MS 2268, pp. 323–331 Journal of Physiology (1994), 476.2

Stretch reflexes in human masseter

Andrew V. Poliakov and Timothy S. Miles

Department of Physiology, The University of Adelaide, Adelaide, SA 5005, Australia

1. The reflex response to stretch in most contracting human muscles includes both a short-latency, probably monosynaptic, excitatory component, and a longer-latency, polysynaptic excitation. However, it has been claimed that stretch of the jaw-closing muscles evokes only the short-latency response in masseter. This question was re-examined, using controlled stretches of varied rates and durations.
2. Very brief, rapid stretches analogous to the stimuli used to investigate the 'jaw-jerk' reflex in earlier studies evoked a prominent excitatory peak in the electromyogram at monosynaptic latency excitation, but little or no longer-latency excitation. This response could be produced even by stimuli that were barely detectable by the subject. However, this prominent electrical response did not produce a measurable increase in biting force.
3. In contrast, slower stretches evoked both a short- and a longer-latency excitatory response in the surface electromyogram, as in most limb muscles. It is shown that the absence of a long-latency excitatory response in earlier studies can be explained by the powerful reflex disfacilitation of the motoneurones that occurred at the end of the brief stretches used. Depending on the duration of the stretch, this disfacilitation is often sufficient to mask or abolish the long-latency reflex.
4. The reflex response to stretches was not markedly affected by blocking the activation of mechanoreceptors around the teeth with local anaesthetic, indicating that receptors around the teeth cannot be playing more than a minor role in the response.
5. The stretch-induced increase in force became greater as the velocity of the stretch decreased.

The jaw muscles are similar in many ways to the limb muscles, but their neural organization has specific adaptations to their particular functions. Like many limb muscles, the muscles of mastication have a postural role, maintaining the mandible in a fairly constant position relative to the maxilla at rest, and resisting the force of gravity during locomotion and other movements (Lund, Drew & Rossignol, 1984). However, the major motor function of the masticatory muscles in man is to break food down into particles of a size that can be swallowed. The jaw-closing muscles are capable of powerful contractions (e.g. Gibbs, Mahan, Lundeen, Brehnanan, Walsh, & Holbrook, 1981), and have a higher mechanical advantage than most limb muscles because they act directly across the joint without the interposition of long, flexible tendons between the muscle and the bones. The masticatory muscles exert force in one direction only, i.e. jaw closing; they rarely work against a load during opening. They must also function under some important constraints which differ in several ways from those for the limb muscles. The jaw-closing muscles exert powerful forces over very short distances to break down food, and the teeth are an immovable end-point to jaw closing. The teeth themselves pose the second important constraint. They are anatomically adapted to cut and to crush food; however, the nearby lips and cheeks can easily move into the path of the teeth during chewing, and be damaged. These factors make it critical for the movements of the jaws during chewing to be precisely controlled.

In most investigations of the stretch reflexes of the jaw muscles, the stimulus has been a tap on the chin with a tendon hammer to elicit the so-called 'jaw-jerk' reflex (e.g. Godaux & Desmedt, 1975; Murray & Klineberg, 1984). The few studies in which controlled stretch of the jaw-closing muscles has been used to evoke stretch reflexes include those of Marsden, Merton & Morton (1972), Lamarre & Lund (1975) and Cooker, Larson & Luschei (1980) in humans, and Goodwin, Hoffman & Luschei (1978) in monkeys. The characteristic response of most limb muscles to stretch is an initial burst of excitation at monosynaptic latency, followed by a more sustained excitation at longer latency. The longer-latency response is believed to be the result of a transcortical pathway (Marsden *et al.* 1976, Wiesendanger & Miles, 1982; Matthews, 1991). However, these earlier investigations of the stretch reflexes of the jaw-closing muscles have concluded that, in contrast to most limb muscles, the human jaw-closing muscles respond to stretch only with a short-latency excitatory reflex. This is an intriguing difference between the limb and the jaw muscles, especially as it is the long-latency component of the stretch reflex that is believed to have the greater functional significance in the co-ordinated response to muscle stretch (Gielen, Ramackers & van Auylen, 1988). This issue was reinvestigated in the present study.

METHODS

The experiments were conducted with the approval of the Ethics Committee for Human Experiments at The University of Adelaide. The subjects were ten volunteers aged 18–46, including the authors, who gave informed consent and participated in twenty experiments.

Subjects were seated comfortably so that they could bite with their incisor teeth on a purpose-built jaw-muscle stretcher. This was based on a servo-controlled, electromagnetic vibrator, whose moving core imposed precise displacements of the lower jaw. The stretcher is described in detail elsewhere (Miles, Poliakov & Flavel, 1993). Particular care was taken to ensure the safe performance of this system, including the provision of mechanical stops to prevent excessive stretches and electronic cut-outs to limit the forces applied to the teeth. The baseline jaw separation was determined by the thickness of the jaw-bars: for stretches, the incisal surfaces of the teeth were about 3 mm apart and for the unloading stimuli they were initially 5 mm apart. The biting force was measured with strain gauges mounted near the teeth on the lower jaw-bar, and the vertical acceleration of the lower jaw-bar was measured with an accelerometer.

Surface electrodes were placed on the skin overlying the right masseter muscle to monitor its electrical activity (bandwidth 2–1000 Hz). The two electrodes were placed approximately in line with the direction of the muscle fibres. One electrode was at the level of the lower border of the mandible, and the other was 25 mm above this, close to the motor point. Preliminary experiments showed that, with this placement, the waveform obtained by triggering an average of the surface EMG on the spikes of a single motor unit in masseter was approximately symmetrical (Poliakov & Miles, 1992). This symmetry is reflected in the averaged EMG response to a jaw-jerk stimulus (e.g. the unrectified average in Fig. 1*A*). During each recording run, the subject maintained a steady biting force of about 10 % of the maximal voluntary biting force (MVC) using visual feedback of the output of the force transducer on the bite bars. Each run consisted of fifty randomly timed trials in which the stimulus was a controlled displacement of the mandible. Stimuli were given at intervals of not less than 1·4 s. The characteristics of the ramp displacements (duration, velocity, rise-time, etc.) were specified in a special-purpose program on a personal computer, and output to the control circuitry through a digital-to-analog circuit. The amplitude of the displacements were 0·5 and 1·0 mm. Unloading stimuli with the same profiles (inverted) were also given in different runs. In addition to the ramp stretches, the responses to displacements produced by square-wave command signals of 1 ms duration were measured. This was to produce high jaw acceleration similar to those in the jaw jerks elicited in most earlier experimental studies, as well as in clinical practice, by tapping on the chin with a tendon hammer.

The electromyogram (EMG), displacement, force and acceleration signals were recorded on digital tape. Both the full-wave rectified and the unrectified masseter EMG were averaged (sampling rate 2 kHz per channel, 12 bits resolution). A mathematical analysis of the EMG has recently shown that, subject to some constraints, the integral of the average of the unrectified EMG mirrors the underlying motor unit activity, i.e. it resembles in shape the combined peristimulus time histograms (PSTHs) of the active units (Poliakov & Miles, 1992). This analysis is ideally used in conjunction with the conventional average of the full-wave rectified signal. The integral of the averaged EMG avoids spurious and/or exaggerated peaks and troughs which can appear in the latter. Both analyses were computed off-line. The displacement, force and acceleration signals were also averaged off-line. All response latencies were measured from the onset of jaw displacement, manifest as the first deflection in the acceleration trace to points of sharp inflexion on the integral of the averaged EMG. These inflexions usually corresponded to those in the average of the rectified record occurring at similar times, although differences were often observed in the relative size of peaks and troughs in the two analyses. In order to determine whether the mechanoreceptors in the periodontal ligament were contributing to the response (cf. Brodin, Türker & Miles, 1993), the reflex response to stretch was recorded before and after these receptors were blocked by infiltration of local anaesthetic (2 % lignocaine with adrenaline 1:80000) around the roots of the incisor teeth in two subjects.

RESULTS

The results of simulating a weak jaw-jerk stimulus by sending brief, square-wave command signals to the stretcher are shown in Fig. 1*A*. In this example, the jaw was displaced about 0·01–0·02 mm downwards. (The amplitudes of such small displacements could not be measured precisely). The acceleration record shows that this stimulus produced a brief (10 ms) burst of vibration in the jaw bars: the force record suggests that some of this vibration was transmitted to the teeth and to the jaw muscles. This stimulus, which was described by the subject as a very weak tap on the teeth, evoked a prominent reflex excitation of the masseter at 9 ms latency, which was followed by a period of reduced activity of about 16 ms duration. The average of the full-wave rectified EMG shows that the amplitude of the response was several times the background excitation level, while the average of the unrectified signal emphasizes the highly synchronous nature of the discharge, i.e. it is closely analogous to the response in the so-called 'tendon jerk' in limb and jaw muscles. With graded stimuli producing peak accelerations of 0·3–1 m s^{-2}, the peak amplitude of the earliest EMG response, measured from the integral of the unrectified average, increased approximately in proportion to the peak acceleration of the stretch.

The pattern of masseter response to a long, slow stretch in the same subject is shown in Fig. 1*B*. The accelerometer record shows that the jaw bar accelerated smoothly at the beginning and end of the 64 ms ramp stretch, and did not vibrate during the ramp phase. The pattern of the reflex response is evident in the averages of both the rectified and the unrectified EMG signals. The initial phase of the response was excitation which began at about 10–12 ms latency and lasted for about 10 ms. Following this initial peak, the activity fell slightly below the baseline, indicating the presence of a so-called 'silent period'. A second peak of excitation then began at about 35–40 ms, and continued until it was strongly depressed at about 70–75 ms.

Thus, there were two distinct phases of excitation, and two periods in which the muscle activity fell below the pre-stimulus level. The short-latency excitation is clearly the conventional, probably monosynaptic, segmental reflex response. Several factors may be involved in the depression in the baseline of the integral that follows this peak. First, the integral reflects the shape of the PSTH of the motoneuronal activity (Poliakov & Miles, 1992), and the effect of an excitatory post-synaptic potential (EPSP) in the parent motoneurone is to move forward in time the unit potentials that would otherwise have occurred: this produces a trough in the PSTH following the excitatory peak (Miles, Türker & Le, 1989). The initial depression in the integral is due at least partly to this phenomenon. Second, it is known that tapping on teeth produces a predominantly inhibitory reflex response in masseter at about this latency (Brodin *et al.* 1993). Hence, it is possible that activation of the mechanoreceptors around the teeth may have contributed to the pattern of reflex responses evoked by this stimulus, including this initial depression.

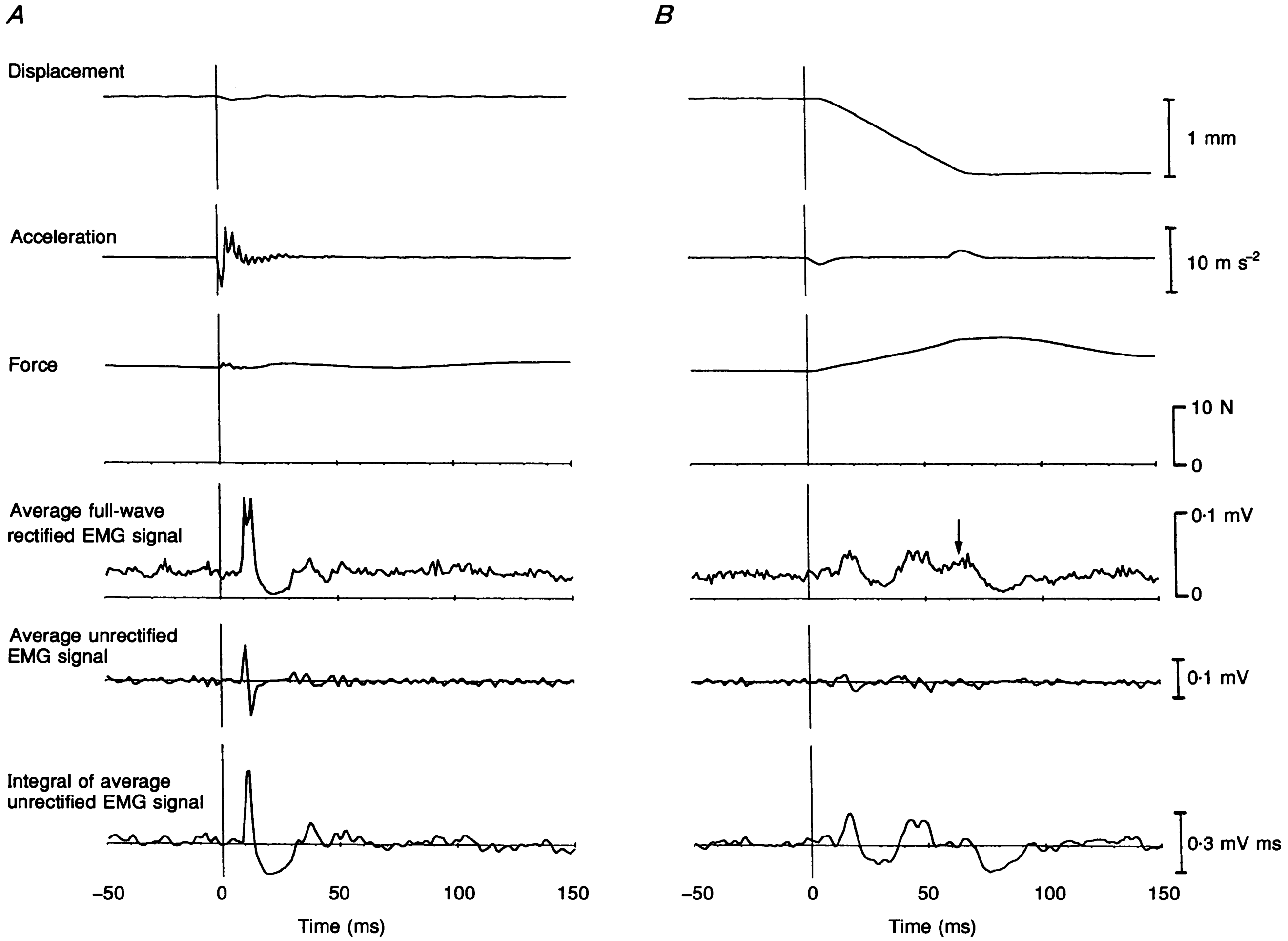

Figure 1. The reflex response of the human masseter to mechanical stimuli during an isometric bite at about 10 % MVC

A, a simulated jaw-jerk, produced by sending a 1 ms square-wave command signal to the stretcher. The uppermost record is the vertical displacement of the mandible, measured at the incisor teeth (jaw opening is downward). Note that the amplitudes of displacements as small as the one illustrated (0·01–0·02 mm) could not be measured precisely from this signal. Below this is the output of an accelerometer mounted on the lower jaw-bar, showing the brief burst of vibration produced in the jaw bars by this command signal. The force record is the output of a strain gauge mounted on the lower jaw-bar about 25 mm from the teeth. *B*, responses of the same subject to a 1 mm stretch of the jaw-closing muscles, at 0·015 m s^{-1}. Same format as *A*. The vertical arrow shows the time at which the deceleration of the jaw-bar began.

However, blocking of the afferents from the receptors around the incisor teeth with local anaesthetic had a negligible effect on the overall pattern of the reflex response in the two subjects in which it was tested.

Third, the integral of the average of the unrectified EMG in Fig. 1*B* shows that the record fell below the baseline about 10 ms after the onset of deceleration of the stretch (arrow). This is shown even more clearly for stretches of different duration in Fig. 3. This point was examined further by averaging the reflex response to unloading the masseter during an isometric bite, by moving the jaw-bar rapidly upwards. Figure 2 shows that this stimulus also elicited a reflex decrease in masseter activity after about 10 ms, which is comparable with the latency of the short-latency stretch reflex. Thus, in Fig. 1*B*, it is likely that the spindles continued to fire throughout the 64 ms ramp stretch, contributing to the longer-latency excitatory response. At the end of the ramp, the reduced spindle excitation during the hold phase led to disfacilitation of the parent motoneurones.

The pattern of reflex responses of one subject to stretches of different lengths and velocities is shown in Fig. 3. The vertical arrows show the time of onset of deceleration (as in Fig. 1*B*). Consider first the longest-duration, 1 mm stretch (*A*). The initial response was the classic monosynaptic response, beginning at 11 ms latency. The second, more prolonged, burst of excitation began at about 40 ms, and was terminated by disfacilitation 10 ms after the jaw-bars began to decelerate (arrow). When the velocity of the 1 mm stretch was increased to 0·03 m s^{-1} (*B*), the amplitude of the monosynaptic response increased. A peak beginning at about 40 ms latency is still visible in *B*, but is segmented into two. The trough between the two peaks is the result of disfacilitation from the deceleration of the jaw-bar. The fastest stretch (*C*) evoked a monosynaptic response of still larger amplitude, while the long-latency peak was almost totally suppressed.

The velocities of the 0·5 mm stretches in Fig. 3*D*–*F* were the same as those in the corresponding 1 mm stretches (Fig. 3*A*–*C*). Despite this, the amplitudes of the monosynaptic reflexes were greater for the longer stretches in this subject. This is presumably due to the different level of pre-stimulus EMG activity. When the data from all subjects were considered, the relative amplitude of the monosynaptic

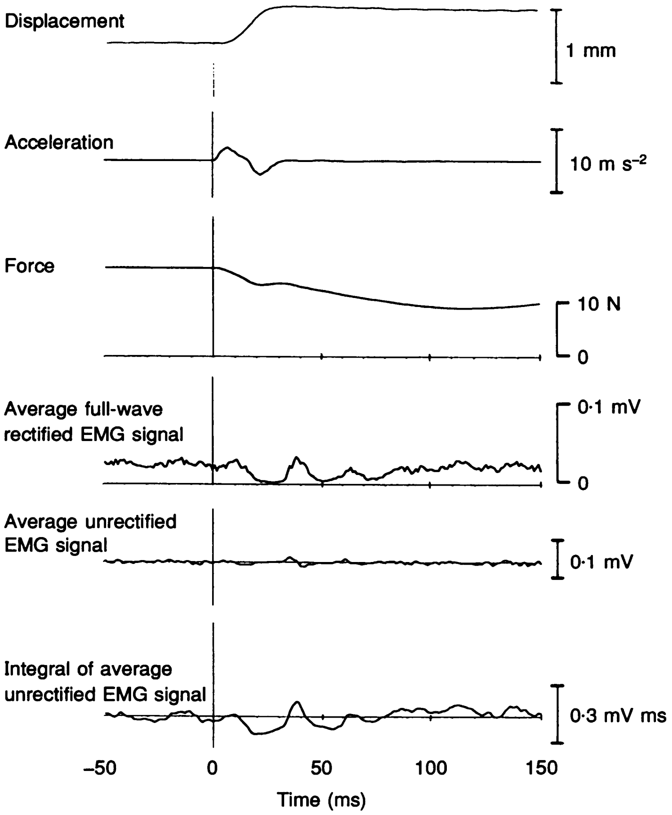

Figure 2. Reflex response of masseter to unloading of the jaw-closing muscles
The jaw-bar was moved 0·5 mm upwards at 0·03 m s^{-1} during an isometric bite at about 10 % MVC. Same format as Fig. 1. Note that the initial fall in biting force due to reduced stretch of the elastic elements in the muscle is followed by a second, longer-latency force decrease which is the result of disfacilitation of the jaw-closing muscles.

response was found to depend only on the initial acceleration, and not on the length of stretch.

The shape of the responses to the 0·5 mm stretches was also complicated by disfacilitation. In Fig. 3*D*, a trough separates the small, brief peak beginning at about 40 ms and the larger peak at 55 ms. This was again the result of disfacilitation, that is, when a stretch of the same velocity was prolonged as in Fig. 3*A*, the long-latency component of the reflex excitation was no longer segmented. In Fig. 3*E*, the disfacilitation (beginning 10 ms after the arrow) delayed the onset of the long-latency response until 60 ms, while in Fig. 3*F*, the disfacilitation began so early that the integral was kept below baseline until about 80 ms.

Consider now the force produced as a result of the stimuli. The synchronous monosynaptic response evoked by the brief jaw-jerk stimuli failed to produce even a low-amplitude twitch in most subjects, e.g. Fig. 1*A*. In contrast, slower stretches evoked measurable reflex force changes in most subjects.

However, the force exerted on the jaw-bars during the slower stretch stimuli was the result of several factors. The total force changes produced by three stretch velocities in the same subject are shown in Fig. 4*A*; jaw-jerk stimuli elicited no reflex changes in force in this subject (data not shown). During the course of each stretch, the force applied to the jaw-bars increased approximately in proportion to displacement at each velocity. This proportional increase results from the elastic properties of the contracting jaw-closing muscles and the related soft tissues. There was also a contribution to the total force from the combined inertia of the jaw-bars and the mandible. The form and time course of the inertial forces are shown by the acceleration records (cf. Figs 1*B* and 2), and are reflected in the shape of the force records in Fig. 4*A*. Although it is difficult to estimate accurately the magnitude of the inertia, the elastic plus the inertial forces produced about 10 N of the total force shown in Fig. 4. The inertia ceased to contribute to the force at the end of the stretch. The mechanical

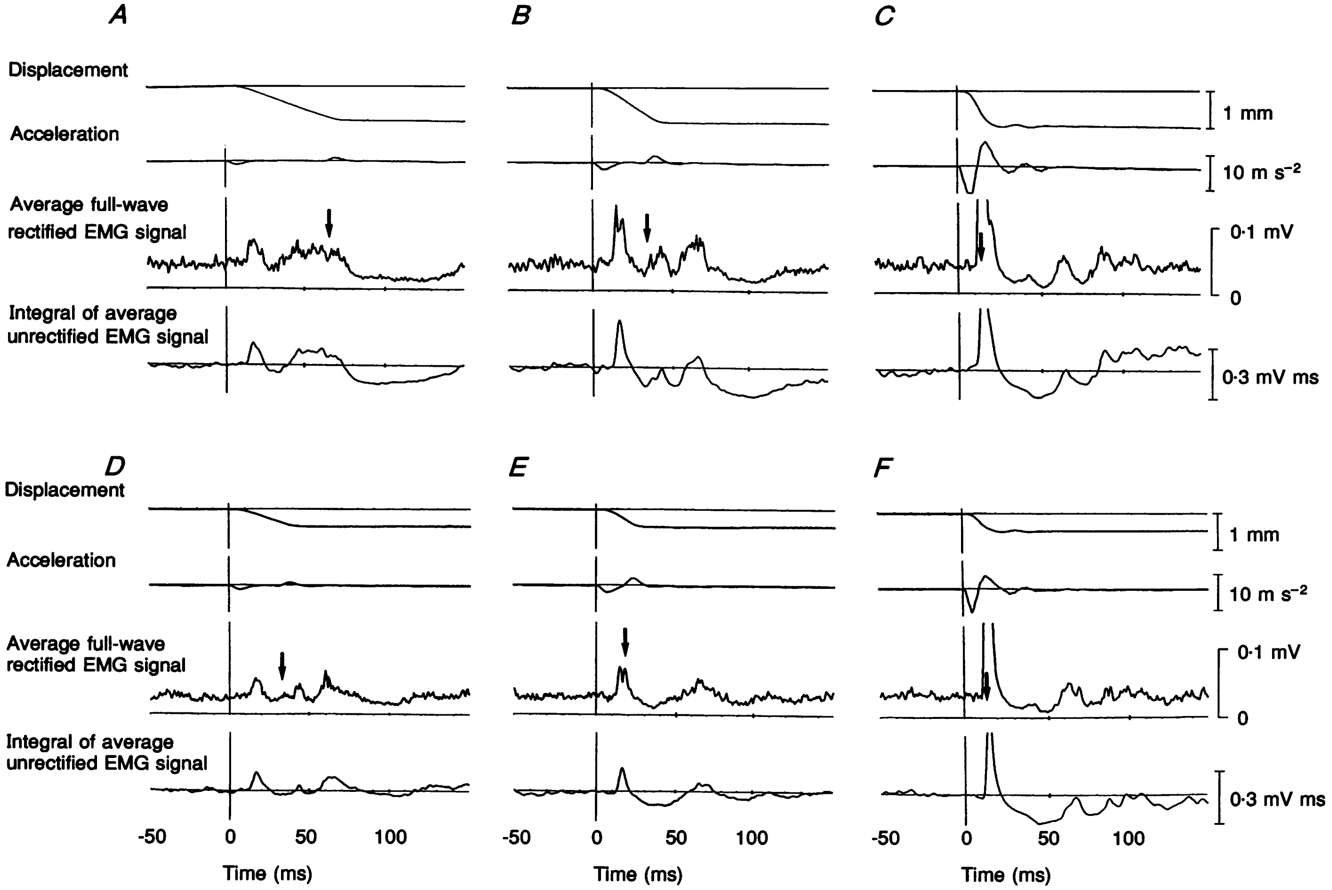

Figure 3. Reflex responses of human masseter to stretches of various lengths and velocities
The amplitude of the stretches was 1·0 mm in *A–C*, and 0·5 mm in *D–F*. The stretch velocities were 0·015 m s^{-1} for *A* and *D*, 0·03 m s^{-1} for *B* and *E* and 0·1 m s^{-1} for *C* and *F*. Vertical arrows show the onset of deceleration. The disfacilitation that occurs about 10 ms after the the onset of the deceleration is a major factor determining the differences in the shapes of the long-latency EMG responses to stretches of different durations.

properties of muscle can cause the force exerted by a stretched muscle to drift upwards after the stretch (Joyce, Rack & Westbury, 1969). However, the length of all three stretches shown in Fig. 4 was the same, and the twitch-like shape of the forces evoked by slow and rapid stretches suggests that they are mainly the consequence of reflex muscle activation. The reflexly induced force increment in this subject was about 2 N for the slowest stretch and 5 N for the fastest.

The inverse relationship between stretch velocity and the reflex increase in force shown in Fig. 4*A* was observed consistently. In Fig. 4*B*, the maximal force occurring 80–110 ms after the onset of 0·5 mm stretches is plotted against the stretch velocity for four subjects. The actual increase in force resulting from the reflex in these four subjects was about 10–40 % of the total increase in force.

The amplitude of the short-latency EMG response increased in proportion to the stretch velocity; in contrast, the reflexly elicited increase in force decreased as the stretch velocity increased. While the decline in peak force with stretch velocity may be due in part to the mechanical properties of the muscle (i.e. yield), the data suggest that the reflex increases in total jaw-closing force induced by the slower stretches were principally the result of the long-latency reflex response evoked by these stimuli.

Reflexly induced decreases in force were regularly observed when the jaw-closing muscles were unloaded by moving the bar 0·5 mm upwards during an isometric bite. In Fig. 2, for example, the force on the jaw-bars initially fell about 3·2 N when the stretch of the elastic element in the muscle was reduced, then another 4·3 N as the result of a late-onset reflex decrease in muscle activity.

DISCUSSION

It has been argued that the feedback control of muscle length in the intrinsic hand muscles is regulated principally by long-latency reflexes, with little contribution from the monosynaptic response (Matthews, 1991). However, it has been claimed that the control of the masticatory system is different in that it is effected principally by the monosynaptic pathway. This claim is based mainly on the earlier observation that the only reflex response to stretch of the human jaw-closing muscles seen in most studies is the segmental jaw-jerk reflex (e.g. Lamarre & Lund, 1975; Goodwin *et al.* 1978; Cooker *et al.* 1980). Marsden *et al.* (1976) reported that the latency of the first excitatory response to stretch occurs at 12–14 ms in masseter. This latency is too short to correspond with the long-latency response found in the present experiments. It is likely that the short-latency reflex was delayed in these records, perhaps because of the difficulty they reported in obtaining 'reasonable rates of stretch' of the jaw-closing muscles.

Reflex pathways

It is clear from the present study that the general pattern of reflex responses to stretch in the human masseter is similar to that in most spinal systems, that is, a burst of excitation at short latency followed at longer latency by a second phase of excitation. The rapidity of onset of the short-latency response indicates that it is at least in part monosynaptic (Lamarre & Lund, 1975). The origin of the longer-latency response has been the subject of intense debate (e.g. Wiesendanger & Miles, 1982; Matthews, 1991), but recent observations on subjects with the rare

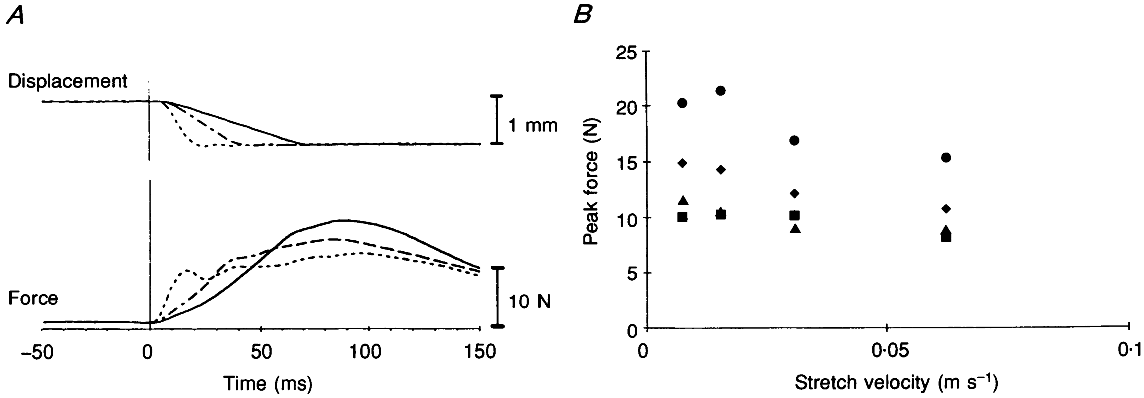

Figure 4. Reflexly evoked changes in the force exerted by the jaw-closing muscles in response to various mechanical stimuli in one subject

A, displacement and force records recorded in one subject during 0·5 mm stretches at different velocities. *B*, the peak force exerted on the jaw-bar by four subjects, represented as ●, ◆, ▲ and ■, between 80 and 120 ms after the onset of 0·5 mm stretches at various stretch velocities. Slower stretches were associated with larger increases in reflex biting force.

Klippel–Feil syndrome confirm that the long-latency response of at least the intrinsic hand muscles is the output of a polysynaptic pathway that traverses the motor cortex (Matthews, Farmer & Ingram, 1990). Is, then, the long-latency excitatory response to stretch in the masseter transcortical? It begins at about 35 ms in the integral of the average of the unrectified EMG (e.g. Figs 1*B* and 3). However, the minimal time for a signal to travel from the muscle to the cortex and back is substantially shorter than this. Non-painful trigeminal stimuli evoke a potential over the sensory cortex beginning about 8 ms (Findler & Feinsod, 1982), and the efferent conduction time from the motor cortex to the masseter is about 6 ms (Cruccu, Berardelli, Inghilleri & Manfredi, 1989), giving a minimal transcortical loop time of about 15 ms. It may be assumed that some temporal summation will be required to activate this polysynaptic pathway. If, however, the long-latency response is the output of a transcortical loop, this summation time would need to be about 20 ms, which seems excessive.

Brodin *et al.* (1993) have recently reported that pressure on an incisor tooth evokes a long-latency excitatory reflex in the human masseter. However, two lines of evidence indicate that this response is distinct from the long-latency response to muscle stretch. The reflex response to pressure begins about 50 ms after the onset of the stimulus, which is significantly later than the long-latency response to stretch; and secondly, the long-latency response to stretch was not materially altered by local anaesthesia of the teeth, whereas this procedure abolished the pressure-evoked response. At the present time, therefore, the pathway traversed by the long-latency response to stretch in the jaw muscles remains unknown. Why should the well-developed long-latency response seen in the present study have eluded most earlier investigators? The answer lies in the stimulus parameters used in the various studies. In the present study, we confirmed that very brief stimuli, similar to the jaw jerks produced by a tendon hammer, evoke principally short-latency excitation. In Fig. 3*C* and *F*, for example, the dominant response in the EMG to brief stretches of 0·5 and 1 mm was the monosynaptic excitation. Longer stretches evoked both the short- and the long-latency excitation. Our data show clearly that the pattern of excitation is critically dependent on the duration of the stimulus. The long-latency excitation evoked by stimuli of less than about 50 ms duration is segmented by a trough that is the result of disfacilitation following the decrease in the stretch velocity (Fig. 3). Hence, the burst of excitation that is evoked by very brief stretches is terminated abruptly by disfacilitation. Moreover, after discharging synchronously, the membrane potentials of many masseter motoneurones will be relatively far from their firing thresholds and thus will not be discharged by an excitatory input that arrives at longer latency (Miles, Türker & Le, 1989).

The extraordinary sensitivity of the monosynaptic reflex to minute vibrations of the jaw-bars may also have contributed to the absence of a long-latency response in the earlier studies. In the present experiments, the presence of vibration was revealed only by the accelerometer on the jaw-bar, and its abolition required careful tuning of the control circuitry (Miles *et al.* 1993). If the stretches in the earlier studies induced even low-amplitude vibration of the jaw bars, they would produce a prominent monosynaptic response with no longer-latency components like that shown in Fig. 1*A*. Thus, the absence of a long-latency reflex in the records of earlier investigators is almost certainly the result of the parameters of their stretch stimuli.

It is interesting that disfacilitation has such a powerful effect on the motoneuronal activity. Figure 2 shows that unloading the masseter by moving it 0·5 mm upward during an isometric bite evokes a reflex reduction in the amplitude of the average of the rectified masseter EMG to less than 20 % of its pre-stimulus level. This indicates that the Ia afferents contribute substantially to the net drive to motoneurones during isometric biting, i.e. that fusimotor drive is high (Appenteng, Morimoto & Taylor, 1980). Miles & Wilkinson (1982) pointed out that powerful, rapidly acting disfacilitation is particularly important in the jaw-closing muscles, as it can reduce the risk of the teeth crashing together during a forceful bite when the resistance to closing is suddenly and unexpectedly withdrawn. However, the major mechanism that prevents the teeth from crashing together when unloaded during a powerful isometric bite is co-activation of the antagonist muscles (Miles & Madigan, 1983).

Relationship of force changes to reflex responses

Lamarre & Lund (1975) and Cooker *et al.* (1980), who were unable to demonstrate a long-latency response in the masseter, concluded that the reflex increase in force evoked by loading the human masseter during an isotonic bite or by stretching the muscle was the result of the monosynaptic response. In the present study, we found that, although jaw-jerk stimuli evoke a high-amplitude monosynaptic reflex in the EMG, little or no force is generated by this electrical response in most subjects. In the jaw-closing system, as in other muscles (Matthews, 1991), slower stretches that evoke a weaker monosynaptic response but a less-synchronous, long-latency EMG response do result in the generation of a significant force response (e.g. Fig. 4*A*). It is not possible to determine precisely the contribution of the reflexly evoked force to stretch, as the contribution of the velocity-dependent mechanical properties of the contracting muscles is not known. However, as much as 40 % of the total resistance to stretch is the result of these two factors combined. The greater part of the total resistance to stretch was due to the elastic properties of the contracting muscles and other soft tissues.

It seems paradoxical that the prominent, synchronous, monosynaptic reflex does not generate much force in the jaw-closing muscles. There are probably a number of reasons for this. First, the tightly synchronized discharge of motor units during the monosynaptic response produces a compound action potential in the surface EMG whose amplitude may lead the observer to overestimate the number of motor units that are involved, in comparison with the broader peak that results from the asynchronous discharge in the long-latency reflex. Second, the effect of the Ia afferent volley is to bring forward the times at which some motoneurones discharge. However, as shown in the integral of the average of the unrectified EMG (which is essentially a representation of the combined PSTHs of the active motoneurones), the effect of the stretch-evoked Ia volley is to bring some motoneurones to threshold earlier than would otherwise be the case (Miles *et al.* 1989). This would normally produce a twitch. After discharging at monosynaptic latency, these motoneurones are silent for a further interspike interval (the silent period), which is manifest in the integral as a depression below the baseline. This period of decreased motor unit activity will produce a decrease in total muscle force immediately after the twitch, thus tending to offset the effect of the twitch. Third, during the moderate masseter contraction in the present experiments, most motor units that are active are already discharging at frequencies at which their contractions are fully fused (Nordstrom, Miles & Veale, 1989). Hence, the effect of a brief Ia volley may be only to bring into synchrony the action potentials of the already active motoneurones, which would not result in the production of much additional force. This is somewhat analogous to the observation that no additional force is produced during a maximal voluntary contraction when a single, supramaximal shock is given to the muscle's motor nerve (e.g. McKenzie & Gandevia, 1991). Moreover, Appenteng, O'Donovan, Somjen, Stephens & Taylor (1978) have shown that, unlike most limb muscles, the masseter Ia afferents innervate principally low-threshold motoneurones: hence the probability that a stretch will recruit additional motoneurones is low. The probability of recruitment is also diminished by the fact that in the masseter individual Ia fibres diverge to excite only about 10% of homonymous motoneurones, compared with 80–100% in limb muscles. It would then be necessary to argue that the additional force that is produced by the long-latency reflex in masseter is due primarily to the asynchronous recruitment of additional motoneurones by the cortico-trigeminal pathway.

In functional terms, the stretch reflexes described in the present experiments may appear rather artificial, since the only stretches that are applied to the modern human masseter in the course of normal activities are the result of the mass of the mandible and the action of gravity, when one is walking or running. The significance of these reflexes may be greater for other species, including primates, when they carry their offspring or heavy items of prey in their mouths as they run and jump. More importantly, however, the present experiments illustrate the operation of fundamental reflex pathways in the masticatory system.

REFERENCES

APPENTENG, K., O'DONOVAN, M. J., SOMJEN, G., STEPHENS, J. A. & TAYLOR, A. (1978). The projection of jaw elevator muscle spindle afferents to fifth nerve motoneurones in the cat. *Journal of Physiology* **279**, 409–423.

APPENTENG, K., MORIMOTO, T. & TAYLOR, A. (1980). Fusimotor activity in masseter nerve of the cat during reflex jaw movements. *Journal of Physiology* **305**, 415–431.

BRODIN, P., TÜRKER, K. S. & MILES, T. S. (1993). Mechanoreceptors around the tooth evoke both inhibitory and excitatory reflexes in human masseter. *Journal of Physiology* **464**, 711–723.

COOKER, H. S., LARSON, C. R. & LUSCHEI, E. S. (1980). Evidence that the human jaw stretch reflex increases the resistance of the mandible to small displacements. *Journal of Physiology* **308**, 61–78.

CRUCCU, G., BERARDELLI, A., INGHILLERI, M. & MANFREDI, M. (1989). Functional organisation of the trigeminal motor system in man. *Brain* **112**, 1333–1350.

FINDLER G. & FEINSOD, M. (1982). Sensory evoked response to electrical stimulation of the trigeminal nerve in man. *Journal of Neurosurgery* **56**, 545–549.

GIBBS, C. H., MAHAN, P. E., LUNDEEN, H. C., BREHNAN, K., WALSH, E. K. & HOLBROOK, W. B. (1981). Occlusal forces during chewing and swallowing as measured by sound transmission. *Journal of Prosthetic Dentistry* **46**, 443–449.

GIELEN, C. C. A. M., RAMACKERS, L. & VAN AUYLEN, E. J. (1988). Long-latency stretch reflexes as co-ordinated functional responses in man. *Journal of Physiology* **407**, 275–292.

GODAUX, E. & DESMEDT, J. E. (1975). Human masseter muscle: H- and tendon reflexes. *Archives of Neurology* **32**, 229–234.

GOODWIN, G. M., HOFFMAN, D. & LUSCHEI, E. S. (1978). The strength of the reflex response to sinusoidal stretch of monkey jaw closing muscles during voluntary contraction. *Journal of Physiology* **279**, 81–111.

JOYCE, G. C., RACK, P. M. H. & WESTBURY, D. R. (1969). The mechanical propeties of cat soleus muscle during controlled shortening and lengthening movements. *Journal of Physiology* **204**, 461–474.

LAMARRE, Y. & LUND, J. P. (1975). Load compensation in human masseter muscles. *Journal of Physiology* **253**, 21–35.

LUND, J. P., DREW, T. & ROSSIGNOL, S. (1984). A study of jaw reflexes of the awake cat during mastication and locomotion. *Brain, Behavior and Evolution* **25**, 146–156.

MARSDEN, C. D., MERTON, P. A. & MORTON, H. B. (1976). Stretch reflex and servo action in a variety of human muscles. *Journal of Physiology* **259**, 531–560.

MATTHEWS, P. B. C. (1991). The human stretch reflex and the motor cortex. *Trends in Neurosciences* **14**, 87–92.

MATTHEWS, P. B. C., FARMER, S. F. & INGRAM, D. A. (1990). On the localization of the stretch reflex of intrinsic hand muscles in a patient with mirror movements. *Journal of Physiology* **428**, 561–577.

MCKENZIE, D. K. & GANDEVIA, S. C. (1991). Recovery from fatigue of human diaphragm and limb muscles. *Respiration Physiology* **84**, 49–60.

Miles, T. S. & Madigan, M. L. (1983). Programming of antagonist muscle stiffness during masticatory muscle unloading in man. *Archives of Oral Biology* 28, 947–951.

Miles, T. S. & Wilkinson, T. M. (1982). Limitation of jaw movement by control of antagonist muscle stiffness during unloading of human jaw muscles. *Experimental Brain Research* **46**, 305–310.

Miles, T. S., Poliakov, A. V. & Flavel, S. C. (1993). An apparatus for controlled stretch of human jaw-closing muscles. *Journal of Neuroscience Methods* **46**, 197–202.

Miles, T. S., Türker, K. S. & Le, T. H. (1989). Ia reflexes and EPSPs in human soleus motor neurones. *Experimental Brain Research* **77**, 628–636 .

Murray, G. M. & Klineberg, I. J. (1984). Electromyographic recordings of human jaw-jerk reflex characteristics evoked under standardised conditions. *Archives of Oral Biology* **29**, 537–549.

Nordstrom, M. A., Miles, T. S. & Veale, J. L. (1989). Effect of motor unit firing pattern on twitches obtained by spike-triggered averaging. *Muscle and Nerve* **12**, 556–567.

Poliakov, A. & Miles, T. S. (1992). Quantitative analysis of reflex responses in the averaged surface electromyogram. *Journal of Neuroscience Methods* **43**, 195–200.

Wiesendanger, M. & Miles, T. S. (1982). Ascending pathway of low-threshold muscle afferents to the cerebral cortex and its possible role in motor control. *Physiological Reviews* **62**, 1234–1269.

Acknowledgements

This work is supported by the National Health and Medical Research Council of Australia. Dr Mike Nordstrom's helpful comments on the manuscript and the assistance of Stan Flavel are gratefully acknowledged.

Received 2 April 1993; revised 23 July 1993;
accepted 21 September 1993.