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ELECTROMYOGRAPHIC RESPONSES TO IMPOSED SINUSOIDAL MOVEMENT OF THE HUMAN THUMB

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SUMMARY

1. The interphalangeal joint of the thumb was driven through sinusoidal flexion–extension movements while electromyograms were recorded from over the flexor pollicis longus muscle.

2. When the subject relaxed his thumb the movement generated no detectable e.m.g. response. When, however, he exerted a voluntary flexing force electrical activity could be recorded from the flexor pollicis longus, the amplitude of which was modulated at the frequency of the movement.

3. As the driving frequency was increased, the maximal e.m.g. activity occurred progressively later in the cycle of movement; for frequencies above about 6 Hz the timing of the averaged e.m.g. was compatible with a reflex delay of 55–65 msec.

4. The frequency–phase plot was not, however, the perfect straight line that would arise from a simple and constant reflex delay. There were some consistent departures from linearity and some random variations. In either case, the timing of the e.m.g. and the timing of the reflex force (Brown, Rack & Ross, 1982*a*) changed together in ways that increased confidence in each of the measurements.

5. The amplitude of the e.m.g. signal was more deeply modulated by movements at 8–14 Hz than by higher or lower frequencies, and it was concluded that the stretch reflex responds particularly readily to signals in that frequency range.

INTRODUCTION

The previous paper (Brown, Rack & Ross, 1982*a*) described the forces which develop at the interphalangeal joint of the thumb in response to imposed sinusoidal movements. These forces were assumed to be the sum of forces which arise as a reflex response to the movement and forces that arise from other non-reflex mechanisms. The timing of these resisting forces varied with the frequency of movement, and most of this variation was attributed to an interaction between the delay around the reflex pathway and a varying cycle time.

In this paper we describe electromyograms obtained from the flexor pollicis longus during the same movements. The results support many of the conclusions of the

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preceding paper and add some further information about the properties of the reflex pathways.

METHODS

The same six subjects were used as in the preceding paper and many of the results were obtained during the same experiments (Brown *et al.* 1982*a*). That paper describes the method of fixing the forearm and imposing sinusoidal movements by the use of a rotating wheel.

Electromyograms were recorded through needles inserted into the subcutaneous tissue over flexor pollicis longus. With the forearm pronated into the same position that was used in the experiments, a pair of needles was inserted at the junction of the middle and lower thirds of the forearm, in front of the palpable border of the radius. The needles were approximately 1 cm apart, and care was taken to keep them superficial to the muscle itself. Signals were amplified (Isleworth type A101 pre-amplifier, gain 1000, pass band 20 Hz–5 kHz) and recorded on magnetic tape (frequency range 0–2·5 kHz), along with force and position signals and pulses generated by the rotating wheel. Phase shifts in the pre-amplifier (less than 30° at 2·5 kHz) were so small in relation to movements at 20 Hz or less that they were disregarded.

The e.m.g. signals were also rectified and integrated by a purpose-built electronic device, whose integration period was controlled by pulses derived from the wheel which generated the sinusoidal movements. By the use of this device the integrated signal was sampled and the integrators reset thirty-two times in each cycle; the samples thus obtained were then divided by the period of time over which they had been collected, to give a measure of the e.m.g. amplitude that was independent of the sampling frequency and the movement. This mechanism introduced a constant phase lag of 1/32 of a cycle (11·25°) which was allowed for in the subsequent analysis of the results.

The results were displayed in three different ways: 'raw' e.m.g. records could be displayed on an oscilloscope and photographed (Fig. 1); the rectified and integrated e.m.g. could be averaged over a number of cycles of movement at the same frequency (Fig. 2); often the rectified e.m.g. signals were analysed by the same method that has been described for the force signals (Brown, Rack & Ross, 1977) to give the amplitude and phase of that component of the rectified e.m.g. that fluctuated at the frequency of the movement (Figs. 3–6).

Quick stretches. To examine the response of flexor pollicis longus to quick stretches, the fly-wheel and crank mechanism was replaced by a powerful spring, the action of which was to pull the thumb into extension. For much of the time this action was prevented by an electrically controlled latch, and it was only when the latch was released that the extension movement occurred. After an extension of 13·5° the movement was halted by a hard rubber stop.

In order to average the responses to a series of extensions, the position signal and the rectified e.m.g. were sampled at 200 μsec intervals and read into a buffer which was used as a signal-delaying mechanism. The averaging process was initiated by the position change, but since the averaged signals had been delayed the display included a section of record that preceded the movement (Fig. 6).

RESULTS

When a subject flexed the terminal phalanx of his thumb, electrical activity could always be recorded from over the flexor pollicis longus; this activity was irregular in amplitude and it often included definite periodic bursts. If the terminal phalanx was driven through sinusoidal movements while the subject maintained this flexing effort the periodicity of the e.m.g. was also affected by the movement and a component of the electrical activity usually became locked to the movement cycle. The situation was then complicated, with some activity occurring regularly in each cycle, but some whose timing was unrelated to the movement. We are concerned here only with those components that occurred repeatedly at the movement frequency, and we use methods of analysis which exclude activity at other unrelated frequencies.

The amount by which joint movement modulated the e.m.g. activity, and the phase relationship between this e.m.g. fluctuation and the joint position depended on the frequency and amplitude of the imposed movement; the depth of modulation also varied from subject to subject.

Although the results of this investigation can be seen most clearly when the responses to a number of cycles of movement are averaged, the main points could

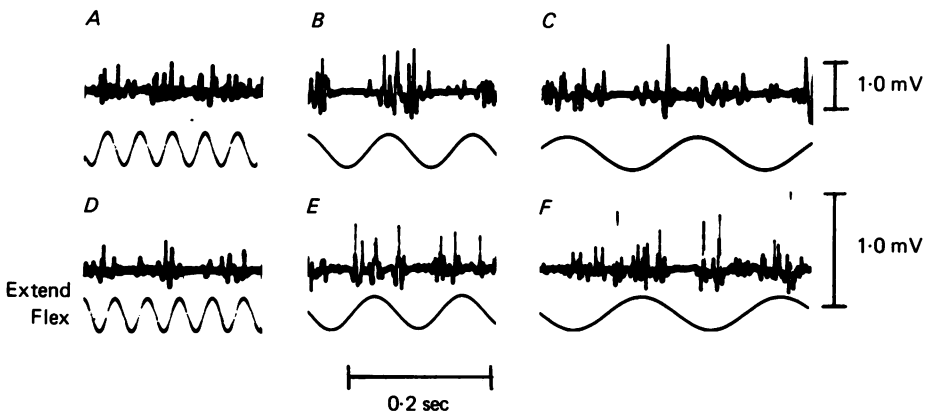

Fig. 1. Flexor pollicis longus e.m.g.s from two different subjects during sinusoidal movements of the thumb at three different frequencies. Subjects exerted a mean flexing torque of 0·5 Nm. Movement was through $\pm 1{\cdot}3°$ (24 mrad). Frequencies were 22 Hz in *A* and *D*, 8·5 Hz in *B* and *E*, and 5 Hz in *C* and *F*.

often be seen also in the 'raw' e.m.g. records. Fig. 1 shows e.m.g. records which were obtained from two different subjects during sinusoidal movements at three different frequencies. The e.m.g. activity was most clearly modulated by movements in a middle frequency range; this may be seen in Fig. 1 *B* where in each cycle of an 8·5 Hz movement there was a burst of activity followed by a period of near silence. At lower frequencies (Fig. 1 *C*) the e.m.g. was still modulated by the movement, though it was less obvious from these 'raw' records. Higher frequency movements (Fig. 1 *A*) also had relatively smaller effects, and in this record it is difficult to detect any modulation of the e.m.g. at the movement frequency.

Although movements in a middle range of frequencies always had the largest effect on the e.m.g. activity, the differences between the frequencies were not always so clear as in the upper records of Fig. 1. Records *D–F* were obtained from another subject during a similar sequence of movements; the e.m.g. was again modulated by the movement, though not so deeply as in *A–C* (note different scales), nor was the difference between the middle frequencies and the lower frequencies so great.

The e.m.g. response to high-frequency movements was sometimes a burst of activity in each alternate cycle, so that the main modulation of the e.m.g. was at half the movement frequency; this may be seen in Fig. 1 *D*, and less clearly in *A*. Bursts of e.m.g. activity in alternate cycles are much more clearly seen during sinusoidal movements of the ankle joint (Agarwal & Gottlieb, 1977; Freedman & Herman, 1975; Rack, Ross & Walters, 1979).

When the thumb was relaxed, and the subject exerted no voluntary force, there was no detectable e.m.g. activity from the flexor pollicis longus, and this was still true when the joint was subjected to sinusoidal movements at frequencies up to 20 Hz and amplitudes up to $\pm 5{\cdot}8°$. This negative result was an interesting demonstration of the low level of stretch reflex activity in the relaxed muscle and it was reassuring to find that no significant artifact arose from movement of the recording electrodes.

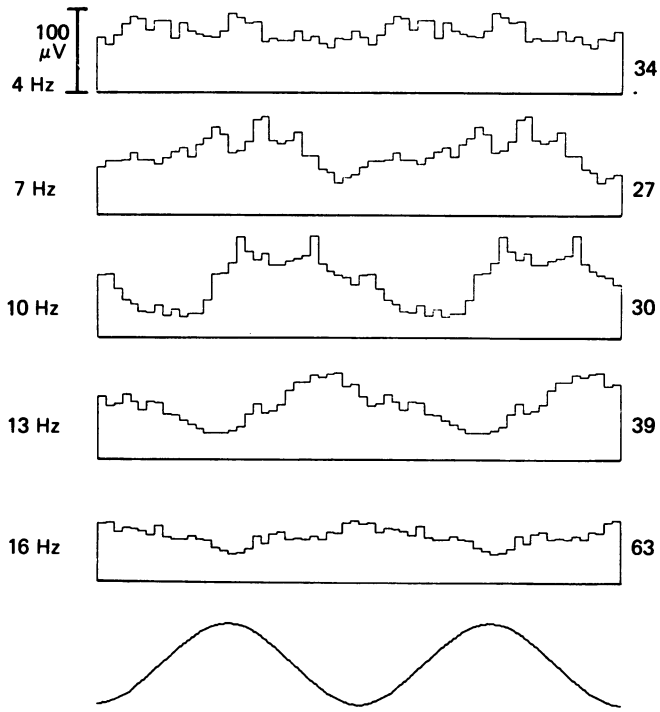

Fig. 2. The e.m.g. activity during sinusoidal movements of different frequencies. The rectified e.m.g.s were integrated and averaged over successive cycles whose frequencies were within 0·5 Hz of the mean values indicated on the left. The number of cycles in each average is shown on the right. Although the results were averaged over successive single cycles they are displayed twice over as a two-cycle sequence for clarity. Mean flexing torque was 0·25 Nm. Movement was through $\pm 1{\cdot}3°$ (24 mrad).

Averaged e.m.g. results

Although cyclical fluctuations of the e.m.g. can be seen in some of the records of Fig. 1, the relationship between joint position and e.m.g. could be seen more clearly when the electromyogram was rectified and the responses to a number of cycles of similar frequency were averaged together. In the experiment of Fig. 2 the frequency of movement was progressively reduced, and all the cycles within each 1 Hz interval were collected together. The 7 Hz record is thus an average of the rectified e.m.g.s of all the twenty-seven cycles whose frequencies lay between 6·5 and 7·5 Hz, and the 10 Hz record was obtained from all the thirty cycles between 9·5 and 10·5 Hz.

Fig. 2 shows how different frequencies of movement modulated the e.m.g. activity. At the lower frequencies (4 Hz in Fig. 2) the modulation was quite slight, but there was some increase in activity during extension of the joint and a decrease during flexion. This result was to be expected, since the afferent discharge from the flexor pollicis longus would reach its maximum during lengthening. With increasing

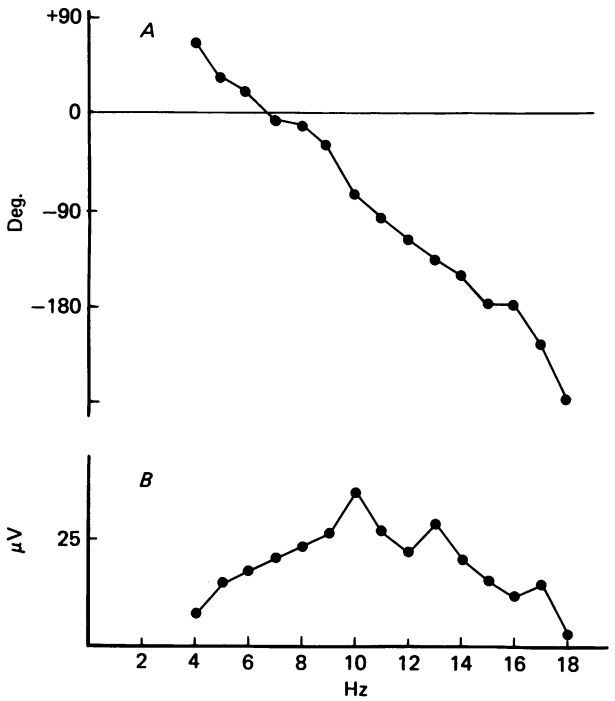

Fig. 3. Sinusoidal analysis of the e.m.g. signal. *A* shows the phase relation of the e.m.g. signal to the movement; *B* shows the amplitude of e.m.g. modulation at the movement frequency. Data from the same experiment as Fig. 2. The integrated e.m.g. was subjected to the same cycle by cycle sinusoidal analysis that was used for the force records (Brown *et al.* 1982*a*) and each phase and amplitude point is the average of all the cycles that fell within 0·5 Hz of the plotted value.

frequency the maximal e.m.g. activity moved later in the cycle, and this too could have been expected, since the delays around the reflex pathway would then be a larger fraction of the cycle time. The depth of modulation of the e.m.g. was clearly greater in the 7–13 Hz records than at either 4 or 16 Hz, and in the 10 Hz record the modulation was such that the e.m.g. activity diminished to quite a low level at one point in the cycle.

Sinusoidal analysis of the e.m.g.

Although the distribution of e.m.g. activity within the cycle was often irregular, the timing of the fundamental component could be conveniently described in terms of its amplitude and its phase relation to the movement. This information was extracted from the results as described in the *Methods*. The process is equivalent to

rectifying and averaging the e.m.g. as in Fig. 2 and then fitting the best sinusoid to it; the values for amplitude and phase then refer to that fitted sinusoid.

Fig. 3 was plotted from the same data as Fig. 2 and each point again represents all the cycles within ½ Hz of the plotted value. The phase of the e.m.g. signal (Fig. 3*A*) is the angle by which the e.m.g. maximum preceded maximal joint extension. The amplitude (Fig. 3*B*) is the amount by which the rectified e.m.g. fluctuated around its mean level; the 10 Hz record of Fig. 2 is thus represented as a sinusoid which has maxima and minima that are 35 μV above and below the mean level.

Records such as Fig. 3 only give information about the depth of modulation of the e.m.g. at the movement frequency; they give no information about the total amount of e.m.g. activity, nor do they record e.m.g. fluctuations at frequencies other than the frequency of movement. The small amplitude of the response to high-frequency movements does not therefore necessarily mean that these movements generate no reflex activity, but it does imply that there is no consistent cyclical response at the movement frequency.

Since the surface e.m.g. gives an indication of the timing and intensity of activity in a considerable part of the muscle, it is a signal that is intermediate in the reflex pathway between the preceding afferent activity and the resulting muscle force. The relationship between the movement and the e.m.g. should thus give information about the neural parts of the reflex pathway, while the relationship between the e.m.g. and the reflex force will depend on the properties of the muscles.

The relationship of reflex force to e.m.g. activity

The resistance to joint movement can conveniently be represented by a stiffness vector. When with changing frequency of movement this vector describes an approximately circular or spiral path, it may be assumed that the resistance includes a component which is a result of stretch reflex activity (Brown *et al.* 1982*a*). When the frequency of movement is high, the position of the stiffness vector is assumed to indicate the timing and amplitude of non-reflex component of the resistance; whereas the direction and distance that separate each lower frequency point from the knot of high-frequency points is taken to be a measure of the timing and amplitude of the reflex component of force at that frequency.

The depth of modulation of the e.m.g., and its phase relation to the movement, give another measure of the amplitude and timing of the reflex activity and this can be compared with the reflex force in those same cycles. The most revealing comparisons were possible when the force and e.m.g. records were obtained from the average of a limited number of cycles, so that the fluctuations that occurred from cycle to cycle were not entirely ironed out.

Fig. 4 shows results that were obtained from the same subject during two experimental runs on the same day. On each occasion the frequency of movement was reduced rather rapidly, so that many of the points represent fewer than fifteen cycles of movement, and the phase–frequency plots (Fig. 4*A*) show more irregularities than records in which larger numbers of cycles had been averaged. The vectors which represent the joint stiffness during these same cycles also followed an irregular path (Figs. 4*C* and *D*), and many of these irregularities correspond quite closely to those seen in the phase–frequency plot.

Comparing the reflex forces in Fig. 4*C* with the e.m.g. activity in the same cycles

(filled circles in Figs. 4*A* and *B*), one can see that between 4 and 6 Hz there was little change in the timing of the e.m.g. (Fig. 4*A*), and the corresponding points in Fig. 4*C* also lie quite close together. Between 6 and 9 Hz, however, the phase of the e.m.g. changed through about 120° and the corresponding stiffness vectors moved widely round the high frequency points through a similar angle. At still higher frequencies

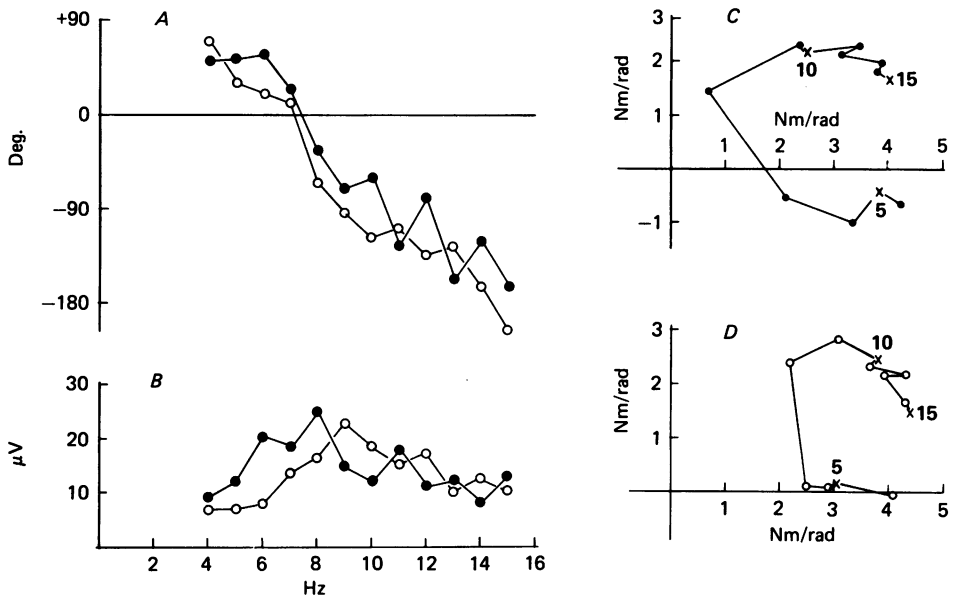

Fig. 4. Reflex e.m.g. compared with resistance to movement. Two records which were obtained from the same subject on the same day. *A* and *B* show the phase and amplitude of the e.m.g., as in Fig. 3; *C* and *D* show the joint stiffness vectors during the same cycles; *C* is from the same experimental run as the filled circles in *A* and *B*; *D* corresponds to the open circles. In *C* and *D* some of the frequencies (Hz) at which resistance was measured are shown in bold type. Each point represents the average of twelve to twenty-four cycles. Mean flexing torque was 0·5 Nm, and movement was ±1·3° (24 mrad).

this relationship between the two records persisted, so that each large increase in phase delay of the e.m.g. signal (10–11, 12–13 and 14–15 Hz) was accompanied by a corresponding clockwise movement of the stiffness vector. There is a similar correspondence between Fig. 4*D* and the phase of the e.m.g. signal (Fig. 4*A* open circles), and this same fairly simple relationship between the reflex force and the e.m.g. phase was regularly seen in numerous other experimental runs.

If one assumes that the relationship of each vector point to the knot of high frequency points gives a measure of the timing of the reflex force, one can compare these values with the measured timing of the e.m.g. activity and arrive at some measure of the phase separation between e.m.g. and force. Such measurements are practicable in a middle range of frequencies (5–10 Hz), where both e.m.g. signal and reflex force are large, and where the high-frequency points may give a reasonable indication of the true non-reflex resistance (Brown *et al.* 1982*a*). These measurements indicate a lag of 150°–170° between e.m.g. activity and reflex force, which is the sort of value that one might expect from comparison with the slower human soleus (Bawa & Stein, 1976), and the faster cat plantaris (Mannard & Stein, 1973).

It was also possible to see a relationship between the amplitude of e.m.g. modulation and the reflex force. This was clearest when the frequency of movement was in the middle range (5–12 Hz); when such a movement was associated with a high level of e.m.g. activity there was usually a corresponding displacement of the joint stiffness vector. In Fig. 4*B* (filled circles) the e.m.g. was more deeply modulated

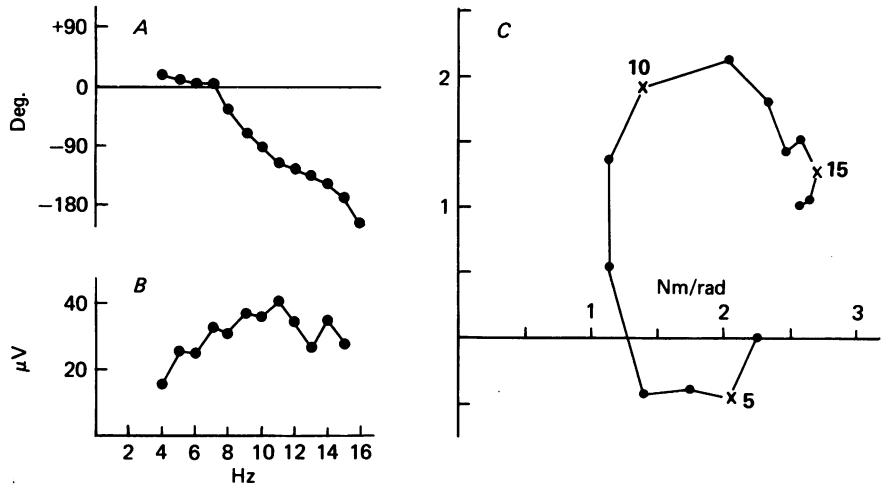

Fig. 5. Reflex e.m.g. and force, plotted in the same way as Fig. 4. Each point represents the average of forty to 100 cycles. Mean flexing force was 0·25 Nm; amplitude of movement was ±0·75° (13 mrad).

at 8 Hz than at 7 or 9 Hz, and in Fig. 4*C* the stiffness vector at that frequency was displaced correspondingly further from the knot of high-frequency points. The relationship between the amplitudes of the reflex e.m.g. and reflex force could also often be seen in records where many cycles of movement were averaged, and the very large reflex forces that we sometimes saw at 8–10 Hz (Brown, Rack & Ross, 1982*b*) were associated with a particularly clear modulation of the e.m.g. activity.

With frequencies of movement above about 12 Hz, the reflex activity seen in the e.m.g. records had only a small effect on the muscle stiffness vector, and at frequencies above 15 Hz such e.m.g. modulation as there was had a negligible effect. This result is to be expected from the 'low-pass filtering' properties of muscles (Marshall & Walsh, 1956; Bawa & Stein, 1976; Brown *et al.* 1982*a*).

In considering the relationship between the e.m.g. and joint resistance, we have concentrated on records in which small numbers of cycles were averaged. A similar result could be seen when the average was from larger numbers of cycles (Fig. 5). This same relationship could also be seen in individual cycles of the movement, though less clearly, because the results were then seriously affected by slower fluctuations as the subject adjusted his mean force.

Relationship of e.m.g. activity to movement

The timing of the e.m.g. activity changed with frequency in a way that one might expect from a pathway which involves significant transmission delays. With increasing

frequency the e.m.g. activity reaches its maximum progressively later in the cycle, and when the response is averaged over sufficient cycles the plots of phase against frequency give a useful indication of the delays that are involved in this neural part of the reflex pathway. These phase–frequency plots are most reliable in a range of frequencies from 5 to 15 Hz, where the e.m.g. is usually well modulated by the movement. The results can then be approximated by a straight line with a slope of 20°–24°/Hz, which intersects the vertical axis between +140° and +170°. The simplest way of interpreting this result is to postulate that in the frequency range 5–15 Hz the afferent activity becomes maximal soon after the beginning of joint extension, and that this afferent activity leads to reflex muscle activation some 55–65 msec later.

Although there was an *approximately* linear relation between phase and frequency, there were some deviations from linearity which repeatedly occurred, and these often became clearer when larger numbers of cycles were averaged. These deviations may be seen in Fig. 5*A*, where the phase–frequency plot has a serpentine shape with particular distortions which we often saw. There was a relatively horizontal section at 4–7 Hz, indicating that the timing of the e.m.g. changed little in this frequency range. At 7–10 Hz, however, there were much larger changes in the timing of the e.m.g. and there was then a steep slope to the phase–frequency plot. These particular deviations from the straight line were more striking, and were more often seen when the movement was accompanied by a vigorous reflex force and by a correspondingly wide excursion of the stiffness vectors.

Fig. 4*A* (open circles) is another record in which the phase of the e.m.g. was much later at 8 Hz than at 7 Hz, and there was a correspondingly large phase change in the accompanying force record (Fig. 4*D*). A similar large change in timing of the reflex response with a small frequency increment was sometimes seen during sinusoidal driving of the ankle joint (Rack, Ross & Walters, 1980), and its causes will be discussed in detail in a later paper.

The response to a rapid extension

Responses to the higher frequencies of sinusoidal movement suggested that the e.m.g. signal might arise from a reflex path which involves a 55–65 msec delay. In order to relate this to reflex delays recorded by other workers who used impulsive stimuli, our subjects undertook another experiment in which the interphalangeal joint was suddenly and rapidly extended. These quick stretches were carried out with the thumb mounted in the same moulds as for sinusoidal driving, and with the subject exerting the same initial flexing force. Under these circumstances, the e.m.g. activity in the flexor pollicis longus began to increase 25–40 msec after the beginning of the extending movement.

Fig. 6 is a typical record which was obtained from the same subject as Fig. 4, while he exerted the same flexing force (0·5 Nm); the results of eighteen successive extensions were averaged. When the whole of the early (30–80 msec) burst of activity is considered together, it follows the movement with a mean delay which is similar to the 55–65 msec that was deduced from the sinusoidal movements. On this occasion, there were two clear peaks in the e.m.g. record, one at 62 msec and one at 80 msec; these two peaks were often, though not always, present.

DISCUSSION

Although the reflex response to sinusoidal movement may be assessed either from the resisting force or from the surface electromyogram each of the methods has its own problems and uncertainties.

Estimates of the reflex component of the resisting force depend on a somewhat

arbitrary separation of the total force into reflex and non-reflex components, and on the assumption that the non-reflex component remains similar in value over a range of frequencies. Modulation of e.m.g. activity by the movement gives clear evidence of a reflex response, but the surface e.m.g. can only be used as a quantitative measure of the reflex activity by assuming that it gives a reasonably reliable indication of the

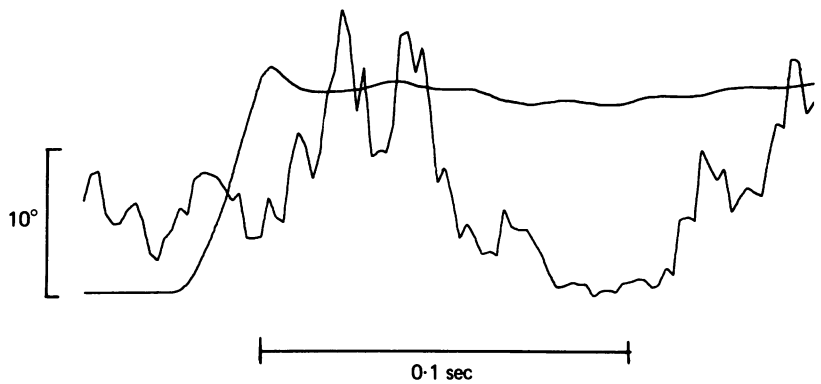

Fig. 6. The response to a rapid extension of the thumb interphalangeal joint. Records of joint position and rectified e.m.g. obtained by averaging the responses to eighteen successive stretches. Amplitude of movement was 13·5° and the initial voluntary flexing force was 0·5 Nm.

amount of muscle tissue that is being activated. Since each of these assumptions is open to some doubt, it is particularly gratifying to find that measurements which are made in these two very different ways support each other, and that the estimates of reflex force and reflex e.m.g. change together as the experimental parameters are altered. In particular, changes in the phase delay of the e.m.g. were reflected by changes in timing of the reflex force in a way that reinforced our confidence in each of the methods of measurement.

The relationship between the e.m.g. amplitude and reflex force was less straightforward, and at high frequencies the reflex contribution to force decreased to low levels while there was still a considerable reflex modulation of the e.m.g. This difference was, however, to be expected, since the 'low-pass filtering' properties of the muscles (Marshall & Walsh, 1956; Bawa & Stein, 1976) would prevent any rapid modulation of motor unit activation from causing a similar modulation of the muscle force.

The amplitude of the e.m.g. signal

The e.m.g. activity was deeply modulated by movements in a middle range of frequencies (8–12 Hz), and at higher frequencies the muscle activation was less clearly locked to the movement cycle; in this respect the thumb stretch reflex differs from the simian jaw muscles (Goodwin, Hoffman & Luschei, 1978) in which the e.m.g. increased in amplitude with increases in frequency up to 20 Hz. Afferent activity from the peripheral receptors is usually more clearly periodic when the frequency is higher, so the neural pathways must therefore transmit the reflex activity more readily when

it is modulated at one of these middle frequencies, and they must presumably serve as a less accessible pathway for higher frequency signals. One can thus regard the neural pathway of the stretch reflex as a filter which has a low impedance for signals in the frequency range 8–12 Hz, but a higher impedance for signals above or below that value.

One could explain this filtering by supposing that with the mean flexing forces that our subjects exerted the motoneurones which contributed most to the e.m.g. had a tendency to discharge action potentials at frequencies within this middle range (Allum, Dietz & Freund, 1978). These neurones would then be readily recruited by afferent activity at a frequency that was close to their own, and would then add to the reflex modulation of the e.m.g. signal. On the other hand, when the frequency of movement was very far from the frequency at which these neurones would readily discharge, they would be less likely to be entrained by the afferent input and more likely to discharge at times that were unrelated to the imposed movement. Mori (1973) has shown that motor units in human calf muscles may behave in this way. The bursts of e.m.g. activity that occurred in alternate cycles of a very fast (20–22 Hz) movement are further evidence that the motor neurones could readily discharge impulses at 10–12 Hz, but would not follow an afferent input that was modulated at twice that frequency. Some of the implications of this frequency-selective reflex behaviour are discussed in succeeding papers (Brown *et al.* 1982*b*).

In comparing the e.m.g. responses to different movements, one should note that a simple measurement of amplitude takes no account of the duration of the cycle. When the amplitude appeared to be the same at two different frequencies, such as the 5 Hz and 13 Hz points in Fig. 3*A* (filled circles), the total amount of e.m.g. response to the displacement was greater in the slower (and therefore more prolonged) cycle. Furthermore, the surface e.m.g. does not necessarily give a reliable indication of the number of motor units that are active during movements of different frequencies. The mode of summation of different action potentials to make up the surface e.m.g. will depend on how closely the activity of the different motor units is locked together. It seems quite possible that the extent of this locking together will depend on the rate at which they are driven to discharge (Mori, 1973), and may therefore be very different at different frequencies of movement.

The timing of stretch reflex activity

At first sight there seems to be a fairly simple relationship between the sinusoidal movement and the subsequent e.m.g. activity. Results obtained with movements faster than about 5 Hz suggest that the maximum reflex activity arose from afferent activity which occurred soon after the beginning of joint extension, and that the reflex pathways involve a delay of 55–65 msec from this afferent activity to the muscle action potential.

This delay which is inferred from the response to sinusoidal movement is similar to the delays which we measured in the same subjects by the quick-stretch method, and it is compatible with the response of the same muscle to a brief extending torque (Marsden, Merton, Morton, Adam & Hallett, 1978). Previous studies of the behaviour of muscle spindle afferents (Matthews & Stein, 1969; Poppele & Bowman, 1970) have shown that their activity reaches its maximum at some point nearer to the middle of the lengthening movement than our results would appear to suggest. The central part of the reflex pathway may, however, behave as a 'phase-advancing' mechanism which lets through only the earlier part of a burst of afferent activity and thus gives

the same result as would an afferent signal whose maximum was earlier in the cycle (Jansen & Rack, 1966; Westbury, 1971).

It is no surprise that at the lowest frequencies the timing of the e.m.g. activity departs from the linear relationship. With low-frequency sinusoids the muscle spindle afferents would have their maximal activity later in the cycle, and the reflex signal would probably be subject to less phase advancement within the spinal cord. A similar result was obtained during sinusoidal movement of decerebrate cat soleus muscle (Jansen & Rack, 1966).

The timing of the e.m.g. activity thus fits reasonably well with the known properties of the muscle spindles and stretch reflex pathway, and the responses to sinusoidal driving give another method of investigating the reflex delays. However some caution is necessary in interpreting results obtained at this joint, since the flexor pollicis longus muscle has a long and compliant tendon whose properties may introduce a phase difference between the movement of the joint and the extension of the muscle spindles; such a phase difference may be frequency-dependent, and could account for the serpentine shape of some of the phase–frequency plots. Further discussion of the timing of the reflex response will therefore be deferred until the properties of the flexor pollicis longus tendon have been described in detail (P. M. H. Rack & H. F. Ross, in preparation).

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