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THIXOTROPIC BEHAVIOUR OF HUMAN FINGER FLEXOR MUSCLES WITH ACCOMPANYING CHANGES IN SPINDLE AND REFLEX RESPONSES TO STRETCH

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SUMMARY

1. Prompted by previous reports on muscle thixotropy, we have investigated changes in inherent and reflex stiffness of the finger flexor muscles of human subjects at rest, following transient conditioning manoeuvres involving contractions and/or length changes of the finger flexors. The stiffness measurements were combined with electromyographic recordings from forearm and hand muscles and with microneurographic recordings of afferent stretch responses in finger flexor nerve fascicles.

2. Finger flexor stiffness was evaluated by measuring (a) the flexion angle of the metacarpo–phalangeal joints at which the system during rest balanced the force of gravity and (b) the speed and amplitude of angular finger extensions induced by recurrent extension torque pulses of constant strength delivered by a torque motor. In the latter case, extension drifts in the resting position of the fingers were prevented by a weak flexion bias torque holding the fingers in a pre-determined, semiflexed position against a stop-bar.

3. Stiffness changes following passive large amplitude finger flexions and extensions were studied in subjects with nerve blocks or nerve lesions preventing neurally mediated contractions in the forearm and hand muscles. Inherent stiffness was enhanced following transient finger flexions and reduced following transient finger extensions. The after-effects gradually declined during observation periods of several minutes.

4. Similar results were obtained in subjects with intact innervation who succeeded during the pre- and post-conditioning periods in keeping the arm and hand muscles relaxed (i.e. showed no electromyographic activity). In these subjects it was also found that the after-effects were similar for active and passive finger movements and that isometric voluntary finger flexor contractions loosened the system in a way similar to finger extensions.

5. In some subjects electromyographic reflex discharges appeared in the finger flexors in response to the extension test pulses. When elicited by small ramp stretch stimuli of constant amplitude, the stretch reflex responses were found to vary in strength in parallel with the changes in inherent stiffness following the various conditioning manoeuvres.

6. The strength of the multi-unit afferent stretch discharges in the muscle nerve,

used as index of muscle spindle stretch sensitivity, varied in parallel with the changes in inherent stiffness. Post-manoeuvre changes in muscle spindle stretch sensitivity were seen also when the spindles were de-efferented by a nerve block proximal to the recording site.

7. The results can be explained in terms of thixotropic behaviour of extra- and intrafusal muscle fibres. The in-parallel changes in reflex and inherent stiffness can be accounted for by assuming that the conditioning manoeuvres have similar mechanical after-effects on intra- and extrafusal muscle fibres, and that the primary spindle endings are more susceptible to the intra- than to the counteracting extrafusal stiffness changes.

8. Loosening of thixotropic bonds in extra- and intrafusal muscle fibres may contribute to the beneficial effects of limbering-up manoeuvres commonly employed by athletes, dancers and physiotherapists.

INTRODUCTION

A thixotropic substance is characterized by the fact that its stiffness or viscosity is dependent on the past history of movement. The word is commonly used for gels which become fluid when shaken or stirred and which then gradually regain their original high viscosity after a period of rest. Stirring forces in such solutions tend to disrupt bonds between molecules which then re-form again when the stirring forces cease.

Lakie, Walsh & Wright (1984) recently reported that human musculo–tendinous structures possess thixotropic properties reminiscent of those previously described for isolated muscle fibres of the frog (Buchthal & Kaiser, 1951). In their studies of the biodynamics of the relaxed human wrist they found that the stiffness of the system was much higher for small than for large movements; also, stiffness was markedly reduced following transient large perturbations. Their findings indicate that the high stiffness for small movements is the counterpart of the short-range elastic component previously observed in frog and cat muscle (Buchthal & Kaiser, 1951; Hill, 1968; Joyce, Rack & Westbury, 1969; Nichols & Houk, 1976). The short-range stiffness of the resting muscle is believed to depend on bonds between actin and myosin filaments in extrafusal fibres, bonds which are broken by movements beyond a certain extent (Hill, 1968) and which then need some time to form again once the motion ceases.

Certain after-effects of fusimotor stimulation on afferent spindle discharge have also been tentatively explained in terms of persisting bonds between actin and myosin filaments. There are a number of animal studies showing that intrafusal contractions may be followed by a persisting tonic spindle discharge and/or a potentiation of Ia spindle responses to subsequent stretch and fusimotor stimulation (Hunt & Kuffler, 1951; Brown, Goodwin & Matthews, 1969, 1970; Hutton, Smith & Eldred, 1973; Smith, Hutton & Eldred, 1974; Baumann, Emonet-Dénand & Hulliger, 1983). A characteristic feature of these after-effects is that they can be abolished by large stretches. It has been suggested that the effects depend on residual filament cross-bridges in intrafusal fibres, bridges which keep the spindle poles stiff and efficient in transmitting stretch stimuli to the primary spindle endings. Large enough perturbations will break the bonds and abolish the after-effects of the stimulation.

However, this explanation is not sufficient to account for the fact that after-effects resembling those following fusimotor stimulation can also be observed following a series of rapid alternating stretches and releases (Proske, 1975; Poppele & Quick, 1981; Emonet-Dénand, Hunt & Laporte, 1983; Morgan, Prochazka & Proske, 1984). According to Morgan *et al.* (1984) most of the observed after-effects on the responses of primary endings of cat muscle spindles are still explicable in terms of intrafusal cross-bridges which in general terms behave like bridges in extrafusal fibres. Pre-existing intrafusal bridges are supposed to be broken by fusimotor stimulation and rapid alternating movements, but when the perturbing stimuli end, new bridges attach within a few seconds at the length at which the undisturbed muscle is being held. As a result of their findings these authors also believe that once bridges have been formed at a stretched length 'the fibre on returning to its rest length will be (stiff but) slack' and it may take up to half an hour before this slack is taken up spontaneously by the formation of new cross-bridges adapted to the short length.

If Ia spindle discharge and sensitivity to stretch are enhanced following a conditioning intrafusal contraction one might also expect a post-contraction enhancement of stretch reflex responses. There are animal experiments indicating that such a reflex potentiation does occur following contractions involving intrafusal fibres (Hutton & Suzuki, 1979; Enoka, Hutton & Eldred, 1980). Enoka *et al.* (1980) also observed a potentiation of the Achilles tendon jerk reflexes in man following isometric voluntary contractions of the calf muscles, and they believe this might be due to post-contraction discharge and increased stretch sensitivity of spindle receptors. So far, direct recordings from muscle spindle afferents in man have provided no definite support for this assumption, even though enhanced spindle discharge has occasionally been seen following a voluntary contraction (Vallbo, 1970).

The present experiments, performed mainly on healthy subjects, were designed to study the after-effects of voluntary finger flexor contractions and large passive and active finger movements on (a) the inherent stiffness of the relaxed finger flexors, (b) the tonic discharge and stretch sensitivity of their primary spindle endings and (c) the strength of the stretch reflexes in the same muscles.

METHODS

Subjects

Twenty-six experiments were carried out on the left arm of ten adult human subjects without signs of neurological disorders. In addition, five experiments were performed on subjects with more or less extensive left sided paresis of the forearm and intrinsic hand muscles. One of these subjects was a patient with a severe plexus lesion causing total denervation of all forearm and hand muscles; in the other instances the paresis was induced experimentally by temporary nerve blocks, as described in the result section. The informed consent of all subjects and the appropriate ethical permissions were obtained.

Mechanical arrangements

The subject was comfortably seated with the left forearm and hand fixed in supinated position to a horizontal support reaching down to the metacarpo–phalangeal (m.c.p.) joints of digits 2–5 (Fig. 1). With the interphalangeal joints extended, these four fingers were fastened to a light aluminium plate and a crank fixed to the spindle of a torque motor (Aeroflex, TQ 34W-33). The axis of rotation at the m.c.p. joints was adjusted to correspond with the axis of the motor. The

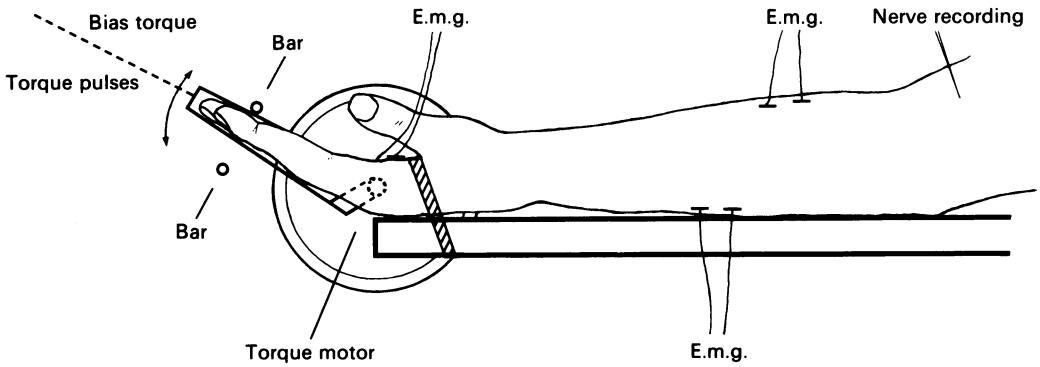

Fig. 1. Schematic drawing of the experimental arrangement.

motor axis was double-ended and connected to a precision potentiometer signalling angular position. In all Figures upward deflexions indicate extension movements at the m.c.p. joints.

The motor was driven by a power amplifier (BBC Axodyn 05LV09) which was fed by square-wave pulses from a stimulator (Grass S 88). Calibrations were performed to ensure that the shape and strength of the torque pulses accurately reflected the wave form and amplitude of the pulses from the stimulator. The polarity of these pulses was always such that the resulting torque pulses produced extension movements at the m.c.p. joints. The power amplifier with the motor could also be adjusted to deliver a constant bias torque.

Testing procedures

Subjects were examined in a warm room (about 20 °C). The tests performed before and after the various conditioning manoeuvres were all carried out with the subject instructed to remain as relaxed as possible in the finger flexor and extensor muscles. The dynamic stiffness of the system was examined by measuring the amplitude of the angular finger excursions induced by recurrent torque pulses of a given strength (within the range 0·10–0·20 N m) with a duration of 1–2 s. In order to prevent the torque pulses or the conditioning manoeuvres from producing drifts in resting finger position (see Results) the motor was set to deliver a constant flexion torque (of about 0·03 N m) which after each test pulse or conditioning manoeuvre pulled the fingers back to their initial semiflexed position (of about 30 deg) against a metal bar (see Fig. 1).

When studying the afferent and reflex responses to the test stimuli, on occasions another metal bar was placed on the opposite side of the fingers, reducing angular range movement to 10 deg between the bars. The torque pulses were then of sufficient strength to produce full amplitude ramp stretches within the pre-determined range. The bars were hinged and could temporarily be removed to allow conditioning movements of large amplitude.

Conditioning manoeuvres

The after-effects of the following conditioning manoeuvres were examined: (1) passive, large-amplitude finger flexion or extension movements. These were manually applied movements, usually reaching the anatomical limits for excursions around the m.c.p. joints; as a rule the fingers were held in maximal extension or flexion for at least 5 s before returning to the resting position; (2) unresisted, voluntary finger flexion or extension movements of similar large amplitude and time course as the passive ones; they were 'unresisted' in the sense that they met with no external obstacle or purposely applied counterforce; (3) resisted, voluntary finger flexor contractions of submaximal strength; these were of three different types – isometric, shortening and lengthening contractions; in the isometric trials the subjects were instructed to press the fingers hard against the upper metal bar, to maintain the force for a few seconds and then relax again; during the shortening contractions, which were of similar strength and duration to the isometric ones, the subject was allowed to flex the fingers to about 90 deg by pulling hard against a yielding manually applied counterforce; during the lengthening contractions the counterforce overcame the flexion

pull exerted by the subject, thereby stretching the contracting finger flexors; (4) occasionally, a vibrator oscillating at a rate of about 100 Hz with an amplitude of 1·5 mm was applied over the tendons or bellies of the forearm finger flexor muscles.

Our primary intention was to study the after-effects of the various manoeuvres in qualitative rather than in quantitative terms. Thus, the conditioning manoeuvres were standardized in the manner described above and we did not systematically examine how the after-effects varied in magnitude with, for instance, the duration and strength of conditioning finger flexor contractions or with the velocity and amplitude of conditioning passive finger excursions.

Electromyography

The electromyographic (e.m.g.) activity of forearm finger flexor and extensor muscles was recorded with bipolar surface electrodes (Disa, 13 L 22), one pair being placed on the ventral and the other on the dorsal side of the left lower arm. The final position of the two electrode pairs was adjusted to maximize the e.m.g. recorded during isometric m.c.p. flexions and extensions, respectively. On occasions we also recorded from the intrinsic hand muscles with a pair of electrodes placed in the palm of the hand. Two e.m.g. channels could be connected simultaneously to identical a.c. amplifiers, full-wave rectifiers and leaking integrators (time constant 0·001 s). Care was taken to check that the e.m.g. gain was always high enough to allow detection of minute contractions in underlying muscles. The e.m.g. signals could also be monitored on loudspeakers.

Nerve recordings

Afferent stretch responses from forearm finger flexor muscles were recorded from the left median nerve, using the microneurographic method of Vallbo & Hagbarth (1968; see also Vallbo, Hagbarth, Torebjörk & Wallin, 1979). In short, insulated tungsten needle electrodes with a tip diameter of 5–10 μm were inserted percutaneously into the nerve a few centimetres above the elbow. The position of the electrode was adjusted carefully until the tip impaled a muscle nerve fascicle innervating forearm finger flexor muscles (flexor digitorum superficialis or profundus). Such fascicles were identified by the following observations: (1) Electrical pulses delivered through the micro-electrode produced distinct flexion twitches at the m.c.p. joint without accompanying skin paresthesias. (2) The adequate stimuli for eliciting multi-unit afferent discharges were taps over the finger flexor muscles in the forearm or extension movements at the m.c.p. joints, whereas skin stroking was totally ineffective.

The present study only includes multi-unit recordings which were stable enough to withstand the minute electrode movements which often occurred during finger flexor contractions and/or large amplitude finger movements. Twitch tests served to elucidate whether signals from muscle spindles were main contributors to the afferent stretch discharges. For these tests stimulating pulses were delivered through a pair of stimulating needles inserted into the forearm finger flexor muscle which was judged to be the prime source of the afferent stretch responses.

After amplification ($\times$ 20000) and band-pass filtering (200 Hz–8 kHz) the neurograms were usually full-wave rectified and passed through an integrator with an adjustable exponential decay (time constant 0·001–0·2 s).

Signal display and analysis

During experiments signals were monitored on a four-channel storage oscilloscope (Tektronix 549). For later analysis all signals were stored on tape by a multichannel FM tape recorder (Sangamo, Sabre VI). To obtain continuous records of the events, taped signals were displayed on paper by an ink-jet recorder (Siemens-Elema, Mingograf 800) or by an electrostatic recorder (Gould, ES 1000). For more detailed analysis of responses to recurrent test stimuli the signals were fed into a universal wave-form analyser (Data Precision 6000 with plug-in unit 611), which was triggered by the pulses to the torque motor. The wave-form analyser, used for averaging and numerical evaluations, presented its results on a digital plotter (HP 7470 A).

RESULTS

Stiffness changes in paretic subjects

In the experiments designed to study the inherent mechanical properties of the finger flexor system it was important to avoid all interference from neurally mediated muscle contractions. On two occasions a temporary partial paresis of the finger flexors was induced by injection of local anaesthetics (prilocaine, 20 mg/ml, 5–10 ml) around the median nerve in the upper arm; on two other occasions a paralysis of all finger

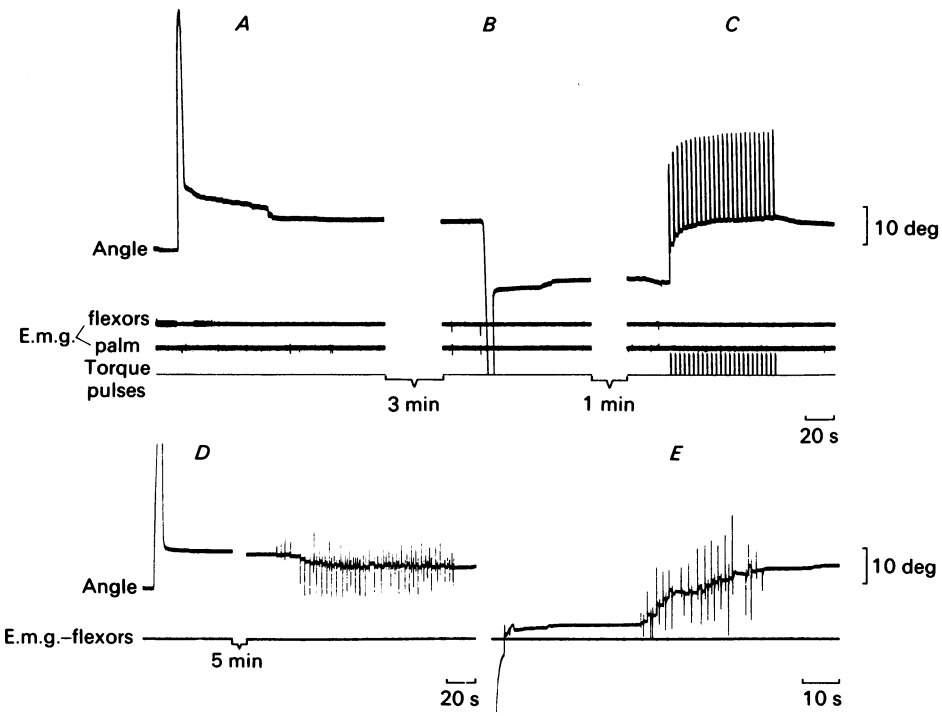

Fig. 2. Slow drifts in finger position after conditioning passive movements in a subject with paretic forearm and hand muscles during a 'cuff experiment' (*A–C*). The retraction movement was slow and sometimes occurred in steps both after a conditioning extension (*A*) and flexion (*B*). *C* shows how repetitive torque pulses caused a drift in the resting position of the fingers. The experiment shown in *D* and *E* was done in a relaxed subject with partial median nerve block induced by local anaesthetics but was otherwise similar to *A* and *B*. The drift towards the original position was speeded up by recurrent taps applied randomly in flexion and extension directions.

flexor and extensor muscles was produced by a cuff around the upper arm inflated above systolic pressure for 30–40 min. A patient with a severe lesion of his left brachial plexus was also investigated. As judged by a routine e.m.g. examination, the forearm finger flexor and extensor muscles and the intrinsic hand muscles were totally denervated. Figs. 2 and 3 summarize the outcome of the biomechanical tests performed on the paretic subjects.

Signs indicative of thixotropy were disclosed by merely observing the resting position of the fingers before and after passively induced joint displacements. The

records in Fig. 2*A*, *B* and *C*, derived from one of the cuff experiments, were obtained after a period of rest with the hand fixed in the standard supinated position and the fingers coupled to the freely moving crank of the unbiassed motor. The initial angular position of the m.c.p. joint, at which the system balanced the force of gravity, was close to 30 deg of flexion. After a manually applied full extension of the fingers, lasting for a few seconds (Fig. 2*A*), the fingers quickly returned about three-quarters of the way to the initial position. This was followed by a period when the fingers continued to retract at a very slow mean speed, often with periods of arrest followed by sudden small steps. After an observation time of about 6 min, when the fingers had not yet returned to their initial position, they were passively flexed to 90 deg (Fig. 2*B*). On release, a quick return to an angle of about 40 deg was followed by a slow drift towards the original, more extended position.

Torque pulses of a moderate strength delivered by the motor had also prolonged after-effects on the resting position of the fingers. As shown in Fig. 2*C*, repetitive extension torque pulses applied to the fingers produced not only rapid extension jerks but also a finger drift towards a more extended position, from which they retracted very slowly when the torque pulses ceased.

Slow return drifts of the fingers similar to those illustrated in Fig. 2*A*, *B* and *C* were seen not only in the cuff experiments but also when the finger flexors were paretic after median nerve block and during relaxation in subjects with intact innervation. The characteristic small step-wise changes in position led to the assumption that the force tending to restore the original position met with some frictional resistance (in joints or tendons) which retarded the return drift. To test this hypothesis small recurrent taps were applied randomly on the dorsal and ventral side of the fingers. With such mechanical 'dither', the return drifts were speeded up as shown in Fig. 2*D* and *E*.

In order to test the dynamic stiffness of the finger flexor system the drifts in resting position had to be avoided. As described in Methods, a stable resting position was obtained by placing a stop-bar on the volar side of the fingers and by using a constant flexion torque of sufficient strength to bring the fingers back to this bar after each extension test pulse or conditioning manoeuvre. This technique was used in the experiments illustrated in Fig. 3. Both in the paretic patient (Fig. 3*B*) and in the nerve block experiments (Fig. 3*A* and *C*), single large finger extension movements were followed by a prolonged reduction of short-range stiffness, as tested by the recurrent pulses. The loosening of the system was maximal immediately following the conditioning stretch movement. As the test pulses were then repeated at regular intervals it could be seen how the system gradually regained some of its stiffness without fully returning to the control level within observation periods of 10–15 min. In the control runs before the conditioning stretch stimuli it was often observed that the test pulses themselves had a tendency to slacken the system so that the angular deflexions increased with repeated test loadings (Fig. 3*A* and *B*). This effect was not seen with torque pulses of minimal strength (Fig. 3*C*). It was also noted that the recovery after the conditioning stimulus occurred faster if the fingers were periodically allowed to rest without being disturbed by the recurrent pulses. Still, in the median nerve block experiment, a rest period of more than 10 min was not sufficient to restore the original short-range stiffness (Fig. 3*A*).

After-effects opposite to those following large extension movements were seen

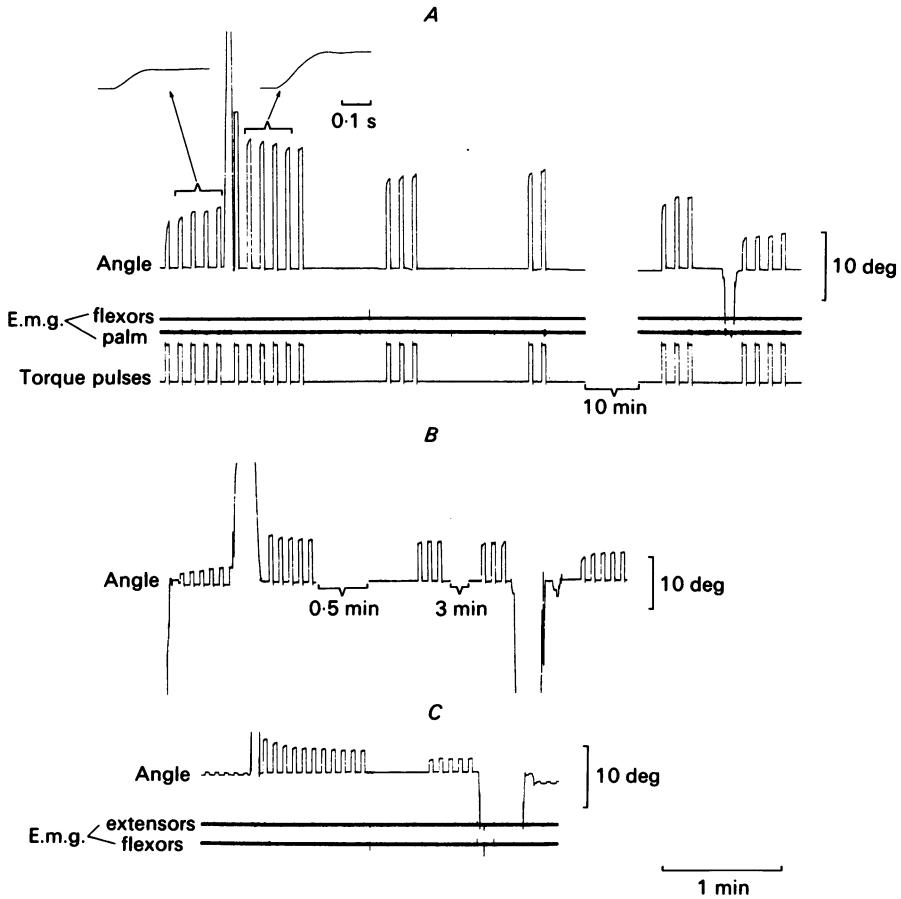

Fig. 3. Stiffness changes induced by passive large finger extensions (left) and finger flexions (right) during total median nerve block with local anaesthetics (*A*), in a patient with severe brachial plexus lesion (*B*), and during total finger flexor and extensor paralysis caused by a cuff inflated around the upper arm (*C*). In each experiment the torque pulses were of constant strength, and the change in stiffness is evidenced by the angular deflexions from the resting position. The inset traces with expanded time scale in *A* were obtained by averaging the angular movements indicated by the square brackets. Besides increased amplitude there was also an enhanced velocity of the extension movements after the conditioning extension manoeuvre.

following large passive finger flexions. After such movements the system became stiffer, as shown by the marked reduction of the finger deviations induced by the torque pulses (Fig. 3, right). This lingering after-effect subsided in a slow manner similar to the opposite after-effect of large extension movements.

Stiffness changes in relaxed subjects

Similar results to those illustrated in Fig. 3 were obtained in subjects with intact innervation following instructions to completely relax the arm and hand muscles. To facilitate relaxation the subjects were often allowed to listen to the audio-monitored e.m.g. with instructions to avoid motor unit activity. Some subjects were more

successful than others in these attempts. The former will be dealt with here, the latter in a following section.

Fig. 4*A* shows the prolonged changes in dynamic stiffness following large passive extension and flexion movements in a subject exhibiting no e.m.g. signs of contraction in the forearm finger flexor or extensor muscles. As in the paretic subjects, stiffness was reduced after an extension and enhanced after a flexion movement. In both

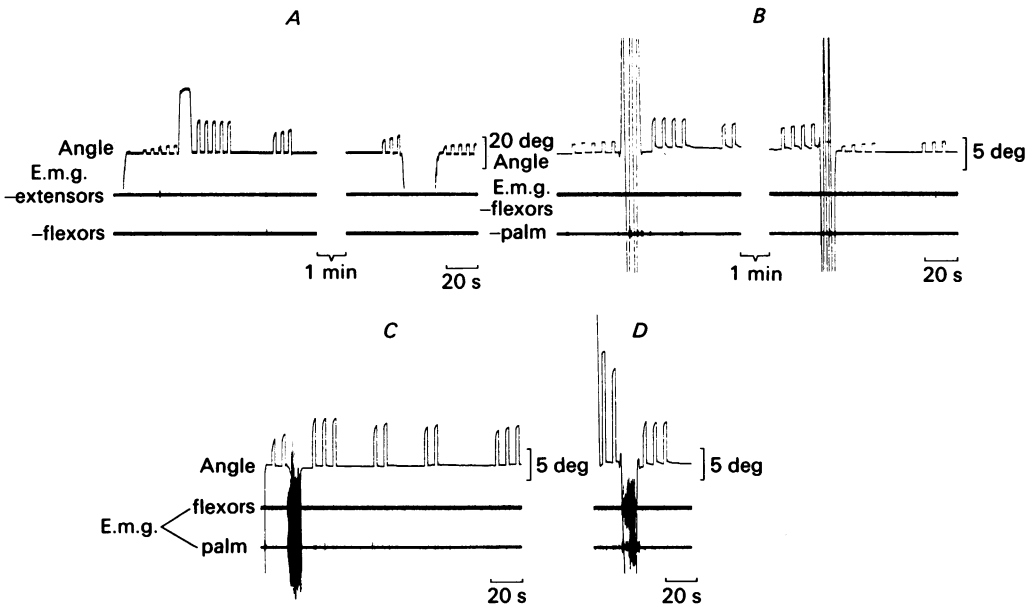

Fig. 4. Stiffness changes induced by conditioning manoeuvres in relaxed subjects. *A* shows the effects of large passive extension and flexion movements. *B* illustrates that stiffness depended on whether the last finger excursion was one of extension (left) or flexion (right). *C* shows the slackening effect of an isometric voluntary contraction and *D* the stiffening effect of a resisted shortening voluntary contraction. Note that the goniometer traces in *A*, *C* and *D* start with return movements from preceding large finger excursions. The torque motor pulses are not illustrated but were kept constant in each trial.

instances the recovery periods lasted for several minutes. The most prominent stiffness changes were seen when the test pulses were weak and the conditioning movements were of large amplitude. The opposing after-effects of extension and flexion movements were particularly apparent in trials where a movement in one direction was applied before the system had fully recovered from a preceding reverse movement (as in Fig. 4*A*). Following a series of slow alternating flexion–extension movements of large amplitude the system became slack or stiff depending on whether the last finger excursion was one of flexion or of extension (Fig. 4*B*).

After-effects similar to those induced by passive movements could be induced by unresisted active finger extension and flexion movements of large amplitude. Thus, the angular deflexions produced by the extension torque pulses were reduced following voluntary unresisted finger flexion movements and enhanced following transient voluntary finger extensions.

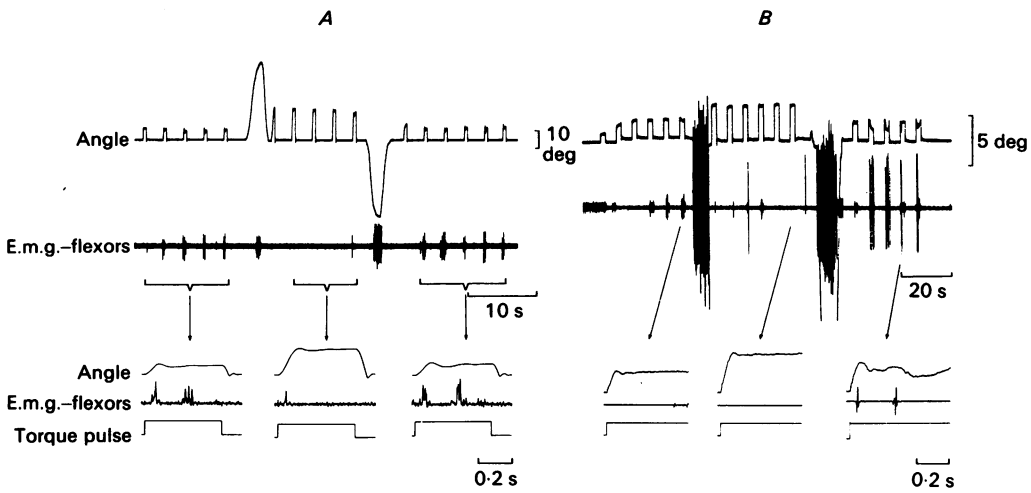

Fig. 5. Reflex changes accompanying variations in stiffness due to different conditioning manoeuvres. *A* shows how a passive extension movement caused disappearance of reflex e.m.g. responses, which then reappeared after a passive flexion. The inset traces with expanded time scale were obtained by averaging the marked five trials. *B* illustrates reduced reflex responses after an isometric voluntary contraction despite increased angular deflexions (left). By contrast, both the inherent stiffness and the reflex responses were increased following a resisted shortening voluntary contraction (right). The inserts in this case depict the response to individual torque pulses. The inset e.m.g. integrated in *A*. See text for further comments.

The system could be slackened not only by large-amplitude extension movements but also by voluntary isometric and lengthening contractions of the finger flexor muscles and by mechanical vibration applied on the bellies or tendons of these muscles. As a rule, the stiffness was reduced to a lesser extent following isometric than following lengthening contractions. The slackening effects were most apparent when, prior to contraction, the system had been stiffened by a previous passive flexion movement (as in Fig. 4*C*). It was also during periods of recovery from a preceding stiffening manoeuvre that the slackening effect of muscle vibration was most apparent. A few seconds of vibration, not sufficient to induce any tonic vibration reflex (Hagbarth & Eklund, 1966), was followed by a stiffness reduction similar to that illustrated in Fig. 4*C*.

After-effects opposite to those induced by isometric and lengthening contractions were observed following shortening voluntary contractions. Fig. 4*D* shows an example where a strong shortening contraction against a yielding resistance was followed by an enduring increase in stiffness, similar to that following passive finger flexion (cf. Fig. 4*A*, right).

Reflex changes accompanying the variations in inherent stiffness

As mentioned above, some subjects had difficulties in relaxing and/or preventing reflex contractions from appearing in response to the recurrent test pulses. The phasic stretch reflexes in the finger flexors were usually seen not only as e.m.g. responses but also as small flexion jerks in the goniometer traces. It was observed that the

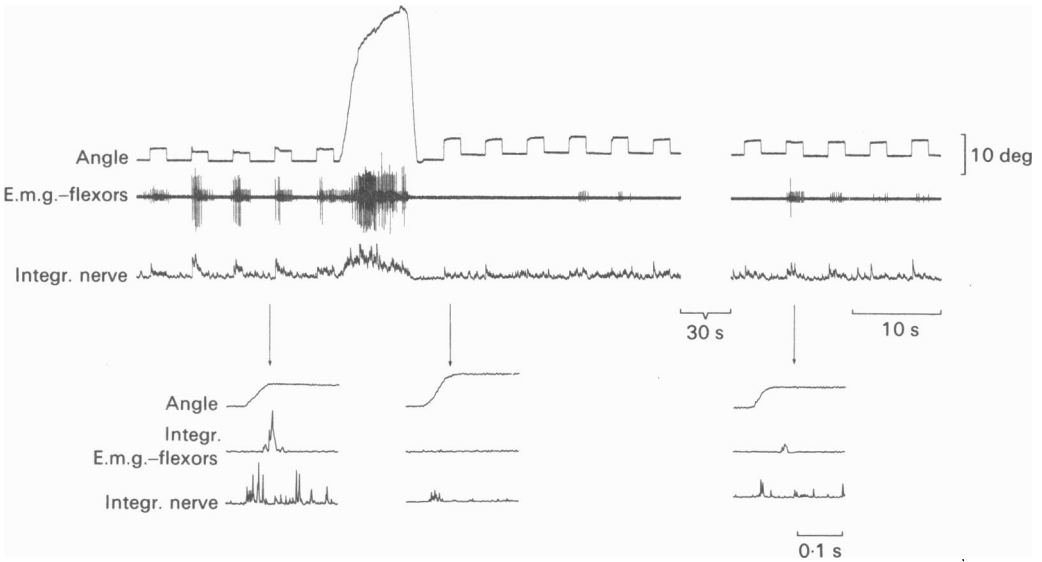

Fig. 6. Reduction of stiffness, afferent stretch responses and reflex e.m.g. responses following a conditioning passive extension movement. During the observation period a slow recovery occurred but the initial levels were not reached. E.m.g. was recorded from the forearm finger flexors, and multi-unit neural activity from a muscle nerve fascicle supplying the same muscles. The inset traces with expanded time scale show the responses to selected individual torque pulses. After the large passive extension an enhancement of the velocity of the extension movements could also be observed. As in previous Figures the torque pulses were unaltered during the trial.

reflexes in these subjects tended to be potentiated by those conditioning manoeuvres which led to a stiffening of the system in paretic or relaxed subjects, whereas a reflex suppression accompanied those manoeuvres which caused a reduction of inherent stiffness. Examples of such persistent reflex changes following different types of conditioning manoeuvres are shown in Fig. 5*A* and *B*.

As shown by the insets traces with expanded time scale in Fig. 5, the conditioning stimuli changed not only the amplitude but also the velocity of the extension movements (slope of the rising phase) induced by the test pulses (cf. also Fig. 3). Apparently, both these variables depended mainly on the passive, inherent stiffness of the system. As the inherent stiffness changed in one direction or the other after the different conditioning manoeuvres, one could observe parallel changes in reflex sensitivity. The stronger the e.m.g. responses the more prominent were the reflex jerks seen as down-going notches in the goniometer traces following the initial peaks. One may deduce that the manoeuvres tended to induce parallel changes in *inherent* and *reflex* stiffness.

Changes in afferent stretch responses accompanying the variations in inherent stiffness

After-effects of passive extension and flexion movements. Fig. 6 illustrates an experiment where the afferent stretch responses to the torque pulses were recorded with a micro-electrode inserted into a muscle nerve fascicle supplying the forearm

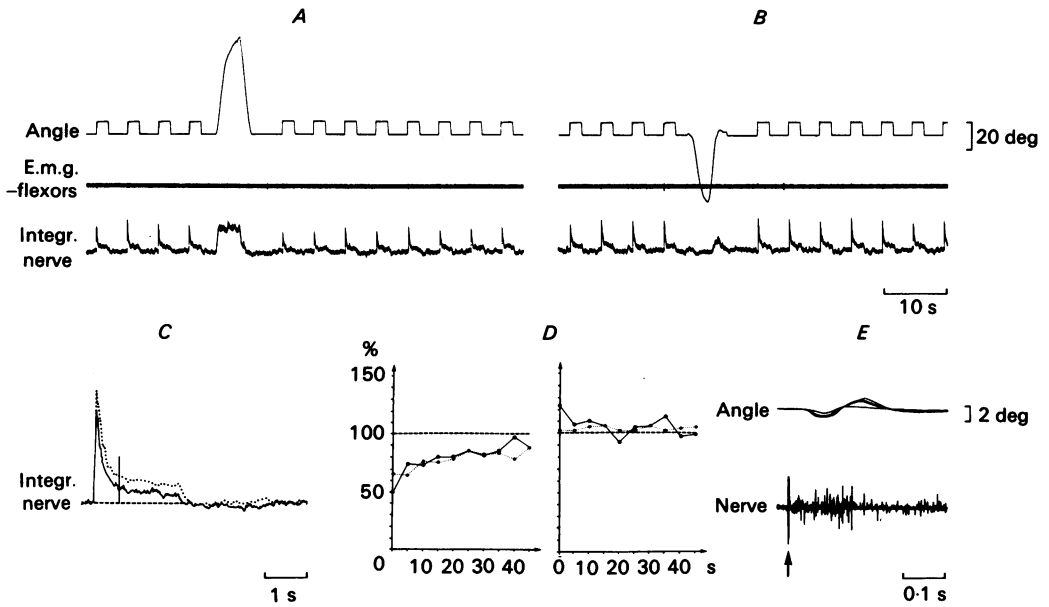

Fig. 7. After-effects of passive conditioning movements on afferent stretch responses. Torque pulses were kept constant and angular movements occurred within a pre-determined range. Multi-unit afferent responses were recorded from a muscle fascicle in the median nerve supplying the forearm finger flexors. The afferent responses decreased following a passive extension (*A*) and increased following a passive flexion (*B*). *C* shows an averaged mean voltage display of the neural responses after conditioning passive finger flexion (dotted trace) and finger extension (continuous trace). For further details see text. In *D* the averaged dynamic afferent response (dotted trace, ●) is plotted together with the averaged static afferent response (continuous trace, ○) after passive finger extension (left) and passive finger flexion (right). The nerve responses are expressed as percentage of the initial level and the abscissa shows the time passed after the conditioning manoeuvre. *E* illustrates a twitch test (four traces superimposed) with the major multi-unit response occurring during the stretch phase following the twitch as expected for muscle spindle afferents.

finger flexors. The conditioning manoeuvre was a manually applied passive finger extension. This manoeuvre had the following after-effects on the responses to the recurrent test stimuli: (i) an enhancement of the velocity and amplitude of the angular finger displacements, (ii) a reduction of the multi-unit afferent stretch responses and (iii) a suppression of the reflex e.m.g. responses in the finger flexors. The after-effects gradually subsided during an observation period of 2 min.

In many of those trials where the enhancement of the finger extensions was more pronounced than in Fig. 6, the neural and e.m.g. responses to the test pulses remained largely unaltered or they could even be slightly potentiated. A modification of the testing procedure was introduced in order to obtain a more accurate measure of the alterations in stretch receptor sensitivity following the conditioning manoeuvres. A stop-bar was placed in such a position that it prevented the fingers from being extended beyond a certain limit, and the torque pulses were made sufficiently strong to produce full amplitude movements within the pre-determined angular range (see Methods).

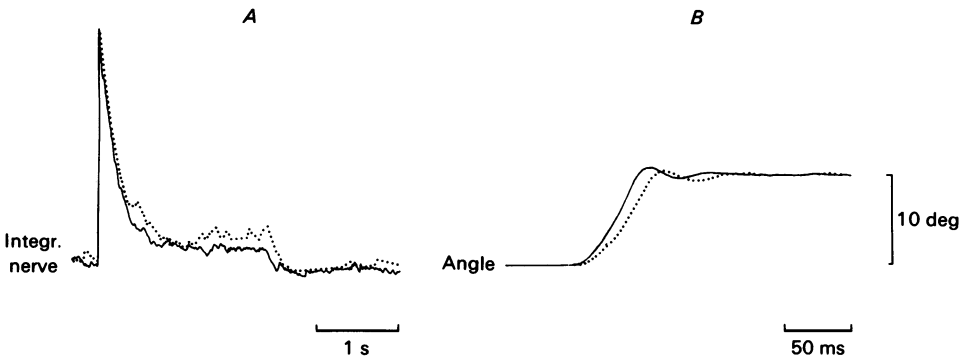

Fig. 8. After-effects of conditioning passive manoeuvres on afferent stretch responses persisting after a total proximal block of median nerve by local anaesthetics. The testing procedure was similar to that used in the experiment of Fig. 7*A* and *B*, but only the averaged multi-unit responses and the goniometer traces are presented (cf. Fig. 7*C*). The continuous trace shows the response after passive finger extension and the dotted trace is the response after passive finger flexion (*A*). Each trace was obtained by averaging four consecutive responses after the conditioning manoeuvre. The static component of the stretch response was stronger in the post-flexion than in the post-extension period. In this case a similar change in the dynamic stretch response was probably hampered by the fact that (as a consequence of a change in inherent stiffness) the standard torque pulses produced faster stretch movements in the post-extension than in the post-flexion period (*B*, continuous and dotted lines, respectively).

When tested with small ramp stretches of constant amplitude, stretch receptor sensitivity was found to be reduced following conditioning passive finger extensions (Fig. 7*A* and *C*) and enhanced following large amplitude finger flexions (Fig. 7*B* and *C*). As shown by the mean voltage neurograms, the multi-unit afferent stretch responses exhibited both a dynamic and a static component. Both components tended to change as a result of the manoeuvres, but they were not always affected to the same extent. The traces in Fig. 7*A* and *B* are derived from an experiment where test runs like those illustrated were repeated three times with similar results. The upper dotted line in Fig. 7*C* shows on an expanded time scale an averaged, mean voltage display of the three afferent stretch responses, each of which was the first in a row after a conditioning flexion movement. This should be compared with the average of the three stretch responses, each of which was the first in a row after a conditioning finger extension (continuous trace). The vertical line shows where the marker on the analyser screen was set to indicate the border between the initial (mainly dynamic) and the later static component of the responses. The areas under the trace before and after this line served as a quantitative measure for the dynamic and static components, respectively. The diagrams in Fig. 7*D* show how the values for the dynamic and static stretch responses (averaged from the three consecutive trials) varied with time after the conditioning stimuli.

In experiments of this type, twitch tests were performed in an attempt to clarify whether muscle spindle afferents were the main contributors to the multi-unit afferent stretch responses. These tests showed that the afferent discharge in the muscle nerve fascicle was more prominent during the falling than during the rising phase of electrically induced finger flexor contractions (Fig. 7*E*).

Similar tests to those illustrated in Fig. 7 were performed in an experiment where the median nerve innervation of the finger flexors had been blocked by local anaesthetics. The afferent stretch responses from the finger flexors, recorded from a muscle nerve fascicle distal to the block, were affected by the conditioning manoeuvres in a similar way to that seen in the experiments where median nerve conduction was intact (Fig. 8).

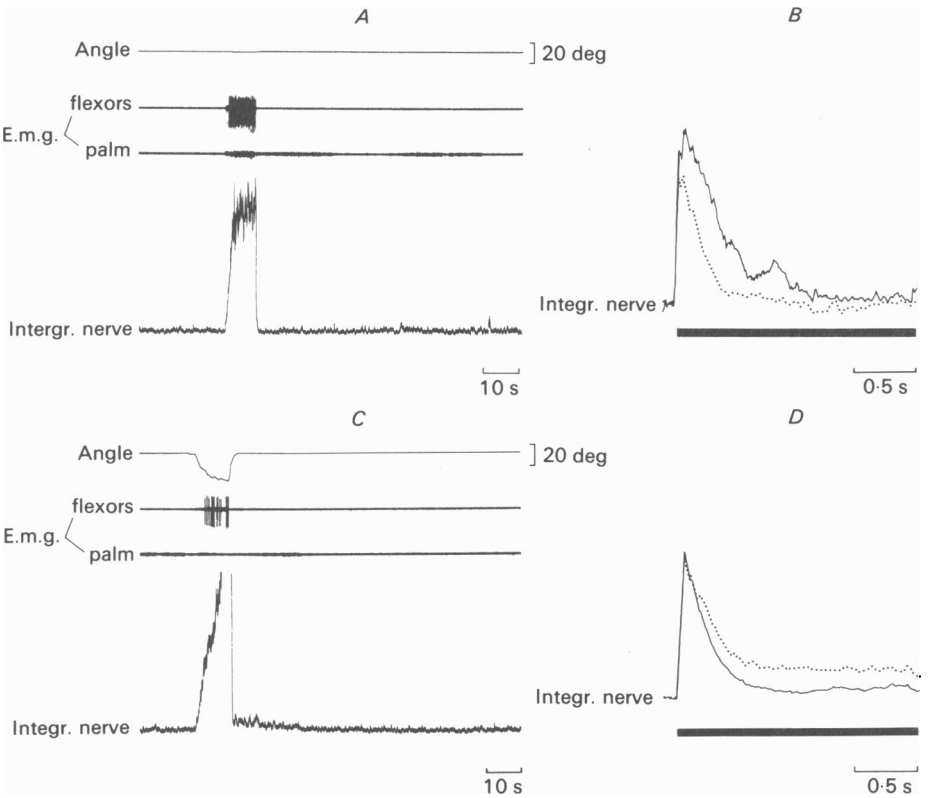

Fig. 9. After-effects of isometric and non-isometric shortening contractions on afferent muscle nerve activity. The sustained multi-unit discharge was unaffected after the isometric contraction in *A*, but was enhanced following the non-isometric shortening contraction in *C*. The nerve response to small stretches of fixed amplitude was decreased after an isometric contraction (*B*, dotted trace) as compared to the initial level (continuous trace). Following a shortening contraction (*D*) the afferent response to small stretches increased (continuous trace before and dotted trace after contraction). Each trace in *B* and *D* was obtained by averaging four and eight consecutive responses, respectively. The filled bars mark the duration of the extension pulses.

After-effects of isometric and non-isometric contractions. According to Hutton *et al.* (1973) and Smith *et al.* (1974) isometric contractions of cat calf muscles are followed by a post-contraction discharge and increase in stretch sensitivity of spindle receptors. In view of these reports, special attention was devoted to the after-effects of voluntary isometric finger flexor contractions on stretch receptor behaviour. In contrast to the findings in the cat, we never found isometric contractions to be

followed by any enhancement of the sustained afferent discharge or of the multi-unit afferent responses to small ramp stretches. On the contrary, the sustained multi-unit discharge in the muscle nerve fascicle was either uninfluenced (Fig. 9*A*) or slightly reduced, and we frequently observed a post-contraction reduction of the afferent responses to small ramp stretches (Fig. 9*B*).

To mimic the technique employed by Hutton *et al.* (1973) we also elicited isometric finger flexor contractions by tetanization of the median nerve; after such electrically induced isometric contractions of different strength again we did not see any post-contraction sensory discharge. However, results similar to those reported by Hutton *et al.* (1973) were obtained with non-isometric, shortening contractions. Such contractions were often followed by an enhancement of both the sustained multi-unit discharge (Fig. 9*C*) and of the afferent responses to small ramp stretches (Fig. 9*D*).

DISCUSSION

Inherent stiffness

As judged by the results obtained in the paretic patient and in the nerve block experiments (Figs. 2 and 3), the human finger flexor–extensor system possesses inherent mechanical properties of thixotropic type (Lakie *et al.* 1984). The system is composed not only of contractile elements in flexor and extensor muscles but also of tendons, joints, ligaments, etc. *A priori*, our observations on stiffness may be considered to reflect inherent properties in any of these structures. However, it seems improbable that variations in joint resistance are responsible for the slow positional drifts and gradual stiffness changes illustrated in Figs. 2 and 3. In this connexion it should be recalled that after-effects on dynamic stiffness similar to those produced by large amplitude finger extension movements could also be produced by strong isometric finger flexor contractions, involving no angular joint movements (Figs. 4*C* and 5*B*). From what is known concerning the mechanical properties of tendons (Alexander, 1981), it is also most unlikely that the thixotropic events illustrated in Figs. 2 and 3 are due to persisting changes in the resting length of flexor or extensor tendons. On the other hand, it is known that isolated muscles have no clearly defined resting length (Hill, 1952). As stated by Buchthal & Kaiser (1951): 'the muscle fibre adjusts itself with considerable retardation to changes in its state, i.e. in length, tension or temperature'. These authors also presented evidence that the contribution of the sarcolemma tube to the total tension of the muscle fibre at rest is of minor importance (see also Podolsky, 1964). We therefore believe that the thixotropic behaviour of the human finger flexor–extensor system reflects properties of the contractile substance rather than the connective tissue.

Many points of agreement, but also some discrepancies, can be noted when our results are compared with those of Lakie *et al.* (1984), who studied the biodynamics of the relaxed human wrist by using sinusoidal torques. They noticed, for instance, that when the hand was driven by a sinusoidal torque, oscillations occurred around a fixed mean position; when the hand was actively or passively displaced from this position it drifted back when the biassing force was removed. This 'self-centring' effect was not seen when the wrist was not kept in motion. We found that after a displacement the fingers did not return fully to the initial position. However, with

a long enough observation time we saw a slow positional drift, indicating that some restoring force was striving to bring the fingers back. The return movement often occurred in small steps and it could be speeded up by small repeated taps on the fingers (Fig. 2*D*). We believe this indicates that the restoring force met with some frictional resistance which could be partially overcome by mechanical 'dither'.

The mechanical after-effects of large-amplitude passive displacements illustrated in Fig. 2 can be explained by postulating that in the extrafusal fibres (of both flexors and extensors) there are pre-existing filament bonds which are broken up by conditioning stretch stimuli and which then need some time to re-form, thereby producing the slow return drift. However, this explanation is not sufficient to account for the stiffening effect of passive finger flexions illustrated in Fig. 3. The increased resistance to extension torque pulses seen after large-amplitude finger flexions must be attributed to an increase in finger flexor stiffness rather than to post-stretch changes in the extensors. We assume that at the same time as bonds are broken in the extensors during a large-amplitude flexion movement, the flexor muscles adjust themselves to the shortening by formation of new bonds. This would cause an after-effect of increased flexor stiffness which, after return to the initial position, slowly subsides as the newly formed bonds gradually dissolve.

With the sinusoidal torque stimuli used by Lakie *et al.* (1984) the amplitude of the resulting angular movements must, in a way different from that in our uni-directional tests, have been dependent on both flexor and extensor stiffness. This can possibly explain why, in contrast to us, Lakie *et al.* (1984) never saw enhancements but only reductions in short-range stiffness after conditioning movements, apparently irrespective of movement direction: 'one movement of flexion followed by extension, or vice versa, was as effective as repeated flapping'. It should also be pointed out that our slow alternating movements (Fig. 4*B*) are probably not analogous to the 'flapping' employed by them. Methodological differences may also explain why Lakie *et al.* (1984) found that 'the memory for past events fades out in 1–2 s', whereas we observed after-effects which often persisted for several minutes. In this respect our observations agree better with earlier findings on isolated frog muscle fibres (Buchthal & Kaiser, 1951).

The increased stiffness following shortening contractions (Fig. 4*D*) might be explained in a similar way to the stiffening effect of passive shortening. The loosening effect of isometric contractions, on the other hand (Fig. 4*C*), can be accounted for by assuming that actively sliding filaments tend to disrupt pre-existing cross-bridges. It is also conceivable that the twitching of individual motor units in unfused contractions can (in a similar way to muscle vibration) cause a disruption of pre-existing bonds.

Afferent stretch responses

There are several reasons for our belief that the multi-unit afferent stretch responses shown in the neurograms of Figs. 6–9 are mainly derived from group Ia muscle spindle afferents: (1) the micro-electrode was properly positioned in a pure muscle nerve fascicle where signals from skin afferents could not be discerned, (2) the comparatively high-amplitude action potentials in the large diameter Ia afferents are likely to stand out better in the neurogram than signals in myelinated fibres of

smaller diameter, (3) as compared to other intramuscular stretch receptors the primary spindle endings possess the highest dynamic stretch sensitivity and are therefore likely to be preferentially excited by minute stretch stimuli, (4) the twitch tests indicated that the signals were derived mainly from muscle spindles rather than from Golgi tendon organs.

Our interpretation of the observed changes in the multi-unit afferent stretch responses would certainly be strengthened if similar changes could be shown also in single-unit recordings from Ia afferents. Unfortunately, we failed in our attempts to obtain such single-unit recordings stable enough to withstand the mechanical impacts caused by the conditioning manoeuvres. Still, on the present evidence, it seems likely that changes in muscle spindle stretch sensitivity were the major but possibly not the sole cause of the lingering changes in the multi-unit afferent stretch responses.

Since the extrafusal fibres lie in parallel with the primary spindle end-organs, changes in the inherent stiffness of these fibres cannot be held responsible for the alterations in muscle spindle stretch sensitivity illustrated in Figs. 6–9. The most plausible explanation is that not only the extra- but also the intrafusal fibres possess thixotropic properties. In general terms, our findings are compatible with the notions recently presented by Morgan *et al.* (1984) concerning cross-bridge formations and disruptions in intrafusal fibres of cat muscle spindles. The present results can be explained simply by postulating that the conditioning manoeuvres have similar mechanical after-effects on intra- and extrafusal fibres and that the primary spindle endings are more susceptible to the intrafusal than to the counteracting extrafusal stiffness changes.

An alternative interpretation would be that the lingering changes in muscle spindle stretch sensitivity depended on changes in static and/or dynamic fusimotor drive. There are, however, a large number of earlier human studies indicating that spindles in completely relaxed human muscles are normally not exposed to any significant fusimotor tone (Vallbo *et al.* 1979). The outcome of the nerve block experiment illustrated in Fig. 8 also indicates that the changes in muscle spindle stretch sensitivity, in this experiment at least, were not due to fusimotor effects but rather to lingering changes in the inherent mechanical properties of intramuscular structures lying in series with the spindle-end organs.

In contrast to Hutton *et al.* (1973) and Smith *et al.* (1974) after isometric contractions we found no signs of enhanced tonic spindle discharge or enhanced stretch sensitivity of spindle endings. As illustrated in Fig. 9, isometric finger flexor contractions had just the opposite after-effect, whereas non-isometric shortening contractions had after-effects similar to those described by Hutton *et al.* (1973) following isometric contractions in the cat calf muscles. We have no definite explanation for the discrepancies between our results and those of Hutton *et al.* (1973). If the finger flexor tendons were less compliant than the Achilles tendon one could possibly understand why an active finger flexor movement was needed to mimic the effect of an 'isometric' calf muscle contraction. However, to our knowledge, there is no direct experimental evidence to support such an explanation (cf. Rack, Ross, Thilmann & Walters, 1983; Rack & Ross, 1984).

Reflex responses

In a similar way to muscle spindle stretch sensitivity, the potency of the stretch reflex varied in parallel with the changes in inherent muscle stiffness. It cannot be claimed, however, that the alterations in muscle spindle sensitivity were the sole cause of the reflex changes. Post-tetanic potentiation of the monosynaptic reflex pathway might for instance contribute to stretch reflex enhancement following powerful contractions (Hagbarth, 1962; but see also Enoka *et al.* 1980). Another contributing factor could be a post-contraction decrease in stretch sensitivity of Golgi tendon organs exerting autogenetic inhibition (Smith *et al.* 1974). It should also be considered that conditioning finger flexion or extension movements may be followed by lingering changes in mechanoreceptive inflows from antagonistic finger extensors, affecting the excitability of the flexor motoneurones.

According to Enoka *et al.* (1980) isometric contractions of human calf muscles are followed by a potentiation of reflex e.m.g. responses to Achilles tendon taps. This after-effect may be analogous to the stretch reflex potentiation we observed in the finger flexors following non-isometric, shortening contractions (Fig. 5*B*, right). It remains difficult to explain why we, in contrast to Enoka *et al.* (1980), found a lingering reflex suppression following isometric contractions (Fig. 5*B*, left).

As judged by the latency, the earliest reflex response in the e.m.g. was conveyed via the spinal stretch reflex arc (Figs. 5 and 6). It was shown earlier that, providing intramuscular oscillations appear in response to a ramp stretch, these oscillations may cause repetitive volleys of Ia discharges and a corresponding segmentation of the reflex e.m.g. responses (Hagbarth, Hägglund, Wallin & Young, 1981). It remains to be seen whether changes in inherent muscle stiffness following different conditioning manoeuvres may affect the proneness of the system to respond to ramp stretches with damped oscillations and repeated spindle volleys.

Implications

A much debated question concerns the problem of whether fusimotor-induced changes in muscle spindle stretch sensitivity normally occur without concomitant changes in α motor outflow to the receptor-bearing muscle (Taylor & Prochazka, 1981). Ia recordings in freely moving animals have shown that the stretch sensitivity of primary spindle endings in a muscle can change independently of extrafusal contraction strength (Prochazka & Wand, 1981). This has been interpreted as a sign of α-independent control of fusimotor neurones. An alternative interpretation is offered by the present results: without involvement of the fusimotor system, there may be lingering changes in muscle spindle stretch sensitivity, which are dependent on the previous history of movement.

The present results may seem contradictory to the theory that a main functional role of the stretch reflex is to compensate for variations in inherent muscle stiffness (Nichols & Houk, 1976). Rather than exhibiting a compensatory function the stretch reflex varied in strength in parallel with the lingering changes in inherent stiffness. It should be noted, however, that in the present study the subjects were instructed to relax, whereas in the experiments by Nichols & Houk (1976) the stretch reflex was 'turned on' by decerebration.

Another implication of the present results concerns the use of averaging procedures

when studying reflex e.m.g. responses to imposed joint displacements. It should be realized that lingering changes in inherent extra- and intrafusal muscle fibre stiffness with accompanying changes in stretch receptor sensitivity may occur following individual stretch movements. On repetition, the reflex e.m.g. responses to individual stretch stimuli may gradually change, possibly not only in amplitude but also in latency and shape. Thus the average picture of a series of reflex e.m.g. responses to stretch may exhibit a pattern which is not representative of the response to any given individual stimulus.

In their training programmes, athletes, dancers and physiotherapists often include different types of stretching manoeuvres to enhance flexibility. The benefit of such manoeuvres may, at least in part, be due to the fact that they tend to reduce both the inherent and the reflex stiffness of the muscles exposed to stretch. There are different opinions as to whether flexibility or muscle relaxation can be further enhanced by so called p.n.f. procedures (proprioceptive neuromuscular facilitation), in which the subject statically contracts the muscles prior to stretch (Kabat, 1950; Knott & Voss, 1968; Moore & Hutton, 1980; Hartley-O'Brien, 1980). Based on the finding that 'isometric' calf muscle contractions in the cat are followed by enhanced reflex stiffness, Moore & Hutton (1980) argue against the benefit of such p.n.f. procedures in promoting muscle relaxation. Also, when testing female gymnasts for hip flexibility they found that conventional stretching techniques were superior to p.n.f. techniques in promoting 'lower absolute e.m.g. magnitudes during stretch'. As judged by the present study, finger flexor stiffness increases after non-isometric shortening contractions and decreases after isometric or lengthening contractions. Thus, in the treatment of stiff finger flexors the latter two types of contractions might be expected to have a beneficial, lingering effect.

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