DIFFERENT TYPES OF TREMOR IN THE HUMAN THUMB

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SUMMARY

1. The upper limbs of normal subjects were immobilized in a way that allowed measurement of forces and movements at the thumb interphalangeal joint without significant movement elsewhere in the limb.

2. When the subject attempted to maintain a steady flexing force at the joint against a rigid stop, the actual force showed the irregular 8-11 Hz fluctuations characteristic of a 'physiological tremor'. This force fluctuation increased when the mean flexing force increased.

3. If the subject exerted his flexing force against a light compliant spring, there was an analogous irregular 8-11 Hz movement at the joint.

4. When, however, an extra inertial load was added to the terminal phalanx, flexion against a compliant spring was often accompanied by a different type of tremor. This was a more regular oscillation, of lower frequency (3-6 Hz), and of much larger amplitude.

5. The precise frequency and amplitude of this type of tremor depended on the characteristics of the added inertia and spring, in a way that could have been predicted from the responses of the joint to an imposed sinusoidal movement (Brown, Rack & Ross, 1982a). The movement appeared to arise from re-excitation within stretch reflex pathways.

6. The irregular 8-11 Hz tremor at this joint could not be attributed to reflex re-excitation, since the responses to sinusoidal movement indicated a stretch reflex whose timing would not support a movement at that frequency. It is, however, emphasized that other joints of the hand and fingers may behave in different ways.

INTRODUCTION

Although the tremors of normal human limbs have been extensively studied, some uncertainty still remains about their natures and origins. The 8–11 Hz tremors of the wrist and fingers have attracted particular attention and particular controversy; some workers have regarded these as an expression of stretch reflex activity (Halliday & Redfearn, 1956; Lippold, Redfearn & Vuco, 1957; Lippold, 1970), while others have thought them a consequence of the intermittent nature of muscle excitation (Marshall & Walsh, 1956; Taylor, 1962), with or without some locking together of the activity

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in different motor units (Allum, Dietz & Freund, 1978; Dietz, Bischofberger, Wita & Freund, 1976; Stiles, 1981). The importance of the mechanical properties of the musculo-skeletal system has been widely recognized (Elble & Randall, 1978; Stiles, 1981), and the possible role of the Renshaw cell feed-back loop has been pointed out (Elble & Randall, 1976). Lower frequency tremors of normal upper limbs have received less attention, though Stein & Oğuztöreli (1976), have suggested that the stretch reflex may play a significant part in some 4–6 Hz pathological tremors, and Stiles (1976) has presented evidence that low frequency tremor may arise in normal subjects as a consequence of stretch reflex activity.

In this paper we describe tremors that occurred at the interphalangeal joint of the normal thumb. The hand and thumb were fixed in a way that confined the movement to that joint, and we were able to control precisely the mechanical loads against which it worked. It was thus possible to examine the effects of load on tremor in a more quantitative way than has usually been done. In previous papers we described the responses of this joint to imposed sinusoidal movements (Brown, Rack & Ross, 1982*a*, *b*, *c*); in the present paper we rely heavily on those responses for our interpretation of the nature of the thumb tremors.

It cannot be assumed that the tremors which we describe at this joint necessarily correspond exactly to those that other workers have described at the wrist and fingers. The thumb does, however, seem to have been a fortunate choice, since it is possible to separate two different types of tremor, one of which can be confidently attributed to a combination of reflex and mechanical factors, while the other appears to have a different origin.

METHODS

Experiments were carried out on the same six normal subjects who were used for the previous investigation (Brown *et al.* 1982a, b, c); we examined both thumbs of three of them.

The forearm, hand and thumb were fixed in the way that has already been described (Brown *et al.* 1982*a*), and the same force and position transducers were used. The wheel and crank that had been used for sinusoidal driving were, however, replaced either by a rigid link or by a compliant spring. The rigid linkage was used in the investigation of isometric tremor, and its length was chosen so that the joint was in its mid-range, with an angle of about 135° between the dorsum of the proximal phalanx and the dorsum of the base of the distal phalanx. The subject was then instructed to maintain some pre-determined flexing force, and to assist him in this the output of the force transducer was displayed to him on a meter of long time constant (see Brown *et al.* 1982*a*).

When the thumb was coupled to a spring, the subject could flex and extend the joint at will, restrained only by the spring and by the inertia of the connecting rods and mountings. Springs of differing stiffness could be used, but in these experiments we usually chose the most compliant one that we conveniently could (equivalent to an angular stiffness of up to 0.1 Nm/radian of joint movement). Since we required the subject to exert some pre-determined force, we adjusted the position of the fixed end of the spring so that he achieved that force when the joint was in a mid-position that was similar to the position employed in the isometric experiments. His task was then to maintain this force-position situation, and either the force or position signal could be used to guide him. With a compliant spring, however, a large position change is associated with only a small change in force, so the position signal made the better monitor, and this was supplied to the meter. The mass of the moving parts was equivalent to a moment of inertia of 0.21 g. m² at the joint, and by adding metal disks to one or other of the swinging arms which carried the connecting rod (see Brown *et al.* 1982*a*, Fig. 1), it was possible to increase this up to 7.5 g. m² without changing the force or position.

Electromyograms were recorded from over the surface of flexor pollicis longus (see Brown *et al.* 1982b). Force, position and e.m.g. signals were recorded on magnetic tape for subsequent analysis. Spectral analysis. Sections of force or position records were digitized at intervals of 9766 μ sec.

The power spectra of successive blocks of 256 points (2.5 sec of data) were computed and averaged together. The resulting spectra had a bin width of 0.4 Hz and an upper frequency limit of 51.2 Hz; in this paper the frequency scales have been truncated where the power in the higher frequency regions was negligible.

RESULTS

When the interphalangeal joint of the thumb was flexed against resistance it was possible to record fluctuations in either the joint position or the flexing force, and corresponding fluctuations could be detected in the e.m.g. of flexor pollicis longus muscle. In the present experiments two different types of irregularity could usually be distinguished, and we shall refer to both of these as tremors whether they appeared as actual movements, or as the force fluctuation during an isometric task.



Fig. 1. Force and e.m.g. fluctuations during a powerful isometric contraction (mean force 0.5 Nm, which was about half maximal). The spectrum was obtained from 50 sec of continuous record.

The 8–11 Hz tremor

When the subject attempted to maintain a constant force against a rigid stop, the actual force fluctuated around the target value (Fig. 1). Within this force fluctuation there was usually a component in the 8–11 Hz frequency range which appears as a band in the force spectrum (Fig. 1). This component appears to correspond to the 'physiological tremor' of the hand and fingers; it was not a regular oscillation at a single frequency, and it was usually of smaller amplitude than the accompanying lower frequency movements.

Electromyograms from flexor pollicis longus were also modulated at these same frequencies, and this could be shown by spectral analysis, though this modulation was not always clear in the 'raw' e.m.g. records, and in this respect the 8–11 Hz tremor differs from the other tremors which we describe below.

When the subject exerted a large flexing force, the amplitude of this 8–11 Hz tremor increased (Sutton & Sykes, 1967), and it increased even further when the force was maintained for a long period (Sutton & Sykes, 1967; Furness, Jessop & Lippold, 1977). (The example illustrated in Fig. 1 was obtained after a series of thirteen previous experimental runs, and it shows a particularly clearly defined peak at 9 Hz.) A prolonged flexion with a *small* force (0.1 or 0.2 Nm) did not, however, cause the notable increase that we shall describe for the lower frequency tremors.

When the subject exerted his flexing force against a compliant spring, so that the terminal phalanx was free to move without any large inertial load, a tremor in this same frequency range could be recorded as an actual movement (see Fig. 4A). Its amplitude was small, and rarely as much as $\pm 1^{\circ}$; this tremor had the same irregularities that we saw in the isometric force fluctuations, and the same rather broad band of frequencies could be seen in the spectral density plot.

Lower frequency load sensitive tremors

In many of our experiments a mass was coupled to the terminal phalanx of the thumb, so that flexion and extension of the joint then involved the movement of a considerable inertial load. If a compliant spring was also added, and the joint was actively flexed against this spring-mass combination, another type of tremor often developed. This was a much more regular oscillation at some definite frequency which was usually in the range between 4 and 6 Hz (Figs. 2C and 3). It was large in amplitude ($\pm 15^{\circ}$ in Fig. 3), and electromyography showed discrete intermittent bursts of activation of the flexor pollicis longus muscle.



Fig. 2. A-C, joint position recorded while the thumb, with an added inertial load, flexed against a compliant spring. Three different flexing forces were used (indicated on the right). In D the joint was subjected to sudden displacements (indicated by arrows). Moment of inertia at the joint 1.6 g. m²; spring stiffness equivalent to 0.1 Nm/rad of joint movement; note different position scales.

The effect of voluntary force

The large low-frequency tremors occurred when the subject was exerting a substantial voluntary force (Fig. 2C). If there were little or no force, then the joint usually remained relatively still even though it was attached to a 'suitable' spring-mass load, so that in Fig. 2A a high recording gain was required to demonstrate the small irregular tremor. With progressive increases in force, however, a point would be reached at which the violent oscillatory movement began. The subject then felt that he was 'losing control' of his thumb, and the tremor would build up to a large amplitude (Fig. 2C). Once this was well developed, the subject could only stop it by changing his mean flexing force, and it often continued until he became fatigued.

When the force was close to this threshold value there were often intermittent bursts of tremor, and the thumb then fluctuated between two different states (Fig. 2B). In this situation, the thumb seemed to be 'on the edge' of a violent oscillation, and the subject could sometimes control the movement; he might for a short time be able to prevent the violent tremor from occurring, though it required considerable concentration to do so, and it usually re-started when his concentration lapsed. At this intermediate force there seemed to be definite transitions between the state of large regular oscillation and the small irregular tremor, and with each transition to the large amplitude movement the subject felt that he was losing control of the joint.

We saw violent tremors of this type in all of our subjects, though there was a good deal of variation in the flexing force that was necessary to provoke them. Whereas in the experiment of Fig. 2A-C, a flexing force of 0.25 Nm or more was required for a large amplitude tremor, there were other occasions when we saw a violent tremor with forces as small as 0.1 Nm (Fig. 3).



Fig. 3. Thumb tremor, and flexor pollicis longus e.m.g. recorded during flexion against a spring mass load. (Mean flexing force 0.1 Nm; moment of inertia 1.84 g.m^2 ; spring stiffness equivalent to 0.1 Nm/rad.)

Even the same subject on the same day would make the transition from a quiet state to a violent oscillation at very different forces. Early in the course of an experiment, the threshold force for a violent oscillation was usually high; later on, however, after he had already actively flexed the thumb for some time, this threshold force was markedly reduced, so that the thumb then oscillated in an uncontrolled manner with quite a small flexing force (less than one tenth maximal in Fig. 3). The threshold force necessary for these large amplitude oscillations seemed to be particularly reduced by a preceding period of such oscillation, so that once well started it tended to go on. Large amplitude oscillations could often be started by increasing the force to a high level, after which it might continue even though the force was then reduced to a considerably lower level. This tendency for tremor to facilitate more tremor complicated any attempt to give a definite value to the threshold force, since tremor usually appeared with smaller flexing forces as the experiment progressed.

When the flexing force was small, and there was no large spontaneous tremor, a sudden displacement was followed by a number of cycles of decaying oscillation (Fig. 2D). If, however, the force was close to the level at which a large spontaneous tremor could anyway be expected, a sudden imposed disturbance was sometimes sufficient to start it off.

The effect of load on tremor

The large amplitude low frequency tremor only occurred when the subject exerted force against particular spring-mass combinations, and the amplitude and frequency depended on the actual spring-mass combination that was chosen. We usually used the most compliant spring that we conveniently could, and kept to the same spring while altering the mass attached to the terminal phalanx. An increase in the mass then reduced the frequency of the tremor, while a reduction in the mass was accompanied by a frequency increase.



Fig. 4. Tremor with four different inertial loads. The subject flexed with a force of 0.5 Nm against a compliant spring (stiffness equivalent to 0.08 Nm/rad). Numbers on the right indicate the moment of inertia at the joint. The spectra were each obtained from 30 sec of continuous tremor. The lines drawn on the spectra of A and B indicate the method of measuring the frequencies and amplitudes that was used to construct Fig. 5.

Fig. 4 shows the tremor that developed when one of our subjects exerted a moderately large force against a compliant spring, but with four different masses attached to the terminal phalanx; the moments of inertia at the joint are indicated on the right. The inertial loads used for B and C gave the largest and most regular tremor movements, and the increase in inertia from B to C was accompanied by a reduction in frequency from 5 to 3.8 Hz.

With larger changes in the inertia (A and D), the frequency changed even further, though the amplitude of movement then decreased. When the mass was small, the large oscillation was virtually abolished, and there remained only the small and irregular tremor that has been described in an earlier section, which included the component at 8-11 Hz (Fig. 4A, note different vertical scale). When the mass was made very large (D), the oscillation was slowed down still further, but again, its amplitude was reduced and it was less constantly maintained.

The relationship between the tremor frequency and the inertia of the moving parts may be shown in a more quantitative way by plotting frequency against moment of inertia (I). In Fig. 5A data from the same experiment as Fig. 4 have been plotted in this way, though the inertia is represented in such a way that the horizontal distance of each point from the origin is proportional to $1/\sqrt{I}$. Fig. 5B shows the amplitude of tremor in those same experimental runs; it was largest with masses that gave a tremor frequency between 3 and 5.5 Hz, but it decreased when with a very small or a very large mass the frequency moved above or below that optimum range. When there was little or no added mass and the tremor was small, it was necessary to use high amplifications in recording and analysing the results. Components of tremor could then often be seen at lower frequencies in addition to activity at 8 Hz or more (see Fig. 4A).



Fig. 5. The effect of inertia on the frequency and amplitude of tremor. In A vertical bars indicate the range of frequency bins in which the amount of activity exceeded a quarter of the amount at the 'best' frequency on the power scale used for spectral density plots; these limits are the points at which the horizontal line in Fig. 4B intersects with the plotted spectrum. These frequencies could be read off without difficulty from most of the spectra; there were, however, some records in which the tremor peak was only part of a more widely distributed activity. The decision about where the peak rose from this noisy background was then somewhat arbitrary, and the method used is indicated in Fig. 4A where the dotted line is taken as a base line and the assumed frequency limits are the points at which the continuous line intersects the plotted spectrum. B shows the r.m.s. amplitude of movement at the frequencies within those limits; where there was more than one peak in the power spectrum (the two points with the smallest inertias), we have plotted the amplitude of the larger (higher frequency) peak. On the horizontal axis, mass has been plotted on a scale in which distance from the origin is proportional to $1/\sqrt{I}$.

The method of plotting frequency against $1/\sqrt{I}$ gives useful information about the elastic resistance at the joint. If one constructed this type of plot for the response of a simple spring with a series of different masses, the points would fall on a straight line through the origin, the slope of which would depend on the spring stiffness (see the dotted lines on Fig. 5A). The points that are actually plotted in Fig. 5A deviate

appreciably from this simple situation, indicating that the effective elastic stiffness at the joint changed appreciably with the changing frequency of tremor. Reasons for these changes will be considered in the Discussion.

DISCUSSION

Since the interphalangeal joint of the thumb resists extension with a force that is partly, and sometimes entirely elastic, a mass that is added to the terminal phalanx creates a spring-mass system which will have a definite natural frequency of oscillation, and this natural frequency can be expected to change as the mass is changed. The changes in frequency of tremor that accompanied changes in the added inertia were therefore to be expected, and may be regarded as alterations in the tuning of the peripheral mechanical system. Changes in the spring would also affect this tuning (Joyce & Rack, 1974), but in the present experiments such changes were seldom made.

It is notable that when the thumb was so loaded that the frequency of tremor was in the range $3\cdot5-6$ Hz, the tremor grew to a large amplitude, but when it was tuned to higher frequencies (above 7 Hz), the tremor remained small, even though there had been definite force fluctuations in that frequency range in an isometric contraction. This contrast between the low frequency tremor which grew when there was an appropriate peripheral load, and the higher frequency tremor which never became very large, can be explained by reference to the response of the joint to imposed sinusoidal movements.

Large amplitude low frequency oscillations

Imposed sinusoidal movements at frequencies at 3-6 Hz were often met by a resistance that was mainly elastic (Brown *et al.* 1982*a*, *c*), so that in the vector plots of joint resistance, the stiffness vectors at those frequencies lay close to the horizontal axis. When the subject exerted only a small flexing force, the vectors were above the axis, but when the flexing force was moderately large (Fig. 6A), the points representing the 4-6 Hz movements were often below the horizontal axis in the region of 'negative viscous' resistance; the force then actually assisted the movement of the joint, and there is no doubt that this downward displacement was a reflex response to the movement.

In Fig. 6A, the resistance to a 5 Hz movement was a force which may be represented as the vector sum of an elastic stiffness of 1.5 Nm/radian, and a smaller 'negative viscous' resistance. An added mass would meet a sinusoidal movement with a resistance that is opposite in its timing to the resistance of an elastic load, and the elastic stiffness of 1.5 Nm/radian could at 5 Hz be balanced by adding an appropriately chosen mass (moment of inertia of $1.52 \text{ g} \cdot \text{m}$). If such a mass were added to the terminal phalanx, the sole response to the 5 Hz movement would then be the small quadrature force which would appear as a negative viscous resistance tending to assist the movement. If a *linear* system with properties similar to those shown in Fig. 6A were coupled to such a mass, and were free to move, one would expect to see an oscillation at 5 Hz which would increase progressively in size, and indeed the system would be unstable. Fig. 6B shows the tremor that did in fact develop when

approximately that mass was added to the terminal phalanx; this was at about the predicted frequency, though it grew only so far, and then continued as an oscillation of limited amplitude. A limit cycle of this type was in fact to be expected, since the system is far from linear, and the reflex forces become relatively smaller as the amplitude of movement increases (Brown *et al.* 1982*c*, Fig. 2). A similar result was



Fig. 6. The relationship between sinusoidal driving and spontaneous tremor. A, vector representation of the resistance to an imposed movement of $\pm 1.3^{\circ}$ (23 mrad). Bold figures indicate the frequency in Hz. B, an example of spontaneous tremor with a compliant spring (stiffness equivalent to 0.1 Nm/radian), and an added inertia (equivalent to 1.64 g.m²). C, the spectrum of 10 sec of the tremor. The mean flexing force was 0.25 Nm for all records.

obtained at the elbow joint where the relative effectiveness of the reflex decreased with increasing amplitudes of movement (Joyce, Rack & Ross, 1974; Robson, 1962), and there were again spontaneous oscillations of limited amplitude (Joyce & Rack, 1974).

Since the 'negative viscous' resistance seen during sinusoidal movements at $3\cdot5-6$ Hz arises as a reflex response to the imposed movement, there can be little doubt that the large amplitude tremors seen in this frequency range are also attributable to the action of a reflex force which is so timed that it sustains the movement, though it is equally clear from Fig. 5 that within this range, the actual frequency of oscillation depended on the mechanical load.

If the joint, along with its inertial load, had merely behaved as an inert linear spring-mass system, which oscillated in response to random disturbing forces, the frequency of that oscillation would be inversely proportional to the square root of the mass, and the slope of a plot of frequency against $1/\sqrt{I}$ would be directly proportional to the square root of the spring stiffness. In the real situation (Fig. 5), the frequency of tremor was only approximately proportional to $1/\sqrt{I}$, indicating

that the effective elastic properties of the muscle changed with changing frequencies of movement. These changes in elastic stiffness with frequency have already been seen in the responses to sinusoidal driving; in this non-linear system, however, the precise relationship between frequency and mass could not have been predicted from the path of the joint stiffness vector for any single amplitude of movement, since that path would describe the resistance at only that amplitude, and the actual tremor had different amplitudes at different frequencies.

Although the addition of inertial loads was accompanied by tremors at the expected frequencies, the amplitude of the tremor was often considerably larger than could have been forecast from the response to sinusoidal driving. Tremor seemed to facilitate more tremor, and after a number of experimental runs our subjects would often exhibit violent oscillations when they flexed with quite a moderate force. Although a similar 'warming up' effect was seen during repeated periods of sinusoidal driving (see Brown *et al.* 1982*c*, Fig. 4), the effect was never so large as with spontaneous tremor. We concluded that the stretch reflex could vary in its sensitivity according to the task which the subject was attempting to perform. It seemed that the stretch reflexes were set up differently depending on the nature of the load against which he was working, and in particular, there was evidence of a more vigorous reflex when he flexed against a load that was freely movable, than when he exerted the same force against a machine which took charge and imposed the movement on the joint.

The 8-11 Hz tremor

Whereas the responses of the joint to sinusoidal driving indicate that a 3-6 Hz tremor may be the result of reflex activity, they indicate equally that an 8-11 Hz tremor of this joint is unlikely to arise in that way. At those frequencies, an imposed sinusoidal movement was met by a positive viscous stiffness, and therefore by forces which tended to oppose it. The timing of the reflex component of force was such that at 8-11 Hz it occurred too late in the cycle of movement to contribute the negative viscous stiffness which sometimes occurred at 3-6 Hz (Fig. 6A). Stretch reflex activity is unlikely, therefore, to play a major part in generating these 8-11 Hz tremors of the thumb. At this point, however, we again emphasize that conclusions drawn from experiments on the thumb may not be correct for other joints of the fingers and hand where the reflex timing is sometimes different (Brown, Rack & Ross, 1976).

Although the thumb stretch reflex was so timed that it would not support a continuing 8–11 Hz tremor, the reflex pathways did quite readily transmit intermittent activity in this frequency range, and in some subjects the reflex pathways appeared to have a particularly low impedance for 8–11 Hz signals, so that the reflex e.m.g.s and forces were both enhanced during sinusoidal movements in this frequency range (Brown *et al.* 1982*b. c*).

It was notable that the subjects who responded to 8-11 Hz sinusoidal movements with a particularly vigorous reflex e.m.g. or force, were the ones who also had the most clearly developed tremor in that frequency range. Possibly the same mechanism that generates the tremor may also enhance the reflex responses; Allum *et al.* (1978) have suggested that this type of tremor reflects the behaviour of the largest active motor units, and that many of these will be discharging at rates less than 12 impulses/sec. When motoneurones that are discharging action potentials at these rates are subjected to the intermittent afferent activity which arises from an imposed sinusoidal movement at a similar frequency, one would expect them to be entrained by the incoming afferent bursts, so that although their rate of discharge remained the same, the action potentials would tend to group together in one part of the cycle, and would thus appear to mediate the particularly powerful reflex response that we sometimes saw.

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REFERENCES

- ALLUM, J. H. J., DIETZ, V. & FREUND, H. J. (1978). Neuronal mechanisms underlying physiological tremor. J. Neurophysiol. 41, 557-571.
- BROWN, T. I. H., RACK, P. M. H. & Ross, H. F. (1976). Sinusoidal driving of finger joints. J. Physiol. 263, 184-185P.
- BROWN, T. I. H., RACK, P. M. H. & Ross, H. F. (1982a). Forces generated at the thumb interphalangeal joint during imposed sinusoidal movements. J. Physiol. 332, 69-85.
- BROWN, T. I. H., RACK, P. M. H. & Ross, H. F. (1982b). Electromyographic responses to imposed sinusoidal movement of the human thumb. J. Physiol. 332, 87-99.
- BROWN, T. I. H., RACK, P. M. H. & Ross, H. F. (1982c). A range of different stretch reflex responses in the human thumb. J. Physiol. 332, 101–112.
- DIETZ, V., BISCHOFBERGER, E., WITA, C. & FREUND, H. J. (1976). Correlation between the discharges of two simultaneously recorded motor units and physiological tremor. *Electroenceph.* clin. Neurophys. 40, 97-105.
- ELBLE, R. J. & RANDALL, J. E. (1976). Motor-unit activity responsible for 8-12 Hz component of human physiological finger tremor. J. Neurophysiol. 39, 370-383.
- ELBLE, R. J. & RANDALL, J. E. (1978). Mechanistic components of normal hand tremor. Electroenceph. clin. Neurophys. 44, 72-82.
- FURNESS, P., JESSOP, J. & LIPPOLD, O. C. J. (1977). Long-lasting increases in the tremor of human hand muscles following brief, strong effort. J. Physiol. 265, 821-831.
- HALLIDAY, A. M. & REDFEARN, J. W. T. (1956). An analysis of the frequency of finger tremor in healthy subjects. J. Physiol. 134, 600-611.
- 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, H. F. (1974). The forces generated at the human elbow joint in response to imposed sinusoidal movements of the forearm. J. Physiol. 240, 351-374.
- LIPPOLD, O. C. J. (1970). Oscillation in the stretch reflex arc and the rhythmical 8-12 c/s component of physiological tremor. J. Physiol. 206, 359-382.
- LIPPOLD, O. C. J., REDFEARN, J. W. T. & VUCO, J. (1957). The rhythmical activity of groups of motor units in the voluntary contraction of muscle. J. Physiol. 137, 473-487.
- MARSHALL, J. & WALSH, E. G. (1956). Physiological tremor. J. Neurol. Neurosurg. Psychiat. 19, 260-267.
- ROBSON, J. G. (1962). An analysis of the human stretch reflex. Ph.D. Thesis, Cambridge.
- STEIN, R. B. & OGUZTORELI, M. N. (1976). Tremor and other oscillation in neuromuscular systems. Biol. Cybernetics 22, 147-157.
- STILES, R. N. (1976). Frequency and displacement amplitude relation for normal hand tremor. J. appl. Physiol. 40, 44-54.
- STILES, R. N. (1981). Mechanical and neural feedback factors in postural hand tremor of normal subjects. J. Neurophysiol. 44, 40-59.
- SUTTON, G. G. & SYKES, K. (1967). The variation of hand tremor with force in healthy subjects. J. *Physiol.* 191, 699-711.
- TAYLOR, A. (1962). The significance of grouping of motor unit activity. J. Physiol. 162, 259-269.