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# THE TENDON OF FLEXOR POLLICIS LONGUS: ITS EFFECTS ON THE MUSCULAR CONTROL OF FORCE AND POSITION AT THE HUMAN THUMB

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## SUMMARY

1. Human flexor pollicis longus tendons obtained at autopsy were subjected to repeated sinusoidal stretching movements. The associated force changes were almost in phase with the movement (force led position by $< 4°$), and alterations in the frequency of movement between 2 and 16 Hz had little effect on them.

2. Examination of the thumbs of formalin-fixed cadavers demonstrated that the tendon exerts its force 7·4–8·0 mm in front of the axis of movement of the interphalangeal joint.

3. From a knowledge of the tendon properties and the joint anatomy, one can calculate the changes in tendon length that would accompany any force change at the joint. Equipped with this information one can re-examine the responses to sinusoidal movements of the thumb interphalangeal joints of normal subjects.

4. When the subject exerts a steady flexing force in which stretch reflexes play no important part, measurements of joint stiffness indicate that only a portion of the imposed movement reaches the muscle fibres. The extension of those (visco-elastic) muscle fibres lags behind the extension of the (elastic) tendon.

5. Stretch reflexes contribute to the mechanical resistance of muscle fibres to low frequency (3–5 Hz) displacements, but in the presence of a compliant tendon the length of the muscle fibres does not determine the angle of the joint in any positive way.

6. It is suggested that the compliant tendons of many thumb and finger muscles simplify the neuromuscular control of forces during gripping and handling movements.

## INTRODUCTION

In many investigations of the stretch reflex, joints of human volunteers have been subjected to mechanical disturbances, and the resulting forces or electromyograms have provided information about muscle properties or about the reflex behaviour. However, these joint movements are transmitted to muscles by elastic tendons (see Elliott, 1965; Alexander, 1981), and one cannot assume that the muscle fibres and muscle spindles see all the movement that is imposed on the joint. When the externally imposed movement is met by an increase in force in the opposing muscles, some of the movement is taken up in stretching the tendons, and only a part of it reaches the muscle fibres. During dynamic stretching of the muscle–tendon combination, the *elastic* nature of the tendon in series with a *visco-elastic* muscle implies that there will be phase differences between the length changes in the tendon and in the muscle fibres. Therefore one cannot assume that the joint movements give a simple indication of the changes that are taking place in the muscle fibres and the associated spindles; indeed, the phase differences between joint movement and muscle fibre extension sometimes become large and they then complicate any analysis of the reflex responses to a perturbation (Rack, Ross, Thilmann & Walters, 1983).

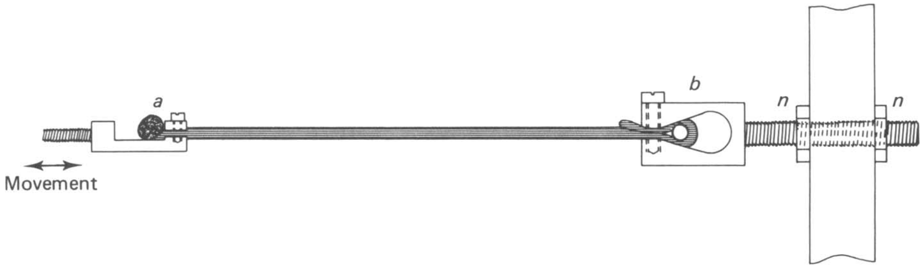

Fig. 1. The method of mounting tendons for stiffness measurements. For description see text.

The human flexor pollicis longus muscle has often been used in the investigations of stretch reflexes (Marsden, Merton & Morton, 1972, 1976; Marsden, Merton, Morton, Rothwell & Traub, 1981; Matthews, 1984; Brown, Rack & Ross, 1982*a*–*c*). This muscle acts through a long tendon which extends far beyond the most distal muscle fibres; in the present paper we describe some mechanical properties of this tendon. With a knowledge of its properties we then return to results obtained during sinusoidal movement of the intact thumb, and compute the forces and movements that occurred at the muscle fibres and spindles. The results of these computations indicate that a large proportion of the imposed movement was often 'lost' in the tendon. The muscle fibres themselves were much stiffer than could have been expected from the 'raw' measurements of joint resistance, and the stretch reflex often made an important contribution to that resistance.

## METHODS

*Measurements of fixed specimens.* The flexor pollicis longus was examined in dissections of four limbs in three formalin-fixed human cadavers; two were female, one was male. After measuring the lengths of the tendons and of the bundles of muscle fibres, the proximal phalanx was held securely by two pairs of steel pins, and a pointer was attached to the distal phalanx. The pointer enabled accurate measurement of the joint angle, while the position of a marker on the tendon was measured with vernier calipers. During these measurements a constant force was applied to the tendon. By comparing these measurements, linear movements of the tendon could be related to angular movements of the joint.

We shall describe the position of the joint in terms of the angle between the dorsal surfaces of the proximal and distal phalanges (proximal to the nail bed). In previous experiments on living subjects this angle was usually about 150° (Brown *et al.* 1982*a*–*c*), and we have therefore made most of our measurements at approximately this angle.

*Fresh specimens.* Measurements were made on six flexor pollicis longus tendons which were removed at autopsy with the permission of the next of kin. The part of the tendon that extended beyond the muscle fibres was removed, along with some of its intramuscular extension. A part of the terminal phalanx was also removed in continuity with the tendon. The tendon was then clamped at both ends and subjected to repeated sinusoidal stretching while the resisting forces were measured.

Movements were generated by a rotating wheel and crank mechanism which has already been described in detail; movements were measured by a photo-electric position transducer, and forces were measured with a device that employed semiconductor strain gauges (see Brown *et al.* 1982*a*; Evans, Fellows, Rack, Ross & Walters, 1983). Movements were applied to the distal end of the tendon, which was held in a purpose-made clamp (*a* in Fig. 1); a fragment of the terminal phalanx engaged behind the clamp and ensured a secure attachment. The proximal end was more difficult to hold securely; the method finally used was as follows: the part of the tendon that received the most distal muscle fibres was folded and fixed back on itself with linen thread and cyanoacrylate glue (Loctite Superglue) to form a loop. This loop was passed round a short steel pin (diameter 2 mm), and both loop and pin were wedged in a tapering slot (*b* in Fig. 1). With this arrangement, tensions of up to 150 N could be applied to the tendon without slippage. This static clamp was attached by a $\frac{3}{8}$ inch screw to a rigid assembly of steel bars; by rotation of nuts (*n*) on this screw the mean length of the tendon and its mean force could be adjusted.

Estimates of tendon stiffness were derived from forces measured during repeated sinusoidal stretching movements. The method was essentially similar to one that has been used for the investigation of living joints (Evans *et al.* 1983) and much of the same equipment was used. The force transducer, clamps and mountings were designed to be rigid, and altogether these elements yielded by 0·71 $\mu$m/N. Our measurements must therefore have underestimated the tendon stiffness by this small amount. This error was usually disregarded.

*Living subjects.* In order to compare measurements of tendon properties with measurements of resistance at the interphalangeal joint, we carried out some additional experiments in which the joints of normal subjects were subjected to imposed sinusoidal movements. The method has been fully described in a previous paper (Brown *et al.* 1982*a*).

## RESULTS

### *Anatomy*

Flexor pollicis longus is a unipennate muscle with bundles of muscle fibres which are 40–50 mm long when the thumb is extended. 100–130 mm of tendon lies on the surface of the muscle, and the tendon extends a similar distance beyond the most distal muscle fibres to reach its insertion into the terminal phalanx. The proximal muscle fibres are in line with the tendon, but the more distal ones join it at an angle which may be as low as 160°. When the wrist is held in a neutral position, the tendon curves round the trapezium to reach its insertion, but its course becomes straight when the wrist is held in ulnar deviation.

When the proximal phalanx was rigidly fixed and the angle between the proximal and distal phalanges was 130–170°, each degree of joint movement was accompanied by 0·13–0·14 mm movement of the tendon. In this part of its range the tendon thus behaved as though it were attached at a point 7·4–8·0 mm from the axis of movement.

### *The elastic nature of tendons*

Fig. 2 shows the forces which developed in a tendon during sinusoidal stretching at two different frequencies. When the mean force was small (Fig. 2*A*), the tendon was relatively compliant and imposed movements led to only small force changes. When the tendon was stretched by adjustment of the nuts (*n* in Fig. 1), the mean force increased, and this increase was accompanied by an increase in stiffness, so that the same sinusoidal movement was then accompanied by larger force fluctuations (Fig. 2*B* and *C*). When, however, the tendon was stretched still further with a further increase in force, the stiffness and the consequent force fluctuations increased by only a small amount (Fig. 2*D*). These effects of mean force on tendon stiffness are well known (Gratz, 1931; Rigby, Hirai, Spikes & Eyring, 1960; Diamant, Keller, Baer, Litt & Arridge, 1972; Ker, 1981); they can be seen more clearly when the stiffness (modulus of force/movement) is plotted as a function of the mean force (Fig. 3*A*). When the force was small the stiffness rose steeply with each increment in force, but above about 70 N the curve tends to level off, and the stiffness then changed less. At these high forces the behaviour of the tendon became closer to that of a linear spring.

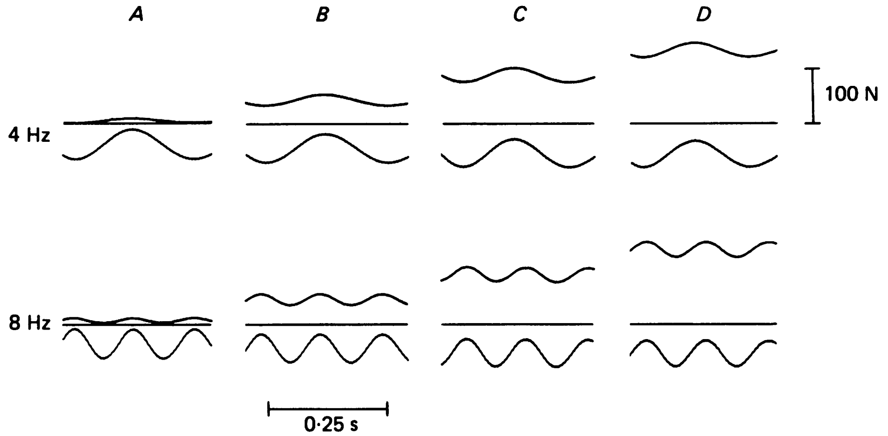

Fig. 2. Sinusoidal stretching of a tendon. In each sample of record the length change appears below (increasing length upward); force records are shown above. The four different mean forces *A–D* were achieved by adjustment of the nuts (*n* in Fig. 1). The upper records were obtained during movement at 4 Hz, the lower ones at 8 Hz. Amplitude of movement ±0·19 mm. The tendon was from a woman aged 35 of medium stature who died in a road traffic accident the previous day.

These results are similar to those that have been obtained for other tendons by other methods (Woo, Ritter, Amiel, Sanders, Gomez, Kuei, Garfin & Akeson, 1980; Ker, 1981).

To construct the more usual length/tension diagram from Fig. 3*A* it is necessary to convert stiffness into compliance, and then integrate this with respect to force. For this tendon a 1 mm extension would have increased the force from 5 to 50 N. In some other tendons a direct measurement of lengths and forces gave a similar result.

In Fig. 2 the force changed approximately in phase with the movement, as one would expect if the tendon were an essentially elastic structure. Sinusoidal analysis of longer records shows that the resisting forces do in fact lead the movement, but only by 2–4°, and it is notable that this phase lead remained small at all frequencies between 1·5 and 16 Hz (see Fig. 3*C*).

Changes in the frequency of movement between 1·5 and 16 Hz had only a minimal

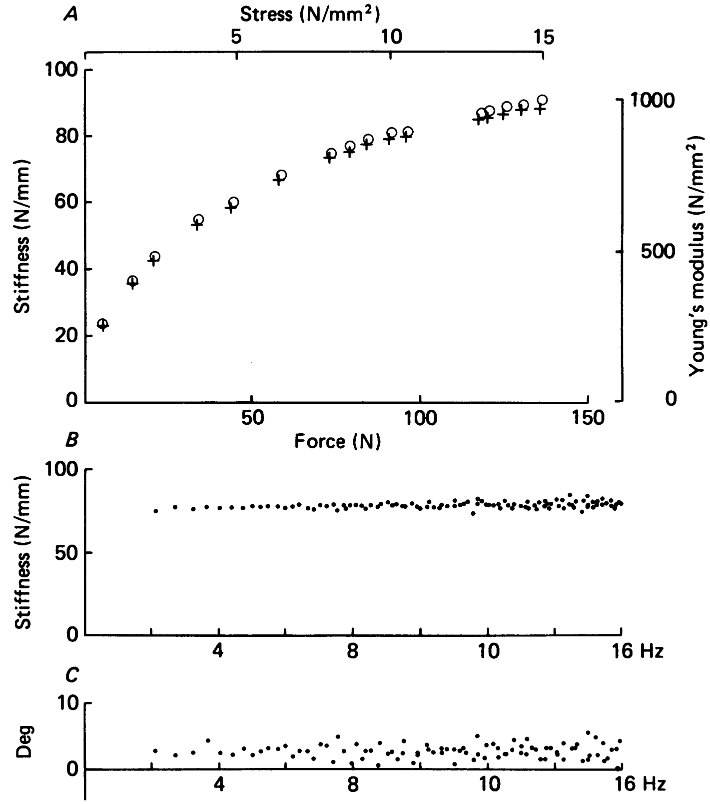

Fig. 3. *A*: the effect of mean force on the stiffness of a 100 mm length of tendon (the same tendon as for Fig. 2). The stiffness was computed from the records of thirty-two experimental runs during each of which the frequency was reduced from 15 Hz to zero. The mean force was adjusted to a new level before each run. At each force ○ indicates the average stiffness for all the cycles of frequencies 10–14 Hz; + is from cycles at 2–6 Hz. Amplitude of movement ±0·19 mm. Force is shown in Newtons on the lower scale, and stiffness is shown as N/mm on the left-hand scale. The cross-sectional area of this tendon was 9·1 mm² (determined by weighing a known length, and measuring its density by flotation in a chloroform–benzene mixture; see Ellis, 1969; Ker, 1981). This allowed us to express the mean force also as a stress (upper scale) and the stiffness as a Young's modulus (right-hand scale). *B*: the amplitude (expressed as stiffness) and *C*: the phase of the force fluctuations at different frequencies. This record shows the responses to all the ninety cycles of movement that made up one sweep of decreasing frequencies. Each dot indicates the value for amplitude or phase that was computed for a single cycle. Mean force was 84 N.

effect on the tendon resistance. There was generally slightly more resistance to the faster than to the slower movements (Fig. 3*B*) and this may be seen as a small separation of the different points in Fig. 3*A*. All the tendons that we examined had mechanical properties similar to those shown in Fig. 3; the stiffness increased with increasing force, and the force sinusoid led length by less than 4°. By chance, it happened that five of our six fresh tendons came from women, and these were all similar in stiffness. The other tendon which came from a large male subject was longer (130 mm of tendon distal to the muscle fibres), and measurement of this longer length gave stiffness values that were similar to those obtained from the shorter female tendons, though the stiffness/unit length was higher.

From a knowledge of the length and cross-sectional area of a tendon it is possible to calculate the stress for each mean force (indicated along the top of Fig. 3*A*) and to deduce a Young's modulus for each force range (the scale on the right). The values obtained were comparable with those that have been obtained for sheep plantaris tendons (Ker, 1981) and for pig digital extensor tendons (Woo *et al.* 1980).

A stiffness that is measured in this way takes no account of the non-linearity of the length–tension relation within the range of each measurement; it is in fact the amplitude of the *fundamental* component of the force record, divided by the amplitude of the movement. However, when the amplitudes of movement are small this measure of Young's modulus approximates to the 'tangent modulus' measured from a length–tension plot.

### *Effects of tendon on muscle properties*

A knowledge of the mechanical properties of the tendon and of its relation to the thumb interphalangeal joint enables one to calculate how much of an imposed movement of the distal phalanx would be taken up in the tendon, and how much would reach the muscle fibres. Such calculations depend on a number of assumptions (see Discussion) and, in particular, one has to apply measurements made on dissected specimens to the joints of living subjects. Even though these calculations are necessarily rather approximate, the results indicate the importance of the effects of an elastic tendon.

Fig. 4 (△) shows the angular stiffness measured at the thumb interphalangeal joint of a normal living subject when he exerted a range of different flexing torques. In this experiment he gradually increased the torque from zero to a high level while the joint was continuously driven through sinusoidal flexion–extension movements at 12·8 Hz. At frequencies of 12 Hz or more, stretch reflexes play little or no part in the resistance to movement (Brown *et al.* 1982*a*), and we assume that these stiffness/torque relationships of Fig. 4 were largely determined by the 'non-reflex' properties of the flexor pollicis longus muscle along with its tendon.

The stiffness of the flexor pollicis longus tendon may also be expressed in terms of resistance to angular movement of the joint, and this is shown by the dashed line (○) drawn on Fig. 4. This line was derived from the 10–14 Hz records of Fig. 3*A*, and it indicates the angular stiffness that one would see if that tendon were attached to the distal phalanx 7·7 mm from the axis of rotation, but with its proximal end anchored to bone without any interposed muscle fibres. This line indicates stiffnesses which are almost double the values that were actually measured at the joint, and it is notable that the tendon stiffness and joint stiffness both increased together as the mean force increased.

In the experiment of Fig. 4 the wrist was fixed in a position of ulnar deviation so that the flexor pollicis longus tendon was as straight as possible (see Brown *et al.* 1982*a*, Fig. 1) and the extensor muscles of the thumb were paralysed by a radial nerve block to prevent any co-contraction. For the moment we assume that friction in the joint can be ignored.

The values plotted in each record of Fig. 4 are for the modulus of stiffness (force/displacement) and they take no account of phase differences between force and position. When the tendon alone was examined, these differences were small (Fig. 3*C*)

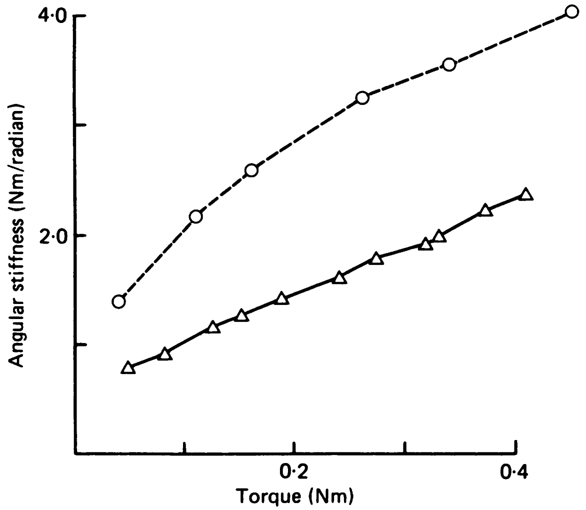

Fig. 4. The effect of mean force on joint stiffness. The thumb interphalangeal joint was subjected to continuous sinusoidal movement at 12·8 Hz while the subject progressively increased his flexing force. The extensor muscles had been paralysed by lignocaine anaesthesia of the radial nerve. The continuous line (△) indicates the stiffness (Nm/radian) in 275 consecutive cycles of movement, each point being an average from 25 cycles. Amplitude of movement ±2·0°. The dashed line (○) was obtained from the data of Fig. 3*A*, and expresses that tendon stiffness as the angular stiffness which it would give if its distal end were attached to the terminal phalanx at a point 7·7 mm from the axis of joint rotation, while its proximal end was rigidly fixed.

but when the intact muscle–tendon combination acts on a normal joint they are often much larger (Brown *et al.* 1982*a*). Fig. 5*A* shows these same results displayed as a polar plot, and again the circles (○) indicate the tendon properties, while triangles (△) show the responses of the intact normal wrist. These are vector plots in which the distance of any point from the origin indicates the modulus of stiffness, while the angular elevation above the horizontal axis indicates the phase advance of force on position. As the mean force increased, each of these vectors moved out further from the origin, but whereas the phase angle of the tendon records remained very small, the force at the intact joint led position by up to 37°.

If (for the present) we ignore the compliance of the part of the tendon which extended onto the surface of the muscle, and assume that our measurements give the stiffness of the complete tendinous attachment, then it is possible from the estimates of tendon stiffness to calculate how much of an imposed movement would be 'lost' in the tendon, and thus to determine the fraction of the movement which would reach the muscle fibres (see the legend to Fig. 5). This calculation was carried out point by point, and the results are shown in Fig. 5*B*. Again, the results are vectors, but in this diagram the distance of each point from the origin indicates the proportion of the total movement which would reach the muscle fibres, while the angular displacement below the horizontal axis gives the angle by which the muscle fibre movement would lag behind the imposed joint movement. Fig. 5*B* shows that the muscle fibres moved through a distance that was about 0·6 of the imposed movement, and lagged behind the joint movement by up to 37°.

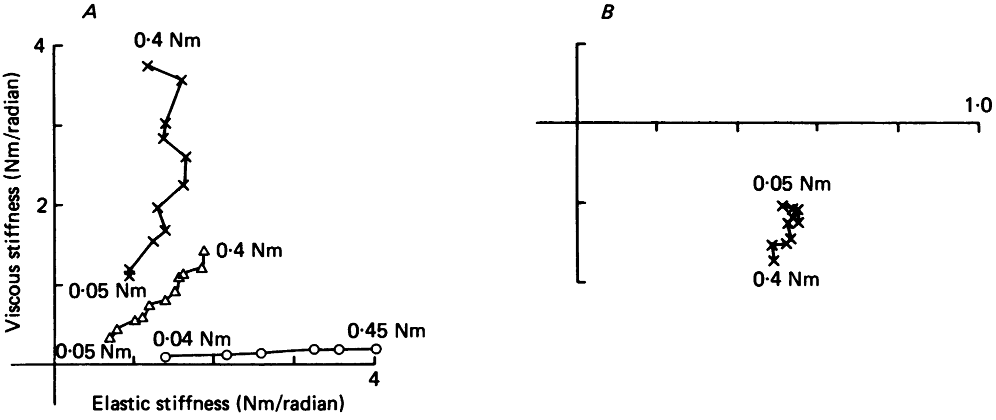

Fig. 5. *A*: the middle record (△) shows how the joint stiffness vectors change with increasing force (the same data as for Fig. 4). Some of the forces are indicated on the Figure. The stiffness of the tendon is also indicated (○). From those two records the stiffness of the muscle alone (without tendon) has been computed, and this is also shown ( × ). *B*: the movements that would actually have reached the muscle are plotted as vectors; their amplitudes are expressed as a fraction of the amplitude of the imposed movement. If the (complex) joint stiffness is $X$, and the tendon stiffness $T$, then the proportion of the movement that reaches the muscle fibres is $1-X/T$, and the muscle fibre stiffness is $X/(1-X/T)$.

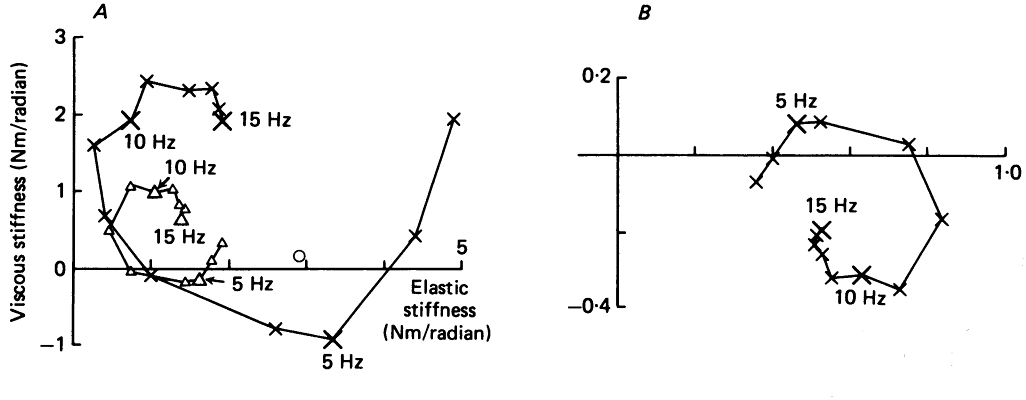

Fig. 6. Reflex responses at the thumb interphalangeal joint. Extensor muscles had been paralysed by radial nerve anaesthesia. The subject maintained a constant mean flexing force of 0·22 Nm, while the thumb was driven through sinusoidal movements of ±2·0° at progressively decreasing frequencies. Each frequency point represents the average of all the cycles within a 1 Hz frequency bin. The 10 Hz point is thus the averaged response to all the fifty-one cycles at frequencies between 9·5 and 10·5 Hz. The 5, 10 and 15 Hz points are denoted by larger symbols. *A*: the smaller C-shaped path (△) shows how the joint stiffness vectors altered with changing frequency; this record is similar to ones that have been shown previously (Brown *et al.* 1982*a*) . The larger C ( × ) shows the stiffness of the muscle fibres, calculated on the assumption that they were coupled to the joint through a perfectly elastic tendon which was attached 7·7 mm from the joint axis (tendon stiffness equivalent to 2·98 Nm/radian of joint movement, indicated by the circle (○) close to the horizontal axis). *B* shows the movement of the muscle fibres at each frequency (expressed as in Fig. 5*B*).

A knowledge of the fraction of the movement which reached the muscle fibres enables us to express their stiffness as force/muscle *fibre* extension; this has been plotted in Fig. 5*A* ( × ). In this Figure one can see that the muscle fibres themselves had a stiffness which was comparable to the tendon (the corresponding points lie at approximately equal distances from the origin). However, the muscle fibre vectors are at a position 50–80° above the horizontal axis, which indicate that the muscle fibres presented a viscous resistance to the movement which was in contrast to the elastic nature of the tendon.

### *The effect of tendon properties on reflex responses*

The distribution of an imposed movement between muscle fibres and tendon becomes particularly complicated if the level of activation of the muscle fibres is itself altering while the movement proceeds. Such a situation arises when muscle activation is the reflex response to an imposed movement; the changes in length will then be accompanied by forces that depend on both the reflex gain and the reflex loop delays. During sinusoidal driving the particular relationship between movement and force will be different with different frequencies of movement. Since the tendon length depends on force, this length will have only an indirect relation to the imposed movement (Rack *et al.* 1983).

Fig. 6*A* (△) is a vector diagram to show the forces that developed in response to sinusoidal driving of the thumb interphalangeal joint at a range of different frequencies. Each point represents the response to a single frequency of movement, and the C-shaped path of the vectors is characteristic of a stretch reflex response to a sequence of different frequencies of movement (see Brown *et al.* 1982*a*, *c*). For this experiment the extensor muscles had been paralysed (as for Fig. 4). The subject maintained a constant mean flexing force of 0·22 Nm, and from Fig. 4 we estimate that his tendon then had a stiffness equivalent to about 2·9 Nm at the joint (indicated by ○ in Fig. 6*A*).

From these data, the distribution of movement between muscle fibres and tendon was calculated for each frequency. The position of each point in Fig. 6*B* shows the fraction of the movement which reached the muscle fibres at that frequency, and the phase lead or lag of the muscle fibre movement in relation to the joint movement (plotted as in Fig. 5*B*). At low frequencies (3–4 Hz) the muscle fibres experienced only quite a small fraction of the imposed movement ($\frac{1}{3}$–$\frac{1}{2}$ in Fig. 6*B*), and it is clear that the stretch reflex activity was then effectively limiting their extension. However, at 7–8 Hz a much larger fraction of the movement reached the muscle fibres, and it is equally clear that stretch reflex activity did not resist movements at those frequencies.

The responses of muscle fibres to different frequencies of movement can be seen more clearly in Fig. 6*A* ( × ) which shows their stiffness (force/muscle *fibre* movement) at each frequency. At 3 Hz the muscle fibres presented a high resistance to the movement, almost double the tendon stiffness, whereas at 7 Hz this stiffness was reduced to less than a fifth of the low-frequency value, and to less than half the tendon stiffness. This result is essentially similar to the responses of calf muscles to sinusoidal movements (Rack *et al.* 1983). At low frequencies the stretch reflex effectively restricts movement of the muscle fibres, but at some higher frequency (7–8 Hz in this experiment) the timing of the reflex response is such that its action reduces the muscle fibre stiffness and thereby permits relatively large movements of the muscle fibres and spindles.

### *Joint friction*

In the foregoing descriptions we have assumed that the friction at the interphalangeal joint was so small that it could be disregarded. The resistance to sinusoidal movements of the passive joint is indeed very small (Brown *et al.* 1982*a*), but there remained a possibility that frictional resistance might increase to significant levels during a forcible flexion, when the articulating surfaces were pressed firmly against each other.

An experiment was therefore carried out in which the resistance to sinusoidal movements was measured in a joint that was subjected to a compression force while the subject made no voluntary effort. The terminal phalanx was fixed to the driving mechanism in the usual way, but the whole hand and forearm were forced down toward it by a strap acting on the elbow, and attached to weights that acted over a pulley. A compressing force of 20 N increased the resistance of the passive joint by about 50 %, but this was still less than a fifth of the resistance measured during a 0·2 Nm voluntary contraction.

## DISCUSSION

In its mechanical properties the flexor pollicis longus tendon is essentially similar to the tendons of other muscles (Woo *et al.* 1980; Ker, 1981), and to the tendinous fibres that extend within the substance of many other muscles (Rack & Westbury, 1984). The fibres are essentially elastic, but their elastic modulus increases when the force on the tendon increases.

The main interest of the present results comes from a comparison of the tendon properties and the properties of the living joints. In comparing these different types of information we are obliged to make use of results obtained from different subjects, many of whom differed considerably in physique; furthermore, our measurements of tendon stiffness were confined to that part of the tendon which extended beyond the most distal muscle fibres. The more proximal muscle fibres are in fact attached through greater lengths of tendon which would thus have a greater total compliance (a lower stiffness) than the specimens that we measured. A true mean value for tendon stiffness would therefore have been lower than the values which we used in the calculations of Figs. 5 and 6.

By using these rather high values for tendon stiffness we have probably underestimated the importance of the tendon properties. The actual muscle fibre movements probably differed from joint movement by more than our calculations indicate, and the muscle fibres themselves were probably stiffer than we have shown.

### *Some mechanical consequences of a compliant tendon*

In the past, investigations and discussions of motor control have often focused on the servocontrol of joint *position*, and there has sometimes been a tacit assumption that mechanisms which could set muscle fibres to particular lengths would thereby determine the positions of the joints. This assumption must be modified when muscles act through compliant tendons, because in that situation a joint would still yield to displacing forces, even if the muscle fibres were quite rigid and remained at exactly the same length. In practice, the extension of a joint will usually stretch both muscle fibres and tendon, but whereas for a given extending force the response of the muscle fibres will be determined by the state of muscle activation and the gain of the stretch reflexes, the tendon will be stretched by some amount that depends only on its inherent mechanical properties.

At first sight it might seem that a compliant tendon reduces the precision of control which the nervous system can exercise over the thumb, and this would be true if joint *position* were the only consideration. It is unrealistic to think of the neuromuscular system as controlling either *position* or *force* quite separately from the other, but there is no doubt that the presence of a compliant tendon will reduce the force changes that accompany any small change in either the muscle activation or the joint position, and in this way it will diminish the *force* errors that would arise from random disturbances, and thus make it easier to control force at the joint, though less easy to control position. This remains true whether the muscle fibre length is determined by a stretch reflex mechanism, or by the stimulus rate/length/tension properties of the muscle fibres themselves. The thumb usually operates as one component of a pincer, in which the control of force is probably more important than the control of position; the flexor pollicis longus with its long tendon seems to be well suited to this task.

It is notable that tendons are at their most compliant when forces are small; the thumb will thus have a softer (more yielding) grip when the force is small. For most purposes this will give an appropriate delicacy of touch, but it is still possible to increase the rigidity of the thumb by contracting agonist and antagonist muscles against each other in a way that produces a high force in each muscle, and therefore a high stiffness in each tendon, but with quite a small resultant force at the joint. Experience suggests that we employ this co-contraction when it is necessary to maintain the *position* of a thumb or finger accurately.

### *The stretch reflex of flexor pollicis longus*

When allowances were made for the properties of the tendon, it became clear that the muscle fibres often presented a high resistance to low-frequency movements; this may be seen in Fig. 6*A* ( × ), where the 3–5 Hz points are displaced far from the origin. Furthermore, the wide circular excursion of that vector path indicates a large reflex contribution to the muscle fibre stiffness. At these low frequencies the stretch reflexes were thus much more effective controllers of muscle fibre length than of the joint position, and this is hardly surprising because it is muscle *fibre* length that the spindles actually 'see'.

For movements of 5 Hz or less, the stretch reflex may thus exert a useful control over the position of the proximal end of the tendon, and to that extent it functions as a moderately effective servocontroller of position. However, reflexes that depend on spindles in the active agonist muscles cannot be expected to provide an effective control of joint position in the face of changing forces. When a precise control of the position of the thumb or fingers is needed, this must presumably be achieved with the aid of signals from joint receptors and skin receptors (Hulliger, Nordh, Thelin & Vallbo, 1979; Moberg, 1983), and perhaps from spindles in antagonist muscles which are passively stretched (Capaday & Cooke, 1981, 1983).

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