative magnitudes of reflex and muscle stiffness represented in Fig. 7 are correct (an analysis that is independent of the line of reasoning discussed above), we would conclude that in the human, the muscle stiffness over the range of frequencies tested is greater than in the monkey (perhaps because the muscles are slower) and the reflex stiffness less.

Since the amplitude and phase of jaw muscle e.m.g. modulation in the monkey are basically similar to those in humans (Goodwin *et al.* 1978), it does not seem likely that the difference in reflex stiffness is due to the stretch reflex *per se*. It seems more likely that the difference is a manifestation of the difference in muscle 'speed' of these two species. In both species, the e.m.g. modulation increases as frequency is increased. In the human the increase does not produce an increase in reflex stiffness because the muscle response is attenuated significantly for frequencies above 3 Hz. In the monkey, however, the attenuation does not become a major factor until 10 Hz is reached; thus the increased input to the muscle at stretch frequencies from 3 to 10 Hz causes a large increase in reflex stiffness in this frequency range.

In summary, we believe that the main quantitative differences in the characteristics of jaw stiffness between the human and monkey can be accounted for by the difference in contraction speed of the jaw muscles between these two species. If this analysis is generally correct, it emphasizes the need to consider muscular contraction dynamics as an important determinant of how much reflexes can contribute, relative to intrinsic muscle stiffness, to postural stability.

#### *Synaptic mechanisms of the jaw stretch reflex*

As noted in the Introduction, afferents from muscle spindles in jaw closing muscles are known to make monosynaptic excitatory connexions to motoneurons of jaw closing muscles. It is reasonable, then, to suggest that the initial e.m.g. response evoked by 'step' stretches is monosynaptic. We did not note any significant peaks of activity following the initial response, so we conclude that a transient stimulus of this type does not evoke activity in long-reflex pathways. Our observations in this regard support those of Lamarre & Lund (1975). The phase and gain characteristics of the jaw muscle e.m.g. modulation produced by sinusoidal stretches are similar to those of modulation of muscle spindle primary afferent firing produced by sinusoidal stretch of cat hind limb muscles (Goodwin, Hulliger & Matthews, 1975; Hulliger, Matthews & Noth, 1977). We therefore think that muscle spindles are the receptors involved in the jaw stretch reflex. There is, however, no way one can be sure that the relevant reflex loop is monosynaptic. Appenteng *et al.* (1978) concluded that the monosynaptic input to cat jaw muscle motoneurons from muscle spindle afferent fibres is relatively weak and have suggested that multisynaptic pathways are perhaps more important for functional responses to stretch.

In our study, the manner in which the phase of e.m.g. modulation decreased for high-frequency stretches suggests that the total delay time in the reflex evoked by sinusoids is relatively short, but such a measure is obviously going to be insensitive to the delays introduced by a few additional synapses. The fact that one individual exhibited a weak response to 'step' stretches but seemed to have a strong reflex when tested with low-frequency sinusoids suggests that the synaptic mechanism tested by these two techniques may be different. We would regard polysynaptic

reflex pathways as a likely possibility but would suggest that such pathways are probably confined to the brain stem. At the very least, one can suggest that the cortex is probably not involved in a direct manner since stimulation of the face area of the precentral cortex of monkeys very predominantly produces short-latency suppression of activity in jaw closing muscles (Clark & Luschei, 1974; Hoffman, 1977). Neurons in this cortical region are affected by sinusoidal stretches of the mandible of monkeys (Hoffman, 1977), but they are only driven effectively by amplitudes and frequencies of stretch well in excess of those necessary to produce a strong stretch reflex.

#### *The human jaw stretch reflex compared with the spinal stretch reflex*

The main conclusion derived from our experiment is that the stretch reflex of the human jaw is strong enough to make a substantial contribution to its postural stability. 'Step' stretches, as illustrated in Fig. 1A, produce in most individuals a vigorous e.m.g. response capable of generating a large force response. Small sinusoidal stretches produce phase-related changes in jaw muscle activity over a range of frequencies of functional importance and, granted certain assumptions about the mechanical properties of human jaw muscle, appear to make a significant contribution to the total mechanical stiffness of the jaw. For large stretches at frequencies between 1 and 8 Hz, we estimate that the reflex stiffness is about the same as muscle stiffness; i.e. the human jaw is considerably stiffer with the reflex than it would be without it.

The mechanical properties of the stretch reflex of the hind limb muscles of the decerebrate cat, determined by imposition of small sinusoidal stretches (Rosenthal *et al.* 1970), are very similar to those of the human jaw stretch reflex. That the properties of the intact reflex were the same in the two experiments implies that the reflex stiffnesses were also about the same. This similarity suggests the possibility that the jaw stretch reflex is basically similar to spinal stretch reflexes when they are freed from the influences of descending neural pathways. Nichols & Houk (1976) have shown that the stretch reflex of the decerebrate cat can compensate for the complex behaviour of muscle when it is pulled beyond the range of 'short-range' stiffness. Houk has incorporated these observations in terms of a more general hypothesis (Houk, 1979), that the function of spinal reflexes evoked by muscle stretch is to maintain the mechanical stiffness of limbs relatively constant. Our observations on the human jaw stretch reflex are consistent with this view although we have used stretch amplitudes that have generally not evoked the highly non-linear 'yield' of muscle when it is pulled beyond its short range (Rack & Westbury, 1974). On the other hand, the stiffness of the intact monkey jaw varies considerably as a function of the frequency of stretch, and for both the monkey and human, the magnitude of stiffness varies with stretch amplitude and mean biting force. Although these latter observations are at variance with the details of Houk's hypothesis, we believe that they do support the general idea that the stretch reflex can compensate for some of the inadequacies of muscle as the sole mechanism for resisting displacements.

The decerebrate cat is a perfectly legitimate preparation in determining what the stretch reflex *can* accomplish, but the study of intact normal subjects is required for

the actual contribution from the stretch reflex to postural stability to be determined. As noted in the Introduction, it appears now that compensatory responses to transient displacements of the limbs depend on long-latency responses. Sinusoidal displacements of the arm (Joyce *et al.* 1974) and sinusoidal force-loading of the ankle (Agarwal & Gottlieb, 1977) of humans have, however, indicated that reflexes capable of following fairly high frequencies can influence the mechanical characteristics of these limb systems. Unfortunately, there is a narrow range of frequencies at which the stiffness of the limb reaches a minimum value. When the human arm is loaded with the appropriate mass, the reflexes can produce sustained high-amplitude oscillations (Joyce & Rack, 1974). These results dramatically illustrate that strong reflexes having long conduction delays that operate on limbs having to move large masses can lead to postural instability rather than stability.

In terms of mechanisms of postural stability, the mandible may be a rather special 'limb' of the body that can, with impunity, utilize relatively simple reflex pathways. The only natural disturbing forces that it is likely to encounter are those associated with acceleration of its mass during locomotion (i.e. walking, running, and jumping). The 'goal' of this stability is invariant: to keep it from bouncing up and down to prevent uncontrolled and possibly traumatic tooth contact. For a person in the modern world, where tooth loss is not a matter of great concern, such a role for the jaw stretch reflex may seem somewhat trivial. In the world in which we and other animals evolved, however, proper functioning of teeth was critical to the survival of the individual. It may also be worthwhile to note that the mechanisms that keep the mandible stable do not have to interact with the rest of the body, and that it is difficult to think of a natural situation in which it would be appropriate for higher control systems to suppress the stretch reflex to minimize the stiffness of the jaw. Another aspect of the mandibular control system that makes simple high-gain reflexes feasible is that the short-conduction pathway for the jaw stretch reflex makes the frequencies of potential instability much higher than the frequencies of input to which the jaw muscles can respond effectively.

From a functional standpoint, a simple, strong, stretch reflex may be quite inappropriate as a mechanism for providing postural stability of the limbs. In the first place, the 'goal' of postural stability is not ordinarily one of keeping the length of a particular muscle constant; it is rather to keep the body from falling over. As emphasized by Nashner *et al.* (1979), interlimb co-ordination is absolutely essential to maintenance of stance posture, and the response patterns must be quite flexible since there are many types of destabilizing perturbations. In some instances, a strong stretch reflex would only tend to produce further destabilization. Given the complexity of the requirements for successful responses to disturbances of the limbs, it seems reasonable that the 'gain' of the stretch reflex would ordinarily be low compared with the 'gain' of higher-order systems, leading to what Crago *et al.* (1976) have called 'triggered reactions'.

Although the considerations discussed above provide some rationale for the apparent weakness of simple stretch reflexes of the limbs compared with the stretch reflex of the mandible, they are not meant to imply that these limb reflexes have no function at all. Muscle receptors and their reflex connexions could act, as suggested by Binder & Stuart (1980), to control the activity of motor units in such a way as to



compensate for internal disturbances of the muscle. At the same time, they could, as suggested by Houk (1979), make the response of a muscle to stretch more linear than it would be otherwise. Limb muscles must be allowed to lengthen appreciably in many circumstances to maintain stability, and the higher-order control of this process may be facilitated if the stiffness of the muscle-reflex system remains uniform during the extension, rather than falls abruptly as the muscle is extended beyond its short range.

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