J. Physiol. (1982), **332**, *pp.* 69–85
With 7 text-figures
Printed in Great Britain

FORCES GENERATED AT THE THUMB INTERPHALANGEAL JOINT DURING IMPOSED SINUSOIDAL MOVEMENTS

BY T. I. H. BROWN*, P. M. H. RACK AND H. F. ROSS
From the Department of Physiology, University of Birmingham,
Birmingham B15 2TJ

(*Received 4 January 1982*)

SUMMARY

1. A method is described for driving the interphalangeal joint of the thumb through repeated sinusoidal flexion–extension movements, while immobilizing other joints of the wrist and hand.

2. The joint met the sinusoidal movement with a force that fluctuated in an approximately sinusoidal manner. This paper is concerned with the relationship between the position and force sinusoids.

3. When the thumb was relaxed the forces were small, but when the flexor pollicis longus was tetanically stimulated there was a large force change in response to each cycle of the movement. In either case, the maximum resistance to extension occurred during the later part of the extension movement, some 20°–45° in advance of maximum extension. A similar result was obtained when the subject exerted a maximal voluntary flexing force.

4. The resistance to movement can conveniently be displayed as a stiffness vector, the amplitude of which is the force/displacement, and the phase is the angle by which the force sinusoid leads the position sinusoid.

5. When the subject maintained a continuous, though sub-maximal, flexing effort the timing of the force fluctuations changed with changing frequency of movement in a characteristic way, and the stiffness vectors described a C-shaped or spiral path. With increasing frequency the stiffness vectors moved round this path in a clockwise direction.

6. For descriptive purposes the resistance to movement can usefully be regarded as the vector sum of a reflex and a non-reflex component. Since the reflex pathway involves significant conduction delays, the reflex force can be expected to appear later in the cycle of a higher frequency movement, and give rise to a vector which moves round in a clockwise direction as the frequency increases. The non-reflex stiffness, however, changes much less with frequency.

7. It is concluded that the size of the C-shaped or spiral vector path gives an indication of the strength of the reflex activity, while the position of the high frequency points gives an indication of the non-reflex resistance to the movement.

---

* Research Fellow. Present address: Department of Medical Physics, London Hospital Medical College, Turner Street, London E.1.

INTRODUCTION

Human limbs resist displacements, and some part of this resistance is attributable to the operation of stretch reflexes. Whereas it is fairly easy to measure the resistance of a limb to an imposed disturbance, it is less easy to determine how much of the resistance is due to reflex activity, because the inertia of the limb and the inherent properties of the muscles and other soft tissues contribute their own resistance which may often outweigh the reflex contribution (Joyce, Rack & Ross, 1974; Bizzi, Dev, Morasso & Polit, 1978). Furthermore, changes in voluntary activity are accompanied by changes in both of these reflex and non-reflex components; with an increase in muscle activation, its inherent (non-reflex) resistance to extension increases (Joyce, Rack & Westbury, 1969), and along with this it frequently also exhibits a more active stretch reflex (Marsden, Merton & Morton, 1972; Joyce *et al.* 1974).

In an earlier paper, Joyce *et al.* (1974) described the resistance to sinusoidal movement of the elbow joint. Although the forces they recorded included components that were due to the non-reflex resistance of the muscles, and a very large component that was due to the inertia of the forearm and hand, there were situations in which a significant reflex force could be identified. At some frequencies of movement the limb muscles exerted a greater force while they were shortening than while they were being lengthened; this is a situation that never occurs in a passive or a continuously activated mammalian muscle, and it indicated a vigorous reflex response to the movement. In those experiments, the reflex action could only be positively identified in a rather restricted frequency range. At other frequencies the force changes often suggested the operation of a reflex, but a lack of precise knowledge about the other non-reflex components of the resisting force prevented more definite measurement of this reflex activity.

In the present paper we attempt to define more clearly the non-reflex resistance to sinusoidal movements, and then to deduce the reflex resistance by a process of subtraction. We have, however, no way of abolishing the stretch reflex activity in our human subjects while preserving the ability to exert a controlled muscle force. In interpreting the response of the thumb to sinusoidal driving, we have therefore been obliged to estimate the non-reflex forces by indirect methods. We have measured the resistance of the interphalangeal joint to sinusoidal movements when the muscles were fully tetanized, on the assumption that they were then inaccessible to any additional reflex inputs; we have then used this result as an indication of the non-reflex stiffness that could be expected when the muscle contracts voluntarily with a lesser force. There were very clear differences between the behaviour of the joint when its reflex pathways were in operation and when the flexor muscles were 'hard on', so that it was possible to draw useful conclusions about the forces contributed by the stretch reflex.

The approximately sinusoidal forces with which the thumb meets sinusoidal movements give useful information about the reflex responses to movement. We do not, however, intend to imply that the only function of the stretch reflex is to control position, nor that the joint would necessarily exhibit a similar reflex response to other movements under other conditions. Although engineers can often use the responses to sinusoids to enable them to make predictions about the behaviour of a system under other different circumstances, we must emphasize that predictions of this sort may be very misleading in so highly non-linear a system as a biological reflex, and although we use elementary sinusoidal analysis as a convenient tool, one cannot safely use some of the associated technqiues that engineers employ in the investigation of more linear systems. Even though non-linearities thus limit the usefulness of our measurements, it is worth noting that when spontaneous tremors do occur, they often have an approximately sinusoidal form, and the method of sinusoidal analysis is particularly useful in defining the conditions under which tremors are likely to appear (Joyce & Rack, 1974) and in explaining their origin. In subsequent papers we make predictions about the conditions which tremors of the thumb may be anticipated (Brown, Rack & Ross, 1982*a*), as we relate these to the tremors that do actually occur (Brown, Rack & Ross, 1982*b*).

There were a number of reasons for conducting this investigation on the interphalangeal joint of the thumb: the primate thumb and fingers are controlled by neural mechanisms which are of particular interest, and may be rather different from those which control the more proximal joints (Phillips, 1969); the stretch reflex of this joint has already been studied extensively by other methods (Marsden *et al.* 1972; Marsden, Merton & Morton, 1976; Marsden, Merton, Morton, Rothwell & Traub, 1981); only a single flexor muscle is involved at the joint; the terminal phalanx is so small that forces due to its inertia can usually be ignored.

Some of the results described here have already been referred to briefly elsewhere (Brown, Rack & Ross, 1977; Rack, Ross & Brown, 1978).

METHODS

Six subjects were investigated; their ages ranged from 23 to 48; five were male, one female. Both thumbs of three subjects were examined.

The terminal phalanx was strapped to a metal lever (Fig. 1) by many turns of thin rubber strip (dental rubber dam). The lever was accurately fitted to the firm dorsal surface of the phalanx with dental-impression compound, and the rubber was applied so tightly that the thumb did not pull away from the lever, even with the most powerful flexing effort. This method of fixation caused some discomfort, and often rendered the tip of the thumb anaesthetic after a few minutes. The lever was mounted on light ball bearings which were co-axial with the interphalangeal joint.

A rotating fly-wheel and crank drove the joint through sinusoidal flexion–extension movements (Joyce *et al.* 1974). Rotation of the fly-wheel was maintained by a variable speed motor acting through a soft plastic coupling. The combination of a heavy fly-wheel and a compliant coupling effectively prevented higher frequency vibrations being communicated from the motor to the thumb. The amplitude of movement could be varied by altering the position of an eccentric driving pin. The other end of the crank was attached to a beam (*b* in Fig. 1) suspended on two swinging arms of unequal length (*x* and *y*). The further end of this beam was coupled to the thumb lever through a beryllium–copper force transducer (Joyce & Rack, 1974). A small helical spring (*b.s.* in Fig. 1) kept the couplings in tension, and thus prevented backlash.

Plaster of Paris moulds were made for the forearm, hand and fingers of each subject; these fitted closely to the palmar surface and to the radial and ulnar borders of the limb, and extended to the proximal phalanx of the thumb to limit movements of the more proximal joints. Free and comfortable movement of the interphalangeal joint was essential; the position of the plaster cast and lever were adjusted, and the dental-impression compound was re-melted (often many times) until this was achieved. The plaster moulds were usually made with the wrist in a neutral position, but for three subjects a second mould was also made with the wrist in a position of ulnar deviation which left the course of the flexor pollicis longus tendon as straight as possible (this is the position illustrated in Fig. 1*A*).

Position transducers. Two different methods of transducing position were used. (1) The beam (*b* in Fig. 1) formed part of a spot follower system (see Gordon, Huxley & Julian, 1966). A window in this beam allowed light from a cathode-ray tube to reach a photomultiplier, the signal from which was amplified and supplied to the deflexion plates to drive the light spot on the tube face toward the fly-wheel. The spot therefore always took up a position under the edge of the window and followed movements of the beam. The voltage supplied to the deflexion plates of the cathode-ray tube then gave a measure of position which was free from any detectable phase shifts at frequencies of movement up to 20 Hz. (2) A disk attached to the fly-wheel was drilled with a circle of 400 holes through which a light source could activate a photo-diode. The spacing of the holes was so arranged that during rotation the train of pulses from the photodiode had a rate proportional to the sine of the angle of rotation. By feeding these pulses to an integrating device an analogue representation of the wheel position was obtained, and by suitable arrangement of the disk this signal was brought into phase with the movement of the crank and the joint. This method of measuring angular position was also the first stage of a device for on-line computation of the dynamic stiffness of the joint (Hollins & Rack, 1976).

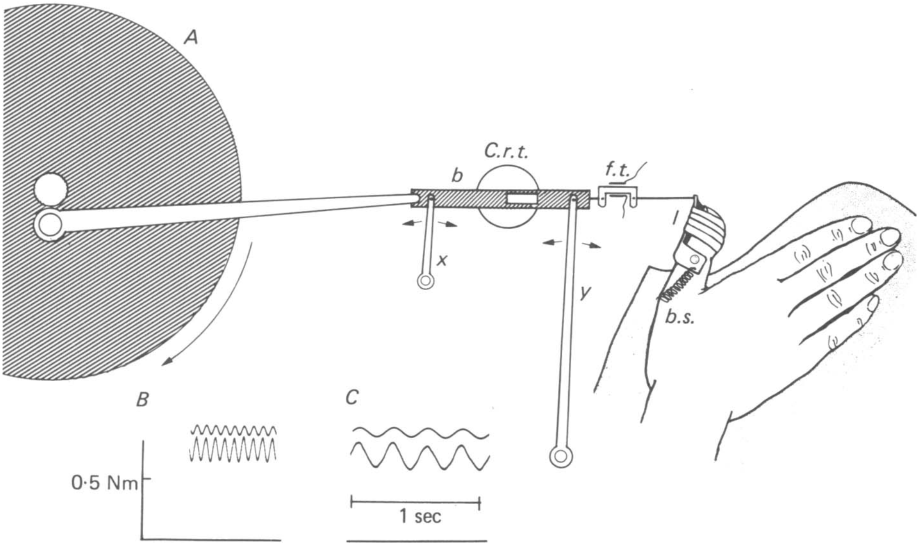

Fig. 1.*A*. The experimental arrangement. Rotation of the fly-wheel acted through an eccentrically mounted driving pin and a crank to cause a reciprocating sinusoidal movement of the bar *b*. This movement was transmitted through a ⊔-shaped beryllium–copper force transducer (*f.t.*) (Joyce & Rack, 1974) to the lever *l* and to the thumb. The bar *b* was attached through bearings to two horizontal beams (*x* and *y*) which swung through small angles as the bar moved. (The use of beams *x* and *y* of unequal lengths reduced the transverse movement and consequent vibration of the strain gauge.) A window in the bar *b* lay over the surface of the cathode ray tube (*c.r.t.*) which formed part of the spot-follower position transducer. The lever *l* was mounted on bearings which were co-axial with the interphalangeal joint; the terminal phalanx of the thumb was fitted to this lever with dental-impression compound and securely fixed with many turns of rubber strip. A back-spring (*b.s.*) attached to the lever kept the couplings in tension at all times. A plaster-of-Paris mould enclosed the palmar surfaces and radial and ulnar margins of the fingers, hand, wrist and forearm. *B* and *C* are samples of position record (above) and force record (below) during movements through ± 1·4° (24 mrad) at 13·5 and 3·5 Hz. The subject exerted a mean flexing force of 0·75 Nm.

The signal from the fly-wheel was used in the subsequent computations, though the spot follower gave a useful check of its accuracy. The spot follower was more important in a subsequent investigation (Brown *et al.* 1982*b*).

The mean voluntary force. In some experimental runs the subject was instructed to relax his muscles as completely as possible; on other occasions he was asked to exert a steady flexing force against the crank. To help him, the output of the force transducer was displayed on a meter whose time constant was much longer than a cycle of the slowest movement (corner frequency of the meter was 0·3 Hz).

Muscle stimulation. In three subjects (the three authors) measurements were made during tetanic stimulation of the flexor pollicis longus muscle. A window was cut in the forearm mould, and a metal ball covered in cloth soaked in electrolyte was pressed against the skin over the muscle; this served as a cathode, and its best position was found by trial and error. The anode was a large plate on the opposite surface of the forearm. Stimulation was through a Devices Mark III isolated stimulator turned up to its maximum pulse amplitude (nominally 90 V): in some experiments two such stimulators were assembled in parallel to increase the current flow, which was then up to 100 mA. Pulses of 0·1 or 0·05 msec were used at rates of 30 or 50 impulses/sec.

Experimental procedure. In many experiments the force records were obtained during a sequence of sinusoidal movements of gradually decreasing frequency, though unlike the previous investigation (Joyce *et al.* 1974) the fly-wheel was continually driven so that the frequency could be reduced in a controlled manner. In other experiments the frequency was progressively increased to achieve a frequency sweep in the other direction and in yet others the frequency was held constant. When the muscle was tetanically stimulated, or when a very high voluntary force was demanded, brief fixed-frequency runs were used to minimize fatigue.

In each experiment we also measured the resistance to sinusoidal movement of the mechanical system when the subject's thumb was not attached to it. The rubber strips, the dental-impression compound and the back-spring remained in position so that these records gave a measure of the properties of all the moving parts except for the thumb itself. From these records it was possible to compute the effective mass of these moving parts and the stiffness of the back-spring. Since neither this mass nor stiffness changed significantly from day to day, these dummy runs served as a useful check on the methods of measurement and computation; any significant component of force 90° out of phase with the lever position gave warning that there was an increase in bearing friction, or some phase lag in the recording equipment.

Treatment and presentation of results

Joint positions and forces were recorded on magnetic tape (band width 0–2·5 kHz) for subsequent analysis. The results were then either displayed on an oscilloscope for photography, or processed with the aid of a digital computer (Digital Equipment PDP 11/34).

Fig. 1 *B* and *C* shows some typical experimental records; the sinusoidal movements (above) were accompanied by approximately sinusoidal force fluctuations (below). The force records were not always quite sinusoidal (see Fig. 1 *C*), but for the present analysis we disregard there irregularities and in both this paper and the two that follow it are concerned only with that component of the force that fluctuates at the same frequency as the movement.

An earlier paper (Joyce *et al.* 1974) describes the method of extracting that part of the force sinusoid that varies at the frequency of the movement, and separating the components that are in phase with and in quadrature to joint position. In this paper we have employed the same method; Fig. 2 *A* shows the results of analysing a sequence of 355 cycles of a movement which gradually decreased in frequency (some parts of this same sequence are illustrated in Fig. 1 *B* and *C*). In Fig. 2 *A* each dot corresponds to a single cycle of movement; in the upper part of the Figure the vertical position of the dot shows the amplitude of the component of force which was in phase with joint position (here expressed as an elastic stiffness) while the lower the part of the Figure indicates the amplitude of the component of force in quadrature to the joint position in those same cycles (here expressed as a viscous stiffness). The additional force required to overcome the stiffness of the back-spring (see Fig. 1), and the forces required to move the metal lever and other attachments have been subtracted (see legend to Fig. 2), so that the results shown in Fig. 2 describe properties of the thumb uncomplicated by properties of the apparatus.

The method of display used in Fig. 2 *A* showed the response to each cycle of movement, and the scatter of the dots gave an indication of the variation between cycles. For many purposes, however, it was convenient to display the same data in a different way (Fig. 2 *B*). To construct this Figure the averaged viscous stiffness for all cycles in a particular frequency range was plotted as a function of the averaged elastic stiffness in the same cycles, as a Nyquist plot. The point labelled 10 Hz was thus obtained from all the twenty-nine cycles whose frequency lay between 9·5 and 10·5 Hz; the elevation of this point above the horizontal axis indicates the averaged viscous stiffness at that frequency, and the displacement from the vertical axis indicates the averaged elastic stiffness. Each of these points is a vector whose distance α from the common origin corresponds to the modulus of stiffness, while the angle ϕ indicates the angle by which the force sinusoid leads the joint position. Sometimes the vector lay between the horizontal axis (the 3–5 Hz points in Fig. 5), the angle ϕ would then have a negative value and the force sinusoid would lag behind joint position by that amount. A similar method of displaying joint stiffness has been used by Rack *et al.* (1978) and by Matthews & Watson (1981).

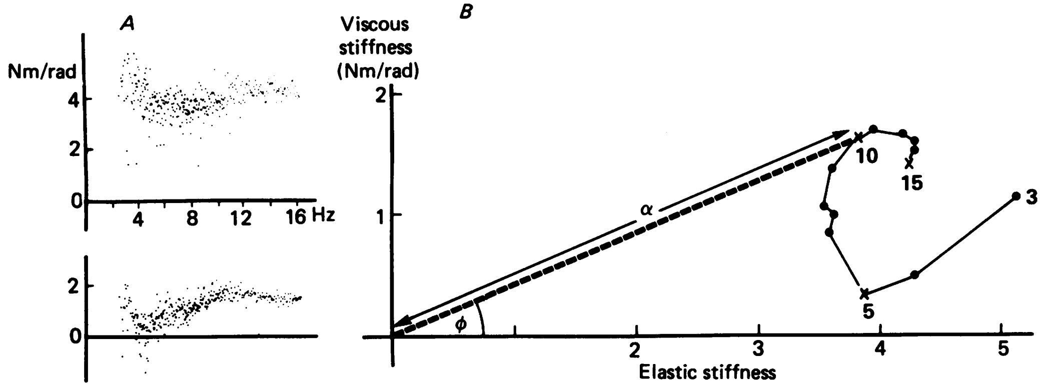

Fig. 2. The resistance to 355 consecutive cycles of movement at progressively decreasing frequencies. (Amplitude ±1·4°; the same experiment as Fig. 1*B* and *C*). *A*, the two components of force are expressed as angular stiffness (torque/angle). The component of force in phase with the movement (elastic stiffness) is shown above, the component in quadrature to the movement (viscous stiffness) is below. Each dot arises from the analysis of a single cycle. Unlike the results presented by Joyce *et al.* (1974), an elevation of the dots *above* the base line here indicates an in-phase flexing force which passes through its maximum when the joint is most extended.

Forces attributable to the inertia of the thumb lever with its coverings (0·1 $g\ m^2$) and to the stiffness of the back-spring (0·07 Nm/rad) had been measured in a preliminary dummy run and these were subtracted from each point before the results in *A* were displayed. *B* the averaged viscous stiffness in each frequency range is plotted as a function of the averaged elastic stiffness in the same cycles. Each point thus indicates the averaged response to all cycles of movement around some (integer) frequency (the 5 Hz point being the average for all cycles with frequencies between 4·5 and 5·5 Hz etc.). The 5, 10 and 15 Hz points are indicated by crosses and the frequency (Hz) printed in bold type in this and most of the other vector plots.

The method of computing and averaging the response to a number of cycles was intended to extract that component of force which varied at the frequency of movement. The results were least reliable for the short records obtained during tetanic stimulation in which rather a small number of cycles were often recorded against a background of a gradually changing mean force. The contaminating effects of a gradual drift in mean force could, however, be avoided or substantially reduced by a method that is described in detail in the Appendix. In brief, the integrations necessary for computing the in-phase and quadrature forces in each cycle were carried out twice over, but with the limits of integration 180° different on the two occasions; the results of the two computations were then averaged.

Units employed. Forces are expressed as torque at the interphalangeal joint (Newton metres), resistance to movement then becomes torque/angle (Newton metres/radian).

RESULTS

The passive joint

When the subject relaxed, sinusoidal movement of a joint was met by a small sinusoidally changing force. Fig. 3*C* shows the forces that developed when the terminal phalanx of the thumb, along with the lever and coverings, were driven through a small movement ± 1·4° (± 0·8 mm at the tip of the thumb). The forces were very small and when the stiffness of the passive joint is represented as a vector, it lies closely to the common origin in the lower left corner of Fig. 4*A*. No e.m.g. activity could be recorded from the flexor muscles during this movement and it was assumed that they were quite passive.

Although the resistance of the passive joint was always small, it changed considerably with small changes of the positioning of the thumb within the mould. Any discrepancy between the joint axis and the axis of the imposed movement added to the resistance, and a high resistance at the passive joint was regarded as an indication of faulty alignment. The force sinusoid always preceded the position sinusoid and this phase advance indicates that the digit combined frictional and elastic resistance to the movement.

An increase in the frequency of movement was accompanied by an increase in the resisting force (Fig. 4*A*), and particularly by an increase in the component of force in quadrature to the movement. A similar increase in viscous stiffness is seen in the passive cat soleus muscle (Rack, 1966).

Although larger movements were resisted with larger forces, the force did not increase in proportion to the amplitude of movement; the passive resistance to large movements was thus relatively less than to small ones, so that the filled squares (larger movements) lie closer to the origin of Fig. 4*A* than do the open squares (smaller movements). Such a result is to be expected if some component of the passive resistance is a simple Coulomb friction.

The terminal phalanx of the thumb has a moment of inertia of about 0·003 g m^2 (This was estimated by measuring the volume of the phalanx at different distances from the joint and assuming a mean specific gravity of 1·0. The inertia was then calculated as $\Sigma m\, l^2$, where m is the mass of each small part of the phalanx and l its distance from the joint). This inertia would resist movement at 10 Hz with a stiffness of about 0·012 Nm/rad, and a movement at 20 Hz with a stiffness of about 0·048 Nm/rad. These forces would contribute so little to the total stiffness at this joint that they have been disregarded.

The fully activated muscle

Flexor pollicis longus was electrically stimulated through a cathode pressed into the palmar surface of the forearm over the radius, approximately 8 cm above its styloid process (the optimum position was found by trial and error). Stimulating currents which were sufficient to give a maximum force at the thumb interphalangeal joint also spread to affect other forearm muscles, and with the supramaximal currents which we used it was necessary to fix the limb securely to prevent flexion movements of the wrist lifting the forearm away from the stimulating electrode.

Flexing forces were recorded with the joint held stationary in a slightly flexed position (there was an angle of about 135° between the dorsal surface of the proximal phalanx and of the proximal part of the distal phalanx). Twitch contractions reached their peak force in 40–50 msec, and this force fell back to half its maximum in 80–100 msec (Fig. 3*A*). The timing of the twitch thus indicates a muscle whose speed

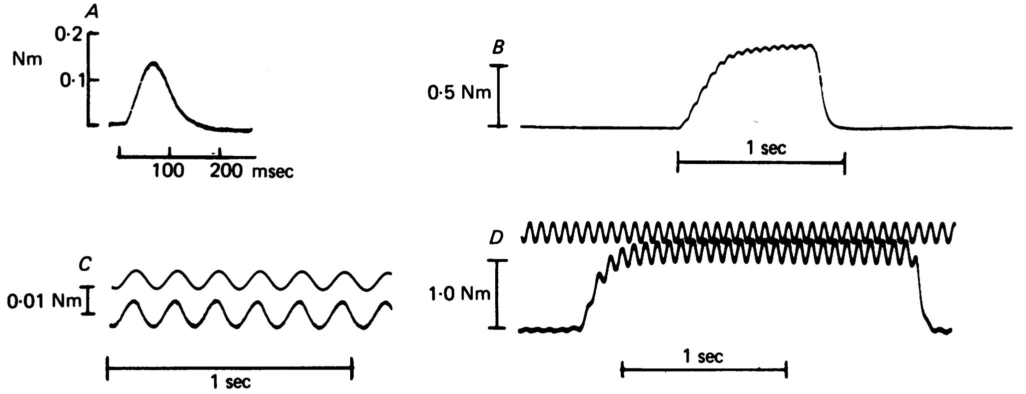

Fig. 3. *A*, an isometric twitch record from the thumb interphalangeal joint on stimulation of flexor pollicis longus. *B*, isometric force during stimulation at 18 impulses/sec. *C*, The response to sinusoidal movement of a relaxed thumb (amplitude ±1·4°); position record is above, force below. With this low force and high recording gain, the inertia of the thumb lever significantly affected the recorded force, which thus differs from the value indicated in Fig. 4*A*. *D*, sinusoidal movement through ±2·7° (47 mrad) at 14 Hz, with tetanic stimulation of flexor pollicis longus (0·1 msec pulses, 50 per sec). All the records in this Figure were obtained with the wrist in neutral position and an angle of about 135° between the dorsum of the proximal phalanx and the base of the distal phalanx.

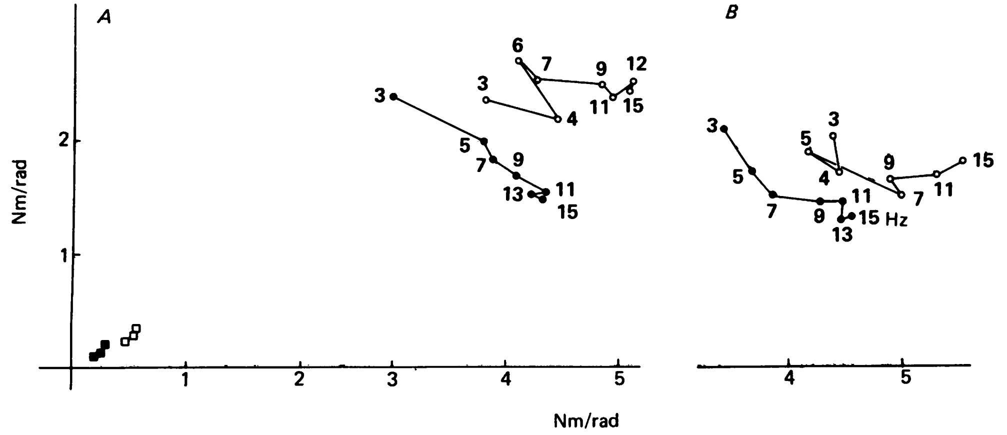

Fig. 4. Stiffness of the thumb interphalangeal joint displayed as vectors. *A*, the squares show the resistance of the relaxed joint to two amplitudes of movement at 2, 8 and 14 Hz; in each case the higher frequency points lie above and to the right. The circles show the resistance to movement when the flexor pollicis longus was tetanized (0·1 msec pulses, 30 per sec). Open squares and circles were from movements of ±1·4° (24 mrad), closed symbols from movements of ±5·1° (89 mrad). *B*, the same movement as in *A*, but with the subject exerting his maximum voluntary force. The frequencies (Hz) at which measurements were made are shown in bold type.

of contraction (as seen through the tendons and the phalanx) is faster than cat soleus but slower than flexor digitorum longus (Buller, Eccles & Eccles, 1960). Repeated stimulation at 18 impulses/sec gave an unfused tetanic contraction (Fig. 3*B*) in which the force fluctuated by about 2 % of the mean value. With this rate of stimulation the mean force was 50–60 % of the maximum value achieved by stimulation at 50 impulses/sec.

Fig. 3*D* is a record that was obtained when during tetanic stimulation the thumb was driven through a sinusoidal movement of 14 Hz. Although the force fluctuations were approximately sinusoidal, other more gradual force changes also occurred; in this record the force reached its maximum after about a second of stimulation and thereafter decreased slightly. Similar slow force changes were often seen. A gradually drifting mean force complicates the computation of the viscous and elastic stiffnesses and may lead to erroneous results. In an earlier report (Rack *et al.* 1978) we presented results which (we now realize) were distorted in that way, and we wrongly concluded that during tetanic stimulation, changes in the frequency of movement are accompanied by little, if any, consistent change in stiffness.

Using the more accurate method described in the Appendix, we obtained the results shown in Fig. 4*A*. As the frequency of movement was increased from 3 Hz to about 11 Hz, there was an associated increase in the elastic stiffness, and the vectors which indicate the properties of the tetanized muscle (circles) moved progressively towards the right. With movements of large amplitude (filled circles) the increase is quite clear; with smaller movements (open circles) the points were more scattered but nevertheless the higher frequency points lie in the region of higher elastic stiffness. We have re-examined the responses to sinusoidal movement during seventy-five tetanic stimulations including those previously presented (Rack *et al.* 1978); when the results are analysed by the method described in the Appendix, each sequence of tetani gave results similar to those shown in Fig. 4*A*, and on no occasion did the stiffness vector describe a C-shaped pattern of the type shown in Fig. 2*B*.

Similar results were obtained when the subject exerted a brief maximal voluntary flexing effort (Fig. 4*B*); again the elastic stiffness increased with increasing frequency, though with the smaller amplitudes there was some scatter of the points in each experiment. This similarity between the maximal voluntary contraction and the tetanus was not surprising. In each case the muscle was fully activated (Merton, 1954), and it is unlikely that any reflex response to the movement will modify the behaviour of a muscle that is already 'hard on'.

Tensions recorded during a maximum voluntary contraction were often higher than the tensions generated by stimulation with very large currents. When these very high currents were used many muscles were stimulated and it was assumed that contraction of the *extensor* pollicis longus was then subtracting from the flexing force at the joint.

In some experiments (including the experiment of Fig. 4*A*) conduction of the median nerve was blocked by compression at the level of the elbow joint, a method used on the ulnar nerve by Marsden, Meadows & Merton (1971). This reduced the pain from stimulation and the subject was unable to exert any voluntary flexing force at the thumb. It was assumed that all reflex responses in the flexor pollicis longus were then completely blocked.

The joint resistance that accompanies a voluntary force

In most of our experiments the subject exerted a pre-determined flexing force, and concentrated on keeping this mean force constant. At some frequencies the sinusoidal movement caused an illusion that the joint was being slowly extended or flexed (Goodwin, McCloskey & Matthews, 1972); the subject was instructed to ignore such misleading sensory cues, and to concentrate on keeping the force at the pre-determined value, as displayed to him on the meter, irrespective of what the joint felt to be doing.

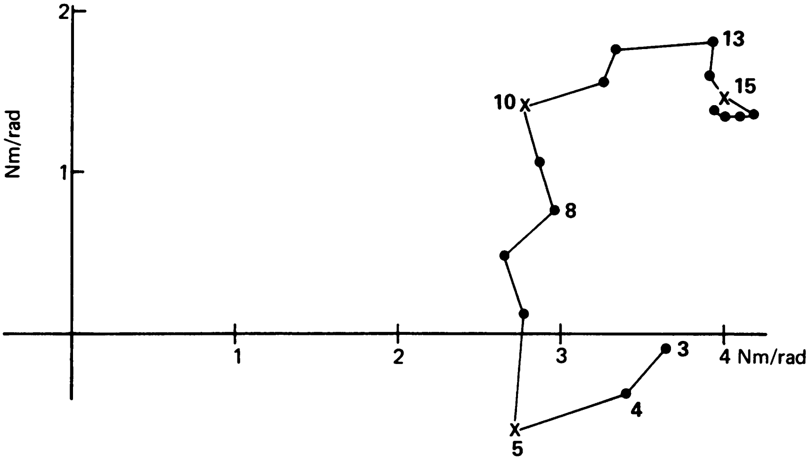

Fig. 5. Stiffness of the thumb interphalangeal joint, plotted in the same way as Fig. 2*B*. Records were made from sinusoidal movements of progressively increasing frequency. Amplitude ±0·65° (11·2 mrad); mean flexing force 0·5 Nm. 360 consecutive cycles were analysed.

The imposed sinusoid added its own forces, and under most experimental conditions this force response to the movement was approximately sinusoidal (Fig. 1*B* and *C*). We are concerned only with the fundamental component of the force wave form, and with the ways that it changed with changing frequencies of the movement. A later paper describes how this response might be further modified by other changes in the experimental conditions (Brown *et al.* 1982*a*).

This principal component of the resisting force can most easily be described and understood when the stiffness (force/movement) is displayed as a polar plot (Figs. 2*B* and 5). In each of these Figures the vectors which denote the joint stiffness traced out an approximately C-shaped pattern, and as the frequency of movement increased, the vector moved around this C-shaped path in a clockwise direction. This type of vector trajectory was seen in all our subjects; the frequency points were always arranged in the same clockwise direction, and the path of the vector usually lay entirely to the right of the vertical axis in the region of positive elastic stiffness. Most of the frequency points lay above the horizontal axis in the region of positive viscous stiffness, though this was not invariable, and at some frequencies the viscous stiffness might be close to zero, or actually negative (Fig. 5, 3–5 Hz). Although the path of the vectors was approximately C-shaped it often spiralled inward at the higher frequencies of movement, and at these frequencies (above about 13 Hz) the points were closely clustered together.

The stiffness vectors followed this type of path whenever our subjects exerted a moderately large flexing force (up to about three quarters maximal), and this was true whether the records were made during a sequence of cycles of decreasing frequencies (Fig. 2*B*) or of increasing frequencies (Fig. 5), or in a number of separate fixed-frequency runs. The regular and repeatable nature of this vector path indicates that movements of different frequencies were met by resisting forces whose timing and amplitude were related to frequency in a predictable way.

It was important to know how far the results depended on the conscious efforts of the subject. When the frequency of the imposed movement was 3 Hz or less, the subject could alter the result by deliberately opposing each lengthening movement, or by deliberately assisting it. This 'interference' required considerable concentration, and could not usually be maintained for long. With higher frequencies of movement it was impossible to interefere in this way, and so long as the subject maintained the required mean flexing force there was little that he could do to alter the path of the stiffness vector.

If the subject made a deliberate attempt to stiffen the joint by co-contracting flexors and extensors, the result was an increase in elastic stiffness with displacement of the whole vector path toward the right. If this stiffening were extreme, the response then changed toward the pattern that was seen when the flexor muscles were exerting their maximum force; the C-shape became small, and might disappear altogether, leaving a record similar to those seen in Fig. 4.

During the course of an experiment the skin of the distal part of the terminal phalanx often became anaesthetic as a result of pressure from the rubber bindings. This anaesthesia did not have any clear effect on the results, and although the response to movements did change as the experiment continued (Brown *et al.* 1982*a*), those changes were unrelated to this sensory loss.

DISCUSSION

In order to establish the relative importance of the reflex and non-reflex resistance to a sinusoidal movement, Goodwin, Hofmann & Luschei (1978) compared the total resisting forces at a joint, with the resisting force that remained after stretch reflex pathways had been interrupted surgically. Their experiments were done on the jaw muscles of trained monkeys, and they were able to measure the non-reflex resistance with the animals exerting the same mean forces as they had done when the reflex pathway was intact. By vector subtraction they were thus able to estimate the timing and amplitude of the reflex component of force.

The non-reflex resistance to movement

In our human subjects we have no way of interrupting the reflex pathway without also preventing voluntary contraction, and it was only possible to measure the non-reflex resistance under conditions of maximal muscle contraction, when additional reflex activity could add nothing to the muscle force and would not therefore affect the result. Our interpretation of the results thus depends on an assumption that the mechanical properties of the fully tetanized muscle give us a reasonable indication of the behaviour of the same muscle when it contracts with a lesser force.

Results obtained from experimental animals are relevant here. Rack & Westbury (1974) found that cat soleus and gastrocnemius muscles resisted sinusoidal stretching with a greater stiffness when they were fully tetanized than when they were activated at lower rates. These authors did not, however, describe the precise effects of movements at different frequencies. We have therefore re-examined tape recordings of their results by the procedures described in the Appendix to this paper. This analysis showed that changes in the frequency of movement were accompanied by similar changes in the muscle stiffness whether the muscle was contracting with a high or with a low mean force. These results encourage us to think that we can use results obtained during maximal contractions (Fig. 4) as an indication of the way that the non-reflex stiffness of muscles would change with frequency when they contract with smaller forces.

The increase in elastic stiffness with increasing frequency of movement (Fig. 4) was to be expected. A simple model, in which 'visco-elastic' muscle fibres act through an elastic tendon, has similar properties since any increase in the frequency of movement meets with increasing resistance from the viscous elements, and more of each extension movement therefore takes place in the elastic tendon, with a corresponding increase in the component of force in phase with the movement. The small decreases in viscous stiffness at the higher frequencies may also be explained in the same way (see Machin & Pringle, 1960).

Changing the frequency of movement had a smaller effect on the tetanized human thumb than on the cat soleus muscle (Rack, 1966, Fig. 6); the length and compliance of the flexor pollicis longus tendon probably accounts for this difference. The relatively small changes in non-reflex stiffness with frequency (Fig. 4) simplify our assessment of the reflex behaviour at the interphalangeal joint; unfortunately it cannot be assumed that the non-reflex stiffness at other joints where tendons are shorter would be so little affected by frequency changes.

In interpreting their experiments on human jaw muscles, Cooker, Larsen & Luschei (1980) used a different method of estimating the non-reflex resistance, which depended partly on the known properties of the jaw muscles, and partly on the response of cat gastrocnemius muscles to sinusoidal stretching.

The reflex resistance to movement

In some of our experiments the force vector passed below the horizontal axis, and for a range of frequencies (3–5 Hz in Fig. 5) there was a phase delay of force on position; the joint then exhibited a negative viscous stiffness, with flexor muscles exerting more force while they were shortening than when they were being forcibly extended. This phase delay of force on position never occurs in a passive mechanical system, and it does not occur when continuously activated mammalian muscles are subjected to sinusoidal movements in this range of frequencies and amplitudes (Rack, 1966); it may be regarded as proof of the reflex response to the movement (Jansen & Rack, 1966; Joyce *et al.* 1974).

We now argue that the progression of the force vector in a clockwise direction around a C-shaped path is in itself evidence for the presence of a reflex response to the movement whether the vectors cross the horizontal axis or not. Futhermore, the size of the C gives an indication of the reflex force, and the distribution of the frequency points around it gives information about the timing of the reflex response.

We shall assume (1) that the force generated in response to the movement may be regarded as the sum of a reflex and a non-reflex component, and (2) that the low-pass filtering properties (Marshall & Walsh, 1956; Bawa & Stein, 1976) of the flexor pollicis longus muscle are such that intermittent activation of the motoneurone pool at 18 impulses/sec or faster, produces little or no modulation of the muscle force (see Fig. 3*B*). Intermittent excitation by a stretch reflex by sinusoidal stretching of muscles at high frequencies cannot then cause any large modulation of muscle force at that same rate, and any considerable force fluctuations that do not occur must be attributed to a non-reflex stiffness. In the present experiments the vectors that represent the joint stiffness at higher frequencies lie close together (Figs. 2*B* and 5), and any further increase in frequency has little effect on stiffness; these vectors are therefore presumed to give a measure of the non-reflex stiffness at those frequencies and under those particular conditions of mean force and amplitude of movement.

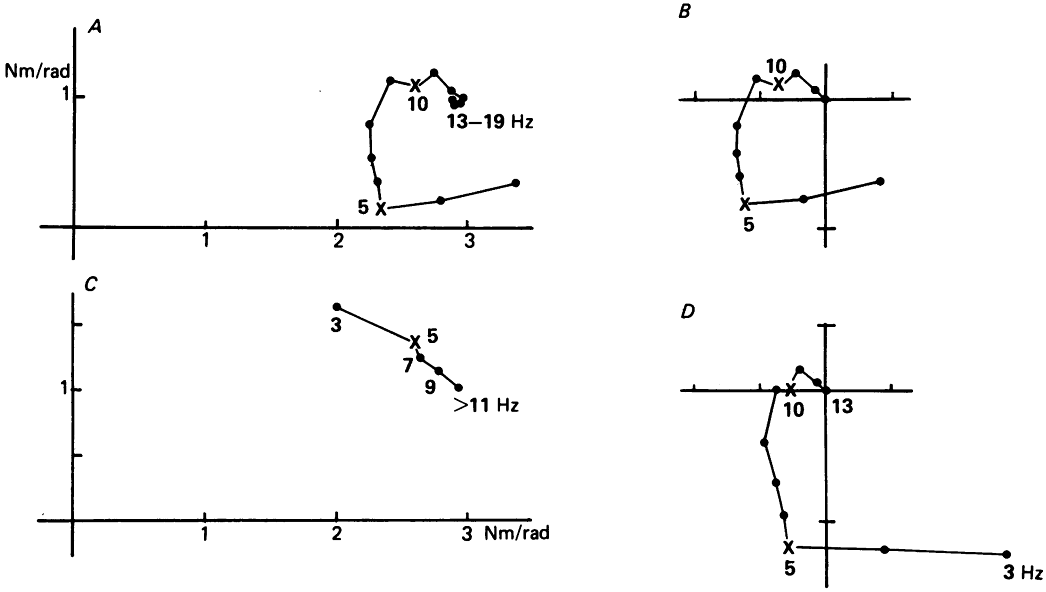

Fig. 6. *A*, stiffness of the thumb interphalangeal joint during movements of ±2·6° (46 mrad), of progressively decreasing frequency. Mean flexing force 0·5 Nm. *B*, the component of stiffness remaining after subtraction of the high-frequency stiffness. *C*, presumed non-reflex stiffness; measurements made during tetani have been scaled down to correspond to the high frequency stiffness in *A*. *D* the non-reflex stiffness in *C* has been subtracted point by point from *A* to leave a reflex stiffness.

If we (for the present) ignore the variations in non-reflex stiffness with frequency which were seen in the tetanized muscle, and suppose that at all frequencies this non-reflex stiffness can be represented by a single point toward which the spirals of Figs. 2*B* and 5 converge, then it becomes easier to see which features of the vector path must be attributed to reflex activity. With this simplification the reflex stiffness may be obtained by vector subtraction of the fixed non-reflex stiffness from the total stiffness. Fig. 6*A* and *B* illustrates this subtraction. The resistance to a sinusoidal movement is shown in Fig. 6*A*; on the supposition that the non-reflex stiffness may be approximately represented by the position of the high frequency points, the vector location of these 13–19 Hz points has been subtracted from each frequency point of Fig. 6*A* to leave the reflex component of stiffness shown in Fig. 6*B*.

The reflex resistance illustrated in Fig. 6*B* amounts to 0·6–1·0 Nm/rad at all frequencies up to 9 Hz, though its timing within the cycle becomes progressively later as the frequency increases. Whereas at 5 Hz the reflex response to extension is a force which reaches its maximum more than halfway through the succeeding flexion movement, at 9 Hz this force maximum occurs almost at the end of flexion, and at 11 Hz it does not occur until the succeeding lengthening movement is already well under way.

The size of the C-shaped path in Fig. 6*B* thus gives a measure of the amount of reflex force, while the distribution of the different frequency points around that path gives an indication of the timing of the reflex force. The behaviour illustrated in the vectors of Fig. 6*B* could have been anticipated from Fig. 6*A* without the need actually to carry out a point-by-point vector subtraction; indeed, the particular advantage of this type of display is the ease with which one can see how the different components of the resisting force combine with each other.

The non-reflex component of force does in fact change with changing frequency, and cannot be represented by a single vector location; the conclusions of the previous paragraph will therefore need some modification. Fig. 6*C* shows changes in the non-reflex stiffness which could be expected on the assumption that the moderately activated flexor pollicis longus changed its stiffness with changing frequency in the same way as the fully activated muscle of Fig. 4. In Fig. 6*D* this better estimate of the non-reflex stiffness has been subtracted point by point from the total stiffness recorded in Fig. 6*A* to give a more reliable picture of the reflex resistance.

Although details of the vector trajectories of Fig. 6*B* and *D* are not the same, the two graphs have a similar general shape and a similar distribution of the frequency points. For an approximate assessment of the reflex force and timing, it is therefore still possible to use the size of the original C-shaped pattern (Fig. 6*A*) and the distribution of the different frequency points as indicators of the reflex force and its timing, without recourse to the explicit vector subtraction of Fig. 6*D*.

Low-pass filtering

Since the low-pass filtering property of muscles was assumed in the arguments which led to the interpretation of the C-shaped patterns, one must exercise care in using the shapes of the vector paths as evidence for the occurrence of low-pass filtering. One can, however, note that the spiral form of the vector trajectories, with its convergence on a single point, is very similar to the Nyquist plots of many linear systems which do incorporate low-pass filters.

The nature of the two components of stiffness

Early in this Discussion it was assumed that the resistance to movement could be divided into reflex and non-reflex components. This division is a matter of convenience and the reflex stiffness is implicitly defined as the part that remains when the non-reflex component of stiffness is subtracted from the total; no difficulties arise so long as the reflex stiffness is defined in this way.

To go a stage further and assume that reflex resistance which is measured in this way gives a simple index of reflex *activation* requires the further assumption that the total resistance may be treated as though it represents the simple addition of a reflex force to another force which arises from stretching continuously activated muscle tissue. This assumption is often made (Bawa, Mannard & Stein, 1975; Robles & Soechting, 1979), and it is probably a reasonable assumption to apply to this joint where the muscle activity is not too deeply modulated by the reflex inputs. We do not, however, suggest that the different components of resistance are attributable to different muscle fibres, nor that they are physically separable in any way. Reflex activity will in fact modulate the stiffness of the muscle fibres as well as their force, and this may contribute to the non-linearity of the system.

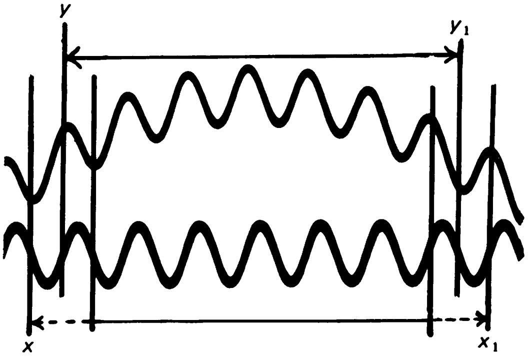

Fig. 7. Illustration of the method of analysis. For description see text.

APPENDIX

In a number of records, particularly those obtained when the muscle was tetanized or was exerting a maximal voluntary force, the sinusoidal force fluctuation was combined with other slower force changes; the number of cycles available for analysis was often small, and the normal method of analysis yielded in-phase and quadrature components of force that were significantly affected by these slower force changes.

On the supposition that the slower force changes were distorting the real response to the imposed movement we have, when necessary, used a method that removes some of their 'contaminating' effects.

The frequency of movement was held constant, and the integrations which were normally used for computing the in-phase and the quadrature forces in each cycle, were carried out twice over. On the first occasion the results from a series of $N+1$ cycles (between x and x_1 in Fig. 7) were added together, the first and last cycles (dotted lines) being given weight 0·5, and all the others weight 1·0. To that sum was added the second series of integrals which began half a cycle later (at y) and ended half a cycle earlier (at y_1). The resulting sum was then divided by $2N$.

One can show that this procedure removes the 'contaminating' effect of lower order force changes as follows.

Consider a record in which the position change $\sin \omega t$ leads to a force change

$$p(t) = a \sin \omega t + b \cos \omega t + c + dt + et^2.$$

Thus a is the amplitude of the in-phase force; b is the amplitude of the quadrature force; c is the coefficient of the constant force contaminant; d is the coefficient of the linear drift force contaminant; e is the coefficient of the quadratic drift force contaminant.

In the normal analysis the in-phase force I and the quadrature force Q are calculated as

$$I = \frac{\omega}{\pi}\int_0^{2\pi/\omega} p(t)\sin\omega t\,\mathrm{d}t \quad \text{and} \quad Q = \frac{\omega}{\pi}\int_0^{2\pi/\omega} p(t)\cos\omega t\,\mathrm{d}t$$

and when the coefficients c, d and e of the contaminating force are zero, $I = a$ and $Q = b$.

In the modified form of the analysis the in-phase (H) and quadrature (U) components of force are given by

$$H = \tfrac{1}{2}N\{I(2,2,N) + 0{\cdot}5I(0,2) + 0{\cdot}5I(2N,2N+2) + I(1,2N+1)\}$$

and

$$U = \tfrac{1}{2}N\{Q(2,2N) + 0{\cdot}5Q(0,2) + 0{\cdot}5Q(2N,2N+2) + Q(1,2N+1)\}$$

where

$$I(R,S) = \frac{\omega}{\pi}\int_{\mathrm{R}\pi/\omega}^{\mathrm{S}\pi/\omega} p(t)\sin\omega t\,\mathrm{d}t$$

and

$$Q(R,S) = \frac{\omega}{\pi}\int_{\mathrm{R}\pi/2}^{\mathrm{S}\pi/\omega} p(t)\cos\omega t\,\mathrm{d}t.$$

Substitution of the full form of $p(t)$ and lengthy but straightforward evaluation of integrals leads to the result that $H = a$ and $U = b$, and therefore that the modified method of analysis is unaffected by linear or quadratic drifts of the force signal.

This work was supported by grant from the Medical Research Council. T.I.H.B. was supported by the National Fund for Research into Crippling Diseases.

REFERENCES

Bawa, P. & Stein, R. B. (1976). The frequency response of human soleus muscle. *J. Neurophysiol.* **39**, 788–793.

Bawa, P., Mannard, A. & Stein, R. B. (1975). Prediction and experimental tests of a visco-elastic muscle model using elastic and intertial loads. *Biol. Cybern.* **22**, 139–145.

Bizzi, E., Dev, P., Morasso, P. & Polit, A. (1978). Effect of load disturbances during centrally initiated movements. *J. Neurophysiol.* **41**, 542–556.

Brown, T. I. H., Rack, P. M. H. & Ross, H. F. (1977). The thumb stretch reflex. *J. Physiol.* **269**, 30–31*P*.

Brown, T. I. H., Rack, P. M. H. & Ross, H. F. (1982*a*). A range of different stretch reflex responses in the human thumb. *J. Physiol.* **332**, 101–112.

Brown, T. I. H., Rack, P. M. H. & Ross, H. F. (1982*b*). Different types of tremor in the human thumb. *J. Physiol.* **332**, 113–123.

Buller, A. J., Eccles, J. C. & Eccles, R. M. (1960). Differentiation of fast and slow muscles in the cat hind limb. *J. Physiol.* **150**, 399–416.

Cooker, H. S., Larsen, C. R. & Luschei, E. S. (1980). Evidence that the human jaw stretch reflex increases the resistance of the mandible to small displacements. *J. Physiol.* **308**, 61–78.

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. *J. Physiol.* **279**, 81–112.

Goodwin, G. M., McCloskey, D. I. & Matthews, P. B. C. (1972). The contribution of muscle afferents to kinaesthesia shown by vibration induced illusions of movement and by the effects of paralysing joint afferents. *Brain* **95**, 705–748.

Gordon, A. M., Huxley, A. F. & Julian, F. J. (1966). Tension development in highly stretched vertebrate muscle fibres. *J. Physiol.* **184**, 143–169.

Hollins, G. W. & Rack, P. M. H. (1976). Measurement of the dynamic stiffness of human limbs. *J. Physiol.* **257**, 77–78*P*.

Jansen, J. K. S. & Rack, P. M. H. (1966). The reflex response to sinusoidal stretching of soleus in the decerebrate cat. *J. Physiol.* **183**, 15–36.

Joyce, G. C. & Rack, P. M. H. (1974). The effects of load and force on tremor at the human elbow joint. *J. Physiol.* **240**, 375–396.

Joyce, G. C., Rack, P. M. H. & Ross, (1974). The forces generated at the human elbow joint in response to imposed sinusoidal movements of the forearm. *J. Physiol.* **240**, 351–374.

Joyce, G. C., Rack, P. M. H. & Westbury, D. R. (1969). The mechanical properties of cat soleus muscle during controlled lengthening and shortening movements. *J. Physiol.* **204**, 461–494.

Machin, K. E. & Pringle, J. W. S. (1960). The physiology of insect fibrillar flight muscle. III. The effect of sinusoidal changes in length on a beetle flight muscle. *Proc. R. Soc.* B **152**, 311–330.

Marsden, C. D., Meadows, J. C. & Merton, P. A. (1971). Isolated single motor units in human muscle and their rate of discharge during maximal voluntary effort. *J. Physiol.* **217**, 12–13*P*.

Marsden, C. D., Merton, P. A. & Morton, H. B. (1972). Servo action in human voluntary movement. *Nature, Lond.* **238**, 140–143.

Marsden, C. D., Merton, P. A. & Morton, H. B. (1976). Stretch reflex and servo action in a variety of human muscles. *J. Physiol.* **259**, 531–560.

Marsden, C. D., Merton, P. A., Morton, H. B., Rothwell, J. C. & Traub, M. M. (1981). Reliability and efficiency of the long latency stretch reflex in the human thumb. *J. Physiol.* **316**, 47–60.

Marshall, J. & Walsh, E. G. (1956). Physiological tremor. *J. Neurol. Neurosurg. Psychiat.* **19**, 260–267.

Matthews, P. B. C. & Watson, J. D. G. (1981). Effects of vibrating agonist or antagonist muscle on the reflex response to sinusoidal displacement of the human forearm. *J. Physiol.* **321**, 297–316.

Merton, P. A. (1954). Voluntary strength and fatigue. *J. Physiol.* **123**, 553–564.

Phillips, C. G. (1969). Motor apparatus of the baboon's hand. *Proc. R. Soc.* B **173**, 141–174.

Rack, P. M. H. (1966). The behaviour of a mammalian muscle during sinusoidal stretching. *J. Physiol.* **183**, 1–14.

Rack, P. M. H., Ross, H. F. & Brown, T. I. H. (1978). Reflex responses during sinusoidal movement of human limbs. In *Cerebral Motor Control in Man: Long Loop Mechanisms*, ed. Desmedt, J. E. Basel: Karger.

Rack, P. M. H. & Westbury, D. R. (1974). The short range stiffness of active mammalian muscle and its effect on mechanical properties. *J. Physiol.* **240**, 331–350.

Robles, S. R. & Soechting, J. F. (1979). Dynamic properties of cat tenuissimus muscle. *Biol. Cybern.* **33**, 187–197.