

## A RANGE OF DIFFERENT STRETCH REFLEX RESPONSES IN THE HUMAN THUMB

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### SUMMARY

1. Imposed sinusoids were used to assess the resistance to movement at the thumb interphalangeal joint.

2. The resistance to high-frequency movements ( $> 12$  Hz) increased when the subject exerted a large voluntary flexing force; this increase was attributable to a greater non-reflex resistance of the contracting flexor muscles. This resistance was essentially 'visco-elastic', and the force was phase-advanced on joint position. At moderately large forces (up to half maximal), however, the resistance changed with changing frequency, and over a range 4–12 Hz the vectors which represented joint stiffness described the wide path that is characteristic of an active stretch reflex (Brown, Rack & Ross, 1982*a*). At frequencies between about 4 and 6 Hz the force was sometimes phase-delayed on position, and the joint exhibited a negative viscous stiffness. When the voluntary flexing force was very large the reflex contributed less to the resisting force, which was then phase-advanced on position at all frequencies of movement.

3. Large amplitude movements did not generate correspondingly large reflex responses; as the amplitude of movement was increased, the reflex component of the resisting force became relatively smaller and the total resisting force was then phase-advanced on joint position at all frequencies.

4. The reflex component of the resisting force (as indicated by the excursion of the joint stiffness vectors) varied from subject to subject and from time to time; the reflex usually became more active late in an experiment when the subject had exerted flexing forces against the imposed movement for some minutes. Extreme fatigue, however, diminished the amount of reflex force.

5. In some subjects the joint-stiffness records indicated a particularly vigorous reflex response at 8–11 Hz, in contrast to a rather feeble response at 6 or 7 Hz. It is suggested that the reflex pathways then had a relatively low impedance to afferent signals that were modulated at 8–11 Hz, related perhaps to the firing patterns of the most recently recruited motoneurons.

6. Under the conditions of these experiments, it appears that the stretch reflex has too small a gain to function as a very effective error-controlled position servo-mechanism.

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## INTRODUCTION

A previous paper (Brown, Rack & Ross, 1982*a*) described the response of the interphalangeal joint of the thumb to imposed sinusoidal movements and showed how these responses might be used in the assessment of stretch reflex activity. The resistance to movement could be described as a stiffness vector, and as the frequency of movement increased this vector described a C-shaped or spiral path whose extent gave a useful indication of the amount of reflex activity.

In this paper we describe some of the variations that occurred in our normal subjects. Sometimes the circular or spiral path of the vector changed in size, and we took this to indicate an increase in the amount of reflex response to the movements; sometimes the whole vector path was transported bodily towards or away from one of the axes. On yet other occasions we saw changes in the shape of the vector path, which was bulged outward or indented inward at particular frequencies, indicating that different frequencies of movement then engendered different amounts of reflex resistance.

The variations in reflex behaviour which we describe throw some light on the normal neuromuscular mechanisms, and this is interesting in itself; an understanding of these variations is also important if the method is to be used in the investigation of subjects with pathological disorders of motor control.

## METHODS

The experimental methods have already been described. (Brown *et al.* 1982*a*). The same six subjects were used as in that paper.

## RESULTS

In a simple invariant linear system the response to movements of a particular frequency remains the same under a range of different experimental conditions. In particular, an increase or decrease in the amplitude of movement is met by a proportional increase or decrease in the resisting force. The thumb interphalangeal joint was far from linear in its behaviour, and in the present experiments the C-shaped vector paths which described resistance at the joint changed appreciably in size, shape and position under different circumstances. There were differences between normal subjects, and differences during the course of a prolonged experiment on the same subject. More predictable and more consistent, however, were the variations that occurred when the same joint was moved through different amplitudes, or when the same subject exerted different mean flexing forces.

*The mean flexing force*

Fig. 1 shows the results of five experimental runs on one of our subjects. The amplitude of movement remained the same, but on each of the five occasions she exerted a different mean flexing force (marked on the Figure). When there was no voluntary force the different frequency points lay so close together that they could not be plotted separately. However, when she exerted a moderate force the stiffness

vectors followed a C-shaped path, and with increases in force up to 0.5 Nm (almost half her maximum) these Cs became progressively larger, indicating an increase in the reflex response to movement. Changes in the mean force had a similar effect on results obtained during sinusoidal movement of the elbow joint (Røbson, 1962; Joyce, Rack & Ross, 1974), and the reflex response to quick stretches is also known to increase in a similar way with increasing muscle activation (Marsden, Merton & Morton, 1972).

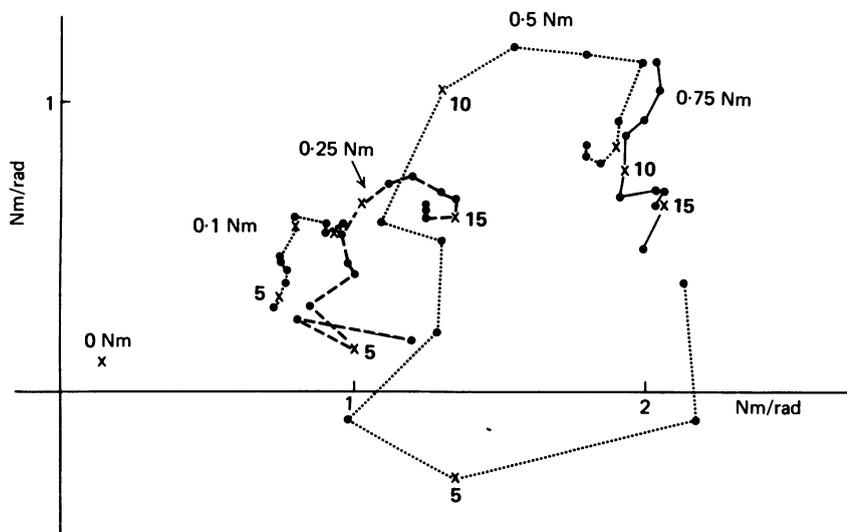


Fig. 1. The effects of mean flexing force on the response to an imposed sinusoidal movement. Resistance to movement is displayed as a number of vector paths, each of which was obtained from many consecutive cycles of progressively decreasing frequency (Brown *et al.* 1982*a*). Each point indicates the resistance at a particular (integer) frequency, and some of the frequencies (Hz) are included in bold type in this and other Figures. The 5, 10 and 15 Hz points are noted by a X in this and all the Figures in this paper. The four different vector trajectories were obtained with mean forces of 0.1, 0.25, 0.5 and 0.75 Nm (indicated on Figure). When the subject exerted no voluntary force, the resistance changed so little with frequency that the difference could not be shown on the present scale, and the resistance of the relaxed limb is indicated by the single X close to the origin. Amplitude of movement was  $\pm 3.9^\circ$  (68 mrad).

When the mean flexing force was increased still further (0.75 Nm in Fig. 1), the different frequency points again lay closer together, indicating that the reflex resistance was then reduced. During a maximum voluntary effort, changes in the frequency of movement had even less effect on the joint resistance and the result was similar to that seen in a motor tetanus (Brown *et al.* 1982*a*); the muscles were then 'hard on' and the reflex activity had no further effect on them.

At the higher frequencies of movement the low-pass filtering property of muscles (Marshal & Walsh, 1956; Bawa & Stein, 1976) attenuated any reflex modulation of the force, and we attribute most of the force changes that accompanied movements at 15 Hz or more to the mechanical properties of the muscles themselves (Brown *et al.* 1982*a*). When the subject exerted a larger mean force, there was more resistance

to these higher frequencies of movement, and in Fig. 1 the high frequency points (13–18 Hz) were displaced further upward and to the right, indicating that the larger muscle force was accompanied by a larger non-reflex resistance.

At lower frequencies, when the reflex could significantly modify muscle activity, the effect of the mean force on the total joint resistance was determined by the interactions between the reflex and non-reflex forces. In Fig. 1, an increase in the mean flexing force from 0.1 Nm through 0.25 Nm to 0.5 Nm displaced the lower frequency points downward and to the right, so that with a mean force of 0.5 Nm the sinusoidal force fluctuation lagged behind the position signal by about  $10^\circ$ , and the joint than presented a 'negative viscous resistance' which actually tended to assist the movement.

Fig. 4, which was obtained from a different subject, also illustrates the effect of increasing the mean flexing force. Again, the vectors described a wider path when the force was larger, though in this experiment the enlargement was particularly toward the origin of the plot, and the vector passed very close to this origin.

The downward movement of the 4 and 5 Hz points in Fig. 1 reflects the greater effect of the mean flexing force on the reflex than on the non-reflex resistance in that subject under those conditions. There were other occasions when the effect on the reflex resistance was smaller, and the Cs increased in size correspondingly less. An increase in the mean force was then accompanied by parallel increases in reflex and non-reflex resistance, so that the low-frequency points moved out horizontally to the right, or upward and to the right; there was then no frequency of movement at which the joint exhibited a negative viscous stiffness and at which the muscles were in danger of sustaining their own oscillatory movements (see Brown, Rack & Ross, 1977*b*, Fig. 1*A*).

#### *Different amplitudes of movement*

In a linear system the amplitude of the force fluctuation would be proportional to the amplitude of the movement, so that the measured stiffness would be independent of these variables. A previous series of experiments on the elbow joint (Joyce *et al.* 1974) showed however, that whereas a small sinusoidal movement might generate a relatively vigorous reflex response, an increase in the amplitude of movement was not accompanied by a corresponding increase in the reflex force. There was in fact a less effective reflex resistance to large disturbances than to small ones.

The thumb interphalangeal joint behaves in a similar way. In Fig. 2 the largest of the C-shaped paths (with the dashed lines) was obtained while driving the joint through a small angle ( $\pm 0.8^\circ$ ); the intermediate C (dotted lines) shows the response when the amplitude of movement was approximately doubled, and the smallest C (continuous lines) is the response to an amplitude that is almost four times the first one. Although there has been little change in the non-reflex stiffness and the 15 Hz points lie quite close together, the decreasing size of the C-shaped paths indicates a relative decrease in the reflex response as the amplitude of movement increased. A significant reflex component did, however, remain at amplitudes of movement which were considerably larger than those which generated a large reflex response at the elbow joint. In Fig. 2 there was sufficient reflex activity to cause a negative viscous stiffness during a  $\pm 1.4^\circ$  movement at 4 Hz, and a similar negativity was

occasionally seen with movements as large as  $\pm 5^\circ$ . These movements are much larger than were normally used at the elbow joint where amplitudes of more than  $\pm 0.25^\circ$  never gave rise to negative viscous stiffness.

Although the reflex resistance was relatively large when the movement was small, one should note that the absolute force changes associated with the movement were

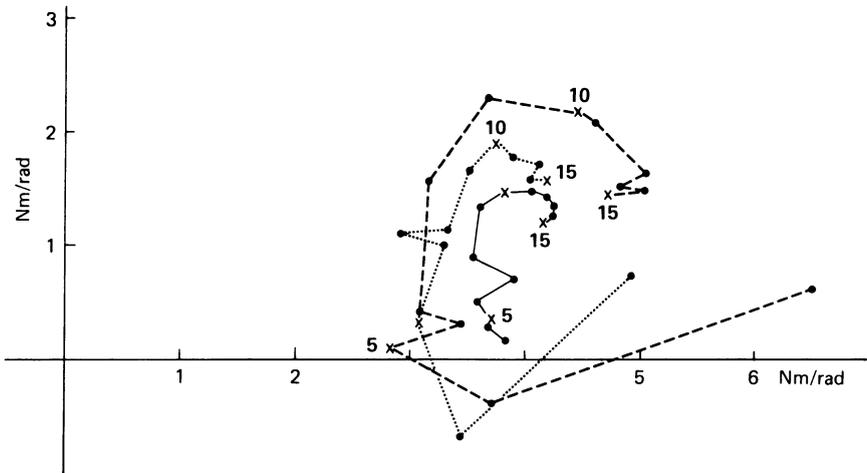


Fig. 2. The response to different amplitudes of sinusoidal movement. Vector plots of the resisting force obtained in the same way as for Fig. 1. Dashed line:  $\pm 0.75^\circ$  (13.5 mrad); dotted line:  $\pm 1.3^\circ$  (25 mrad); continuous line:  $\pm 2.6^\circ$  (46 mrad). Mean flexing force was 0.75 Nm, which was about a half of this subject's maximum.

still quite small. Indeed, the spontaneous force fluctuations of the contracting muscles were often comparable with the forces due to the movement, and the total force record was then complicated and far from sinusoidal. Under these circumstances the present method of analysis extracts only that part of the response that is locked to the movement, and does not necessarily give a complete picture of the forces at the joint. Interactions between spontaneous tremor and an imposed sinusoidal movement will be more fully described in a later paper.

#### *Spontaneous variations in reflex activity*

A progressive change in reflex activity often occurred during the course of a series of experimental runs, and this was most often seen in experiments where the subject maintained a relatively small flexing force for long periods. When the mean flexing force was small the amount of reflex activity, as judged by the size of the C-shaped vector path, often increased with successive experimental runs. In the experiment of Fig. 3 the subject exerted a mean force of less than a fifth of his maximum, and in the first sequence of movements (A) the small excursion of the stiffness vector indicates a rather feeble reflex response. Fig. 3 B was obtained under exactly similar experimental conditions, but later in the day after the subject had exerted the same force for twelve 2 min periods. There was then a well developed C-shaped trajectory, indicating much more vigorous reflex activity. It seems that a period of muscular

activity was necessary to 'warm up' the reflex mechanism; a similar effect of muscular exertion on physiological tremor has been reported (Furness, Jessop & Lippold, 1977). Although this increase in reflex activity was often seen during the course of an experiment it was never so evident as at the ankle joint (Rack, Ross & Walters, 1980).

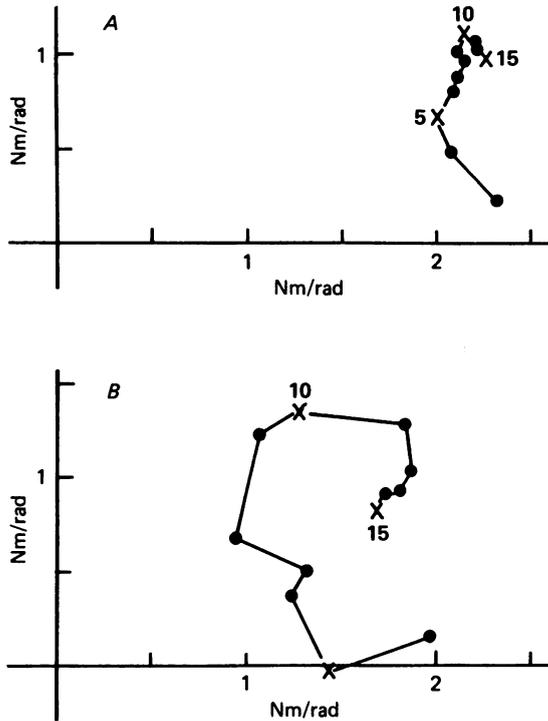


Fig. 3. Two records from the same subject on the same day. Stiffness vectors plotted as in Fig. 1. The movement was through  $\pm 1.4^\circ$  (24 mrad), while the subject exerted a mean force of 0.25 Nm. *A* shows the resistance to the first experimental run of the day. After this the subject exerted the same force for twelve 2 min periods, and *B* shows the resistance to the same movement when he returned to the experiment after a 2 hr rest.

When the subject exerted a large (half-maximal) flexing force, we usually saw vigorous reflex activity right at the beginning of the experiment, and this did not then increase as the experiment went on; in fact the amount of reflex activity (the size of the C) often decreased as the subject became fatigued and experienced difficulty in maintaining the force. The fatiguing muscles were presumably then approaching their maximal force and behaving in a way that was comparable with a rested muscle which was almost fully activated (Fig. 1, 0.75 Nm).

#### *The different behaviour of different thumbs*

There were quite wide differences between different subjects. Some showed a considerable reflex response even when the mean flexing force was quite small, and

this grew into a very large response at high forces (Fig. 4). In others there was little reflex activity with small forces, and it was only when the subject exerted a much larger force that any appreciable reflex response could be recorded. In the subject of Fig. 4 a mean force of 0.25 Nm was accompanied by a considerable reflex response (continuous line), but when some other subjects exerted the same force under the same conditions the reflex response to the movement could hardly be detected; even with a very much larger force the stiffness vector might still describe a relatively small circle which always remained above the horizontal axis (see Brown *et al.* 1982a, Fig. 2).

#### *The different paths of the force vector*

We have hitherto described the force vector as following a C-shaped path, and we have related the size of its excursion to the amount of reflex activity. There were sometimes irregularities in this path, indentations into it, or outward bulges, so that adjacent frequency points might lie at very different distances from the knot of high-frequency points. These displacements of the path of the vector towards, or away from the assumed non-reflex stiffness were taken to indicate that the muscles generated very different amounts of reflex force in response to movements of different frequencies.

One fairly common distortion of the vector path is illustrated in Fig. 1 (0.5 Nm record). Here the 7 and 8 Hz points were displaced to the right to give the appearance of a 'bite' into the C-shaped path. Although this inward displacement did not always occur, it was far from exceptional and we saw it at some time in each of our subjects. This 'deformation' of the vector path usually occurred with the same conditions that led to a well developed reflex response, so that it was often seen when the movements were small and the subject exerted a moderately large flexing force. It was presumed that on those occasions the inward displacement of the 8 Hz point indicated a smaller reflex response to an 8 Hz movement than to a movement at 6 or 9 Hz.

Two of our subjects sometimes showed a very marked displacement of certain frequency points, so that the vector path bulged outward in a wide loop. In Fig. 5 the 8–11 Hz points form such a bulge, while the 6 Hz point is displaced inward toward the high-frequency points. Another example is shown in Fig. 4 where the 7–9 Hz points were widely separated and the vector path may actually encircle the origin. The subjects who showed these wide excursions of the stiffness vector also had a considerable spontaneous tremor of the joint. During the experiments shown in Figs. 4 and 5 force fluctuations unrelated to the imposed movement often had an amplitude that was comparable to the forces at the frequency of movement. Records such as these were usually obtained when the subject exerted a high force and the movement was small.

The interactions between spontaneous tremors and driven sinusoids will be described in a later paper; for the present it should be noted that when records showed an outward displacement with wide separation of the frequency points, as in Figs. 4 and 5, the force fluctuations were often far from sinusoidal, so that the force responses to successive cycles of the movement might appear to be very different from each other. The 8–11 Hz points of Fig. 5 thus represent the average response from widely different individual cycles.

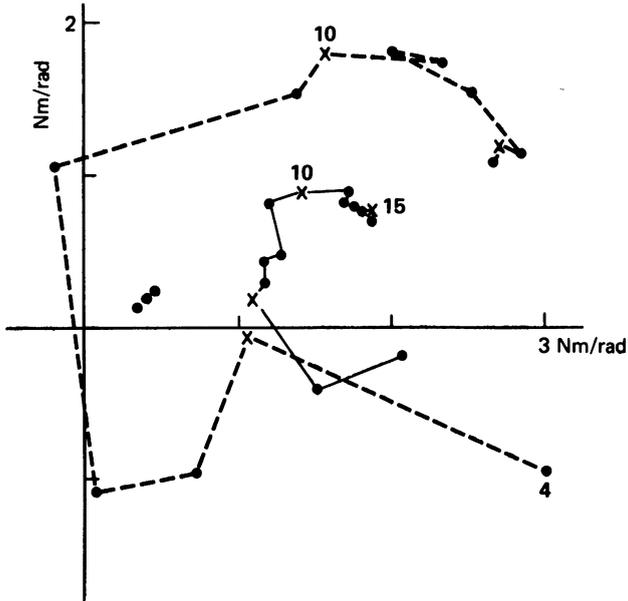


Fig. 4. The effect of mean flexing force on the resistance to sinusoidal movement. Plotted in the same way as Fig. 1, but from a subject with particularly active reflex. Mean flexing forces were 0.5 Nm (dashed line), 0.25 Nm (continuous line) and zero (the three points near the origin). Movement  $\pm 1.3^\circ$  (22.5 mrad.).

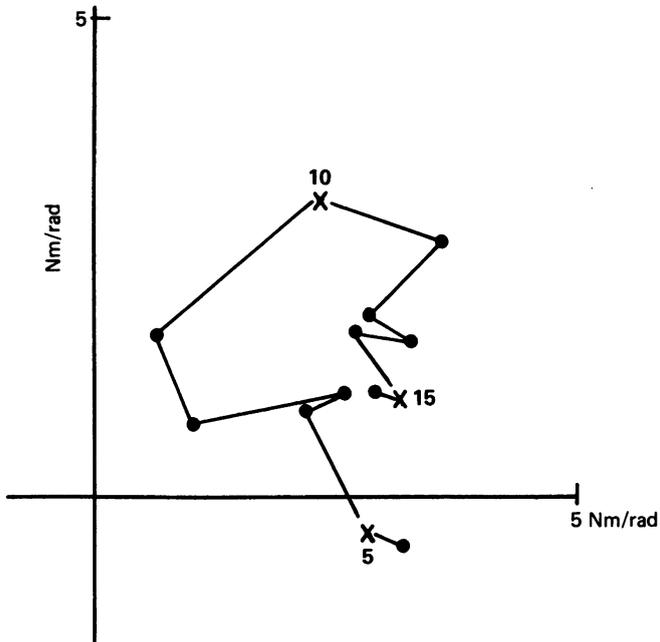


Fig. 5. The response to a movement of  $\pm 0.5^\circ$  (9 mrad) while the subject exerted a moderately large mean flexing force (0.5 Nm).

## DISCUSSION

Changes in the mean flexing force altered the resistance to movement in ways that might have been expected. The increase in non-reflex resistance to the high-frequency movements corresponds to the higher level of muscle stiffness that normally accompanies more intense activation, and an increase in reflex activity is known to accompany a vigorous effort (Marsden *et al.* 1972).

At frequencies 4–6 Hz the two components of force have opposite effects on the viscous stiffness and tend to offset each other, so that the reflex force can increase as the mean force increases without necessarily leading to a state of negative viscous resistance. In practice, however, the increase in reflex activity was often so great that at high forces the joint did exhibit negative viscous stiffness at some frequencies. A similar result was found during some experiments on the elbow joint (Joyce *et al.* 1974).

*The shape of the vector path*

When there were distortions in the shape of the vector path, and slightly different frequencies of movement were met by a very different resistance (the 7 and 8 Hz points in Fig. 5), one must assume that it was the reflex component of force that changed so abruptly, since no large alteration in non-reflex stiffness would accompany these small frequency changes. There is, however, no reason to suppose that the activity of the muscle spindles would change dramatically with this small change in the frequency, so one must presume that the intermittent afferent signals were handled by the spinal cord in ways that depended heavily on the movement frequency. In the case of Fig. 5, the reflex pathway seems to have behaved as a filter which passed signals at 8–11 Hz quite freely, to give a large reflex force, and the vector path bulged far outwards. By contrast, signals at 7 Hz must have been attenuated, since at that frequency the vector path moved in toward the high frequency points. Electromyograms were not recorded during the experiment of Fig. 5, but on other occasions e.m.g.s from this same subject were modulated much more deeply by movements in this middle frequency range than by higher or lower frequencies (Brown *et al.* 1982*b*).

The outward bulge seen in Fig. 5 is a striking example of something that was often present, though it was seldom so well developed as in that Figure; the same phenomenon may be seen in Fig. 3*B*. An inward indentation of the vector path at 7 Hz may also be seen in Fig. 3*B* and in Fig. 1 (0.5 Nm).

Although we lack information about the properties of the flexor pollicis longus motor units, there is detailed information about the behaviour of the first dorsal interosseous muscle (Freund, Budingen & Dietz, 1975), and in this muscle the largest motor units that are active in a sustained contraction have a discharge rate that is usually between 7 and 10 Hz. If the flexor pollicis longus motor units behave in the same way, then it seems likely that during movements in the 8–11 Hz range the incoming bursts of afferent activity are entraining these motoneurons so that they then discharge in a more synchronized way and in a particular part of the cycle of movement, and thus appear to mediate a particularly vigorous reflex activity. In support of this suggestion is the fact that this distortion of the vector path is usually

seen when the subject exerted rather a large force in which the larger motor units must certainly be employed, and this result is particularly clearly seen in subjects with a pronounced 'physiological tremor' whose motor units might be expected to show a degree of synchronization (Dietz, Bishcofberger, Wita & Freund, 1976).

Conversely, these same motor units may be relatively inaccessible to bursts of afferent activity at rather low frequencies if they are already discharging spontaneously at their 'own rate'; this may account for a reduction in the amount of reflex activity at or about 7 Hz in many of our records.

### *Stability*

Vector representations of the joint stiffness make a useful starting point for a consideration of the stability of stretch reflexes. When the vector passes through the origin of the plot the stiffness is zero (see Fig. 4), and at that frequency the sinusoidal movement proceeds without any corresponding fluctuations in the driving force, and with no external energy being required to sustain the movement. One would expect that such a joint would continue to oscillate indefinitely if it were de-coupled from the driving mechanism. Such spontaneous oscillations do indeed occur when the thumb flexes against an appropriate compliant load (Brown, Rack & Ross, 1977*a*), as is described in detail in a later paper (Brown, Rack & Ross, 1982*c*).

When the path of the stiffness vector actually encircles the origin, one would anticipate spontaneous oscillations whose amplitude would increase in succeeding cycles. However, when, the vector approaches close to the origin without encircling it this indicates a system which (when de-coupled from the driving mechanism) would respond to perturbations with a decaying oscillation. In a linear system knowledge of the open-loop response to sinusoidal driving enables one to predict the behaviour of the unrestrained system quite precisely. Human limbs are far from linear in their responses, and predictions about spontaneous oscillations should probably be confined to those situations when the vector path passes quite close to the origin; even then these predictions apply only to spontaneous oscillations at amplitudes similar to those for which the vector path was determined.

It is in fact unusual for sinusoidal movement of this joint to require so little force that the path of the stiffness vector passes close to the origin; there were, however, many occasions when the path of the stiffness vector passed below the horizontal axis, so that at some frequencies there was a negative viscous stiffness though the elastic stiffness remained positive and fairly large. The presence of a mass would affect the resistance to movement in a way that would tend to offset the elastic stiffness and displace the vectors towards the left; by adding mass to the terminal phalanx one could thus create a situation in which the path of the joint-stiffness vector would often pass through or encircle the origin. Spontaneous oscillations were therefore to be expected in most of our subjects when a sufficient mass was attached to the terminal phalanx, and they exerted an appropriate force (see Brown *et al.* 1982*c*).

### *The loop gain*

So far, we have described our results and their implications without assuming that the stretch reflex has the 'purpose' of controlling any particular variable. The stretch reflex has, however, often been regarded as a position controlling servo-mechanism

(Hammond, 1960; Merton, 1953), and it is pertinent to ask how far the present results can support that suggestion. More specifically: is there sufficient gain in the position-correcting mechanisms to maintain an effective servo-control of limb position?

The (dimensionless) loop-transfer function cannot be measured directly in human subjects, but for a particular amplitude of sinusoidal movement it is related to limb stiffness as follows.

Suppose the digit (or limb) to meet the movement with a reflex resistance  $R$  and a non-reflex resistance  $N$ , where both  $R$  and  $N$  are complex functions of frequency with the dimension torque/displacement, and  $N$  includes the additional resistance arising from the properties of the moving parts, whether within the digit, or in some external attachment (experimental apparatus, or an object held in the hand). The stiffness which we measure is then the vector sum of these two quantities ( $R + N$ ).

If the digit (or limb) were free to react to displacement (which for convenience we take to have unit amplitude), the force  $R$  would generate its correcting movement by acting through the compliance of the load (distance/force) which has the value  $1/N$ ; the loop-transfer function would be the product of the reflex force and the load compliance  $-R/N$  (the negative sign arising from the fact that a lengthening movement generates a shortening response).

When the total stiffness ( $R + N$ ) is zero (the vector passes through the origin), then  $R = -N$  and the loop-transfer function  $-R/N$  has the value  $+1$ . The reflex loop then provides a position feed-back with a gain of 1, which is so timed that it supports an oscillatory movement; in fact this is the critical condition under which a continuing oscillation will occur.

For other situations, when the total stiffness  $R + N$  is not zero, the loop-transfer function can only be deduced by performing the vector division  $R/N$ , and this requires an estimate of the separate values of the reflex and non-reflex stiffness at that frequency. If one assumes that the position of the high-frequency points gives an approximate indication of the non-reflex stiffness (Brown *et al.* 1982*a*), then it becomes clear that in the present experiments the modulus of the loop-transfer function  $R/N$  was always small (seldom greater than 1), and it never approached the values that an engineer would expect to see in an effective error-controlled position servo-mechanism. Quite different experiments on other joints have also led to the conclusion that the gain around the stretch reflex pathway is rather low (Valbo, 1974; Matthews, 1972; Bizzi, Dev, Morasso & Polit, 1978).

Implicit in the above discussion is the assumption that the resistance to joint movement can be divided into reflex and non-reflex components, and that the muscle properties will impede a reflex movement with the same stiffness that one measures with an externally imposed sinusoid. If the vector actually passes through the origin (and there is no large force fluctuation at other harmonically related frequencies) the above assumption is probably quite safe. The sum of  $R$  and  $N$  is zero, so that the quotient  $-R/N$  must therefore be 1, and this will remain true however the reflex and non-reflex responses of the muscles are involved with each other. When the stiffness vector is well away from the origin, deductions about loop gain come to depend much more heavily on choosing the correct value for the non-reflex stiffness and on the assumption that the resisting forces can be divided up in this simple way.

We therefore stop short of giving actual values for reflex loop gains, and merely conclude that in this experimental situation they remain small.

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