

GROUPED SPINDLE AND ELECTROMYOGRAPHIC RESPONSES TO ABRUPT WRIST EXTENSION MOVEMENTS IN MAN

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SUMMARY

1. Different techniques were used to generate sudden ramp extension movements of the wrist while the subjects were either relaxed or maintaining a weak voluntary contraction in the wrist flexors. Afferent responses to the displacements were recorded with a tungsten micro-electrode inserted into a fascicle of the median nerve supplying one of the wrist flexor muscles, and e.m.g. responses were recorded with needle electrodes inserted into the same muscle.

2. With the wrist flexors either relaxed or contracting, extensions at 100–200°/sec for 60–70 msec (generated by either an hydraulic motor or a torque motor) produced segmented afferent responses with two to four afferent bursts, separated by intervals of 20–30 msec. The successive neural peaks, occurring during the stretch phase, were correlated to mechanical vibrations sensed by a strain gauge and sometimes also by a wrist goniometer. With the flexor muscles contracting, the successive peaks in the neurogram were followed by similar peaks in the e.m.g., the delay between neural and e.m.g. peaks being 20–25 msec.

3. Small abrupt extension movements of 1–2° lasting only 10–15 msec often produced segmented afferent responses with one neural burst occurring during the stretch phase and another 15–20 msec later, corresponding to a mechanical oscillatory event succeeding the stretch. The oscillation and the second neural burst were not present with small extension movements of smooth onset and halt. With the flexor muscles contracting, stimuli producing one afferent burst produced only one e.m.g. peak, whereas double-peaked afferent discharges produced double-peaked e.m.g. responses, the delay between individual neural e.m.g. peaks being 20–25 msec.

4. Similar segmentation of the neural stretch responses was seen when abrupt displacements were produced by electrically induced muscle twitches, by manual pulls on a spring attached to the hand or by the subject making fast voluntary wrist extensions. This grouping of afferent discharges was seen in both multi-unit and in single-unit recordings from fibres identified as group Ia afferents.

5. It is concluded that mechanical vibrations in the moving parts are initiated by

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abrupt joint movements and that these vibrations are sensed by the primary endings. With initial background contraction in the stretched muscles, synchronous volleys of spindle discharges produce, via segmental reflex arcs, modulation of the e.m.g. with the appearance of two or three e.m.g. peaks separated by intervals of 20–30 msec. Possible causes for the mechanical oscillations are discussed.

6. For imposed movements with a duration of 60–70 msec the successive e.m.g. peaks caused a fused reflex contraction, appearing as a torque trace deflexion, starting at about the time when the movement ended and reaching its peak within about 40 msec. With longer-lasting movements the mechanical reflex response accompanying the successive e.m.g. bursts, appeared as a decelerative force, starting to oppose the ongoing movement about 60 msec after its start. Mechanical consequences of stretch reflex contractions starting after, rather than during, the stretch movement are discussed.

INTRODUCTION

An abrupt angular displacement of a limb joint in man or alert monkeys tends to evoke successive bursts of electromyographic (e.m.g.) activity in contracting muscles being stretched by the displacement. The initial burst is generally ascribed to the spinal stretch reflex whereas the nature of the later responses remains conjectural. The second e.m.g. burst, originally described by Hammond (1954), has by several investigators been interpreted as a supraspinal 'long-loop reflex' (Hammond, Merton & Sutton, 1956; Evarts, 1973; Marsden, Merton & Morton, 1972, 1976*a*). Since this e.m.g. burst contributes significantly to the mechanical reflex response it has also been denoted 'the functional stretch reflex' (Melvill-Jones & Watt, 1971; Marsden, Merton & Morton, 1976*b*). A third burst with latency close to the reaction time has been interpreted as either a 'long-loop reflex' (Lee & Tatton, 1975; Marsden, Merton, Morton, Adam & Hallett, 1978) or a 'voluntary' or 'intended' response (Evarts & Tanji, 1976; Evarts & Granit, 1976; Evarts & Vaughan, 1978).

Other investigators challenge the view that the later e.m.g. peaks reflect neural conduction through supraspinal pathways. Thus, Ghez & Shinoda (1978) conclude from their studies in intact and spinal cats that supraspinal 'long-loop' actions cannot be inferred from the peaks and troughs of the e.m.g. record, and that receptor properties and, or, spinal mechanisms are sufficient to produce the segmented e.m.g. responses. Criticism of the 'long-loop reflex' hypothesis has also been raised by Houk (1978, 1979), and in a recent study, Bawa & Tatton (1979) discuss the possibility that the successive e.m.g. bursts result from successive afferent volleys evoked by the displacement.

For proper interpretation of the segmented e.m.g. response it is obviously of importance to record the afferent response to the displacement – in particular the response from the spindle endings. In the present study, the micro-electrode technique introduced by Vallbo & Hagbarth (1968) was used to record afferent neural stretch responses arising from human wrist flexor muscles in response to abrupt wrist extension movements. Evidence is presented that mechanical vibrations in the moving parts are initiated by an abrupt joint movement and that these oscillations are sensed by the primary spindle endings in the stretched muscles. Provided there

is initial background contraction in the flexor muscles, successive synchronous volleys of spindle discharges, occurring during the stretch, produce reflex modulation of the gross e.m.g. with the appearance of two or three e.m.g. peaks separated by intervals of 20–30 msec. A preliminary report of the study has been published (Hagbarth, Young, Hägglund & Wallin, 1980*a, b*).

METHODS

Data were obtained from seventeen experiments on three healthy subjects (the authors, K.-E. H., J. H. and R. Y.) aged 41–53 yr. During experiments the subjects reclined in a comfortable position with the left forearm strapped to a rigid support and the hand attached to a plate or handle which could be rotated to produce extension movements of the wrist.

Mechanical stimuli. Two different types of electromagnetic devices were used to generate joint movements. One consisted of a step motor connected to an hydraulic power amplifier (Electric Company 6H-HS 50, Slo-Syn Superior), turning a rotating disk to which the hand with extended fingers was securely attached. With its torque capability of about 50 Nm this device was designed to generate reproducible angular displacements with preset speed and amplitude, largely independent of muscle resistance (Löfstedt, 1978). Alternatively, wrist extensions were produced with a disk armature DC torque motor (CEM, AXEM, M 19), generating torque pulses of preset strength and duration. The maximal torque generated was 2 Nm and the amplitude and speed of the resulting wrist movement were dependent on the degree of contraction in the wrist flexors resisting the movement. A handle, grasped by the subject, was eccentrically attached to the axle of the motor in such a way that anticlockwise rotation of the axle generated wrist extension.

With the wrist placed at midposition (about 180°), subjects were instructed either to remain passive with relaxed wrist flexor muscles or to maintain a moderate sustained flexor contraction, thus exerting an active wrist flexion torque against the plate or the handle (which was prevented from moving in the clockwise direction past 180°). The subjects received no instruction to react in any specific way (with for instance 'resist' or 'let go' reactions) to the imposed movements, which were delivered at irregular intervals (5–30 sec) after repositioning the wrist at 180°. Care was taken to avoid clues which could help the subject predict the timing of individual stretch stimuli.

In some experiments wrist extension movements were generated without assistance of any electromagnetic devices. Such trials involved manually applied rapid pulls on a spring attached to the hand (with the finger joints splinted) or dropping weights onto a shock-absorbing material in the palm of the outstretched, supinated hand. Wrist jerks were also produced by electrically induced muscle twitches or by letting the subject make voluntary ballistic wrist movements.

Goniometers, accelerometers, strain gauges. In all experiments a low-inertia goniometer was securely attached with adhesive tape on the ulnar side of the wrist. It contained a conductive plastic element potentiometer (Sakae Tsushin Kogyo Co. FCP 12 AC) with almost infinite resolution. Another potentiometer was connected to the shaft of the hydraulic motor. Even though attempts were made to secure the hand as tightly as possible to the plate, compliance of tissues made it impossible to avoid some mechanical play in transmission of the impact. Thus, even though the shaft potentiometer did not display irregularities or oscillatory variations in speed of the movements, such oscillations were usually sensed by the wrist potentiometer. Only signals from the wrist potentiometer are illustrated.

The hand plate of the hydraulic machine had a built-in strain gauge, monitoring the force between hand and plate (14 cm from the axis of rotation). Its bridge amplifier had an upper frequency limit of 75 Hz (3 db). Phase distortion introduced by the filter was measured and compensated for in the Figures. An accelerometer was attached to the handle of the torque motor; its amplifier was linear up to frequencies of > 1 kHz.

Electromyography. two needle e.m.g. electrodes with 5 mm long uninsulated tips were inserted 2–3 cm apart in one of the wrist flexor muscles, the muscle chosen being the one supplied by the fascicle impaled by the micro-electrode in the median nerve (see below). Most recordings were made from *m. flexor carpi radialis* and *m. palmaris longus*.

Nerve recordings. The micro-electrode recording technique was the same as described in previous reports (Vallbo, Hagbarth, Torebjörk & Wallin, 1979). A tungsten needle electrode (tip diameter

< 5 μm) was manually inserted through the skin into the median nerve, medial to the biceps tendon in the proximal part of the cubital fossa. The reference electrode was a tungsten needle with a 5 mm long bare tip (low impedance) inserted subcutaneously within 1 cm of the micro-electrode. Electrical test shocks delivered through the electrodes provided guidance when searching for the appropriate type of nerve fascicle. The following criteria for impalement of a wrist-flexor nerve fascicle were used: (a) Cathodal pulses (0.2 msec) of less than 4 V delivered through the micro-electrode tip caused twitches in one of the wrist flexor muscles without concomitant skin paresthesias; (b) distinct multi-unit bursts of afferent impulses were recorded in response to light taps over the muscle or its tendon and in response to minute extension movements of the wrist; but no afferent signals could be detected in response to mechanical skin stimuli or to weak taps on neighbouring muscles or tendons. When these criteria were fulfilled it could as a rule also be demonstrated that, in response to electrically induced muscle twitches (by shocks delivered through the e.m.g. electrodes), afferent neural bursts appeared not during the rising but only during the falling phase of the twitch. This supports previous claims that the recording technique involves a bias favouring detection of impulses in the large group Ia afferent fibres from muscle spindles, whereas signals from smaller myelinated fibres (afferent and motor) are often hidden in the noise (Hagbarth, 1979). Occasionally single unit recordings were obtained from fibres in the wrist flexor nerve that could be identified as Ia afferents, but with a few exceptions (one illustrated in Fig. 4A) such single unit recording sites were lost during repeated abrupt extension movements. One recording from the radial nerve on the lateral side of the proximal forearm was included, since in this case an exceptionally stable recording was obtained from a unit that could be identified as a group Ia fibre (Fig. 4B). It came from a spindle in *m. extensor carpi ulnaris* and the recording site remained stable during a long series of brisk wrist flexions. Care was taken to assure that neurograms were not contaminated with any motor unit potentials from neighbouring muscles which the subject was instructed to keep relaxed.

To obtain an optimal signal-to-noise ratio the amplifier used for the nerve recordings operated within a frequency range of 300–5000 Hz and, with guidance from the loudspeaker, noise was further reduced by a discriminator eliminating deflexions below an adjustable level.

Signal analysis. Neural and electromyographic responses to wrist perturbations were together with signals from mechano-transducers, displayed on a four-channel storage oscilloscope (Tektronix type 549). Motor driven perturbations were preceded by prepulses triggering the oscilloscope sweep. These prepulses together with the recorded neural, electromyographic and mechanical events were stored on a multi-channel FM-tape recorder (Sangamo, Sabre VI) for subsequent analysis and averaging.

Multi-unit neural and e.m.g. signals from the tape recorder were rectified and passed through an integrator with exponential decay (time constant 0.001 or 0.005 sec) providing one-directional 'integrated' traces of neural and electromyographic events. Single unit neural impulses were converted to standard pulses before analysis.

An averager (Disa, 14 G 11) connected to a X-Y plotter (HP 7046 A) or a PDP 11/40 minicomputer and an incremental plotter (Versatec 1100) were used for display of individual traces, for averaging and for plotting of time-interval histograms. Triggering events were either recorded prepulses, initial deflexions in the accelerometer signals or time-locked pulses delivered by a time code and tape search unit (Systron Donner 8100).

RESULTS

Grouping of multiunit stretch discharges from relaxed wrist flexor muscles during abrupt wrist extension movements. In thirteen experiments, recordings were made from nerves of relaxed wrist flexor muscles, while wrist extension movements with a speed of 100–200°/sec and an amplitude of about 10° were generated by the hydraulic machine or the torque motor. The afferent muscle nerve responses to individual stretch stimuli of this type were always of complex shape, most of them exhibiting two or three successive peaks of neural activity, separated by intervals of 20–30 msec (Fig. 1). The successive peaks of neural activity, occurring during the stretch phase, were also

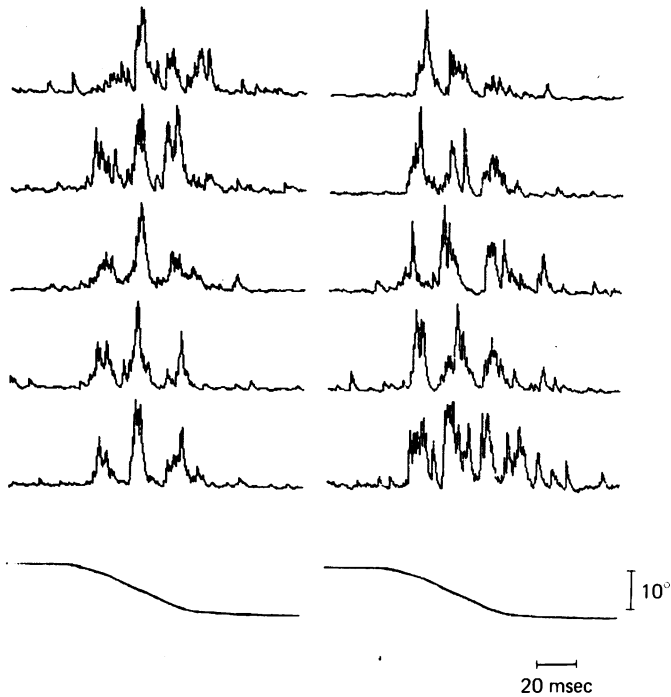


Fig. 1. Grouping of multiunit afferent discharges from relaxed wrist flexor muscles during abrupt wrist extensions generated by hydraulic motor. Neural responses to ten individual stretch movements with averaged wrist displacements shown in bottom traces.

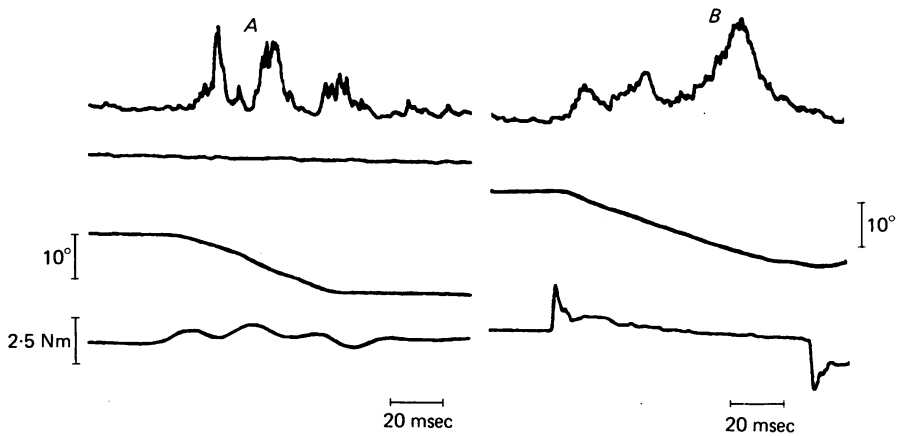


Fig. 2. Grouping of afferent discharges from relaxed wrist flexor muscles during abrupt wrist extensions generated by hydraulic motor (*A*) and torque motor (*B*). *A*, average of four events like those illustrated in Fig. 1. Top to bottom: neural response, e.m.g., wrist angle, torque. Note oscillations in torque signal (and small stepwise changes in speed of movement) relating to successive neural bursts. *B*, average of eight events. Top to bottom: neural response, wrist angle, acceleration (accelerometer attached to handle).

clearly seen after averaging responses to series of similar stretch stimuli (Fig. 2). An initial assumption that this segmentation of afferent responses depended on oscillatory tendencies inherent in the moving parts of the mechanical systems could not be verified. Segmentation of neural stretch discharges remained uninfluenced by changes in mass or spring constant of the hand plate, and, as judged by potentiometer traces

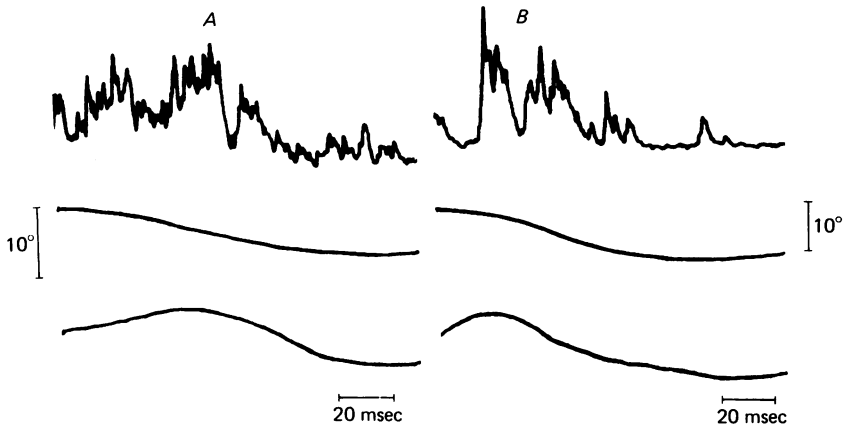


Fig. 3. Grouping of afferent discharges from relaxed wrist flexor muscles during wrist extensions generated by manual rapid pulls on a spring attached to the hand (*A*, average of eleven events) and by quick voluntary contractions of the wrist extensor muscles (*B*, average of four events). Top to bottom: neural response, wrist angle, acceleration (accelerometer attached to handle).

from the axle of the hydraulic motor, there was no mechanical ripple in displacement of the axle relating to the neural bursts. However, the strain gauge signal did oscillate during the stretch phase, indicating rhythmical repercussions of the hand against the hand plate during the stretch. Such fluctuations, sometimes reflected also in the goniometer trace from the wrist, were temporally related to the neural bursts (Fig. 2*A*).

Both the strain gauge oscillations and the peaks and troughs in the neural discharge became more apparent with increasing speed of the stretch movements. A small increase in frequency of the mechanical and neural oscillations also occurred when speed of movements was raised from 100 to 200°/sec.

Segmented stretch responses in wrist flexor nerves similar to those evoked by motor-driven wrist displacements were also seen in five experiments during abrupt extensions produced manually by sudden pulls on a spring attached to the hand (Fig. 3*A*) and during voluntary wrist extension movements (Fig. 3*B*). In these instances individual extension movements in a series were not quite identical with respect to speed and amplitude, and the timing of the neural bursts varied more from one stretch movement to the next than with motor-induced movements. In averaged records, segmentation of the neural response was therefore not displayed as distinctly as during the motor-induced movements and the averaged goniometer and accelerometer traces usually did not reveal any obvious notches or deflexions temporally related to the neural bursts.

Unitary spindle responses to abrupt wrist movements. Two single unit recordings from Ia afferents in the wrist flexor nerve remained stable during repeated wrist extensions generated by the torque motor. For both these units the impulses occurring in response to abrupt stretch were grouped in a similar way to the impulses seen in multi-unit recordings. The unit illustrated in Fig. 4*A* often fired once in the very beginning of the perturbation (even before the wrist goniometer signalled start

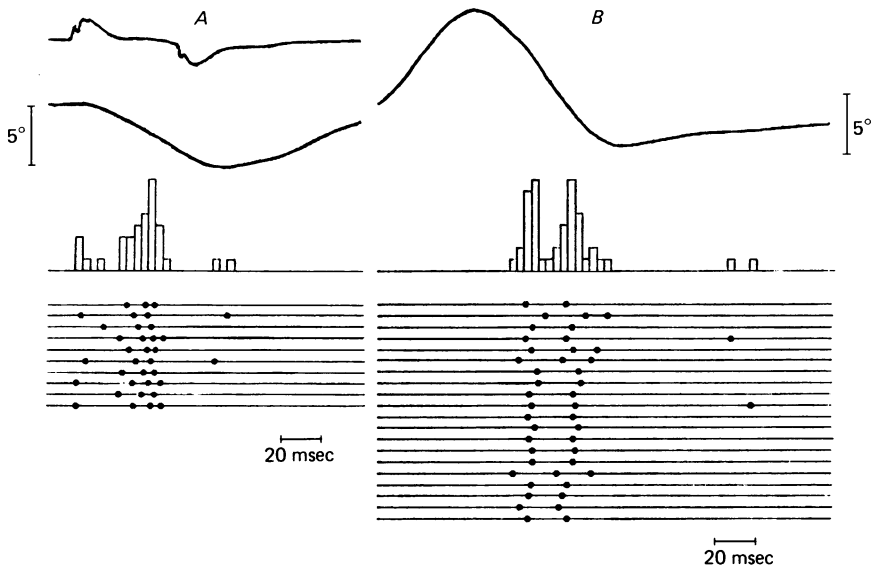


Fig. 4. *A*, timing of single unit discharges from a primary spindle ending in relaxed wrist flexor muscle during wrist extensions generated by torque motor. Lower dot displays show impulses during each of ten successive displacements. Traces above (top to bottom): acceleration, wrist angle, time-interval histogram of impulses shown individually in dot displays. Note how timing of neural discharges relates to deflexions in accelerometer trace. *B*, timing of single unit discharges from a primary spindle ending in wrist extensor muscle during passive wrist flexions following electrically induced wrist extension jerks. Lower dot displays show timing of impulses during each of twenty successive jerks. Upper traces (top to bottom): wrist angle, time-interval histogram of impulses shown individually in the dot displays. Note how timing of neural discharges relates to 'angle' on falling phase of goniometer trace and to low-amplitude second 'hump' following the main jerk.

of movement). Then, after a period of relative silence, a short train of impulses occurred 25–30 msec later, and occasionally single discharges occurred after another 25–30 msec. In this case the peaks and troughs in the time-interval histogram correlated with deflexions seen in the accelerometer trace.

Another group Ia unit, which was found in the radial nerve and originated from a spindle in a wrist extensor, exhibited grouped discharges during abrupt stretch, correlated to minute mechanical fluctuations sensed by the wrist goniometer. With the wrist muscles relaxed and the hand in pronation, electrically induced extensor twitches caused abrupt extension movements of the wrist, followed by rapid stretch of the extensor muscles as the hand fell back to its original position. Twenty such twitches were applied and the unit regularly fired during the stretch phases (Fig. 4*B*).

It seldom fired more than twice during a stretch phase, and as shown by the double-peaked interval histogram most discharges occurred at 20 and 40 msec following the start of the stretch, i.e. at intervals corresponding to the repetition rate of the multi-unit bursts in Figs. 1 and 2. About 20 msec following the start of the stretch, there was also a small change in the slope of the averaged goniometer trace, indicating that the movement did not proceed quite smoothly. Following the main

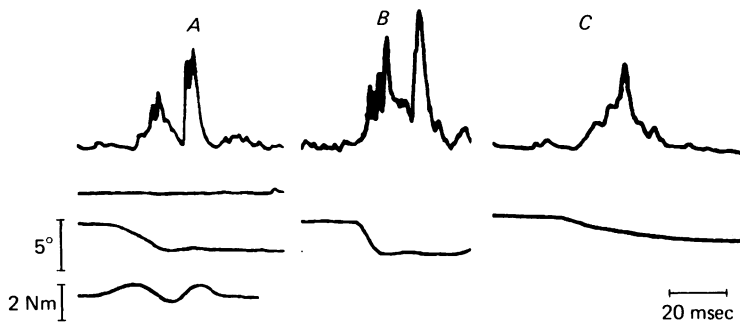


Fig. 5. *A* and *B* illustrate neural bursts from relaxed finger flexors related to repercussions following small fast wrist extensions. *A*, small, rapid wrist extensions generated by hydraulic motor. Average of ten events. Top to bottom: neural response, e.m.g. (from relaxed wrist flexor), wrist angle, torque. *B*, wrist extensions generated by torque motor. Average of six events. Top to bottom: neural response, wrist angle. *C*, illustrates low amplitude, slow stretch movements, (generated by torque motor) producing only one neural burst without repercussion response. Average of twenty-eight events. Top to bottom: neural response, wrist angle.

stretch phase there was also a low-amplitude oscillation which on a few occasions was sensed by the spindle ending which then fired a third time during the stretch phase of that movement. As an indication of this primary ending's high dynamic sensitivity, it also responded to arterial pulse waves in the muscle.

Multiunit neural bursts related to oscillations occurring after the end of an imposed wrist movement. With motor-driven movements, mechanical and neural oscillations were often seen not only during but also after the halt of the stretch movement. Such 'bouncing' phenomena were most apparent in response to small fast joint movements which started and stopped suddenly as in Fig. 5*A* and *B*. With such stretch movements, which did not last longer than 10–15 msec, there was only one burst in the nerve during the stretch phase; then a second and sometimes also a third burst appeared concurrent with oscillatory events sensed by the strain gauge (Fig. 5*A*) or the goniometer (Fig. 5*B*). The repetitive bursts resulting from such short brisk movements usually occurred with intervals of 15–25 msec. Similar goniometer and neural events to those illustrated in Fig. 5*A* and *B* were also seen when minute sudden wrist extensions were produced by a small weight (30 g) falling into the palm of the outstretched hand from a distance of about 20 cm. Fig. 5*C* illustrates a type of wrist extension movement which generally did not produce more than one synchronized neural burst. Movements of this type had a smooth onset and stop, they did not exceed a speed of 25°/sec and they did not last longer than about 30 msec.

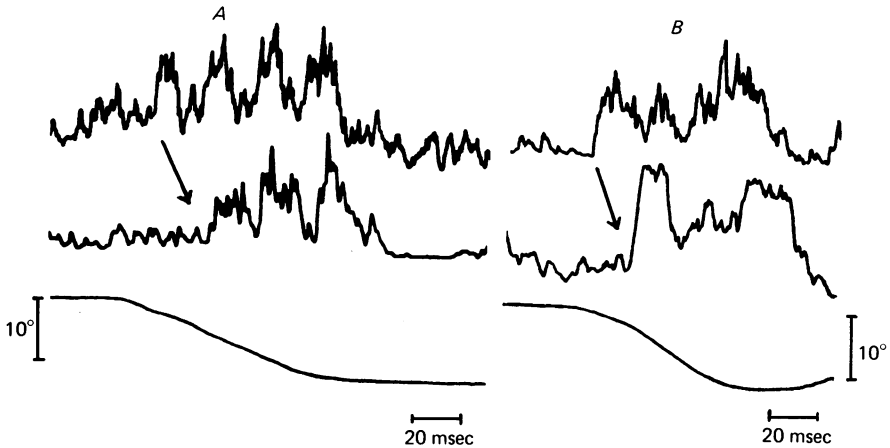


Fig. 6. *A* and *B*, grouping of afferent discharges and e.m.g. responses from contracting wrist flexor muscle during abrupt wrist extensions (lasting 60–70 msec) generated by hydraulic motor (*A*) and torque motor (*B*). Five events averaged in both *A* and *B*. Top to bottom in each case: neural response, e.m.g. response, wrist angle. Arrows indicate reflex delay between afferent bursts and succeeding e.m.g. peaks.

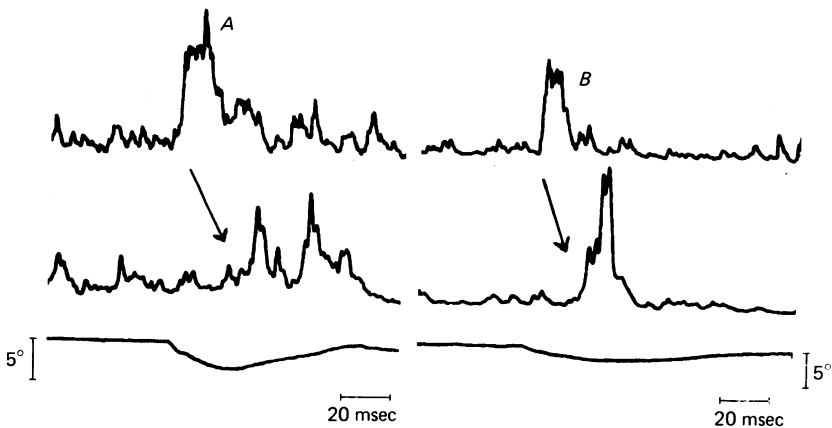


Fig. 7. *A*, grouping of afferent discharges and e.m.g. responses from contracting wrist flexor muscle following a short lasting (20 msec) wrist extension, generated by torque motor. Average of five events. Top to bottom: neural response, e.m.g., wrist angle. *B*, minute wrist extensions (generated by torque motor) producing only one distinct neural burst and one distinct e.m.g. peak. Average of five events. Top to bottom: neural response, e.m.g., wrist angle. Arrows indicate delays between afferent bursts and succeeding e.m.g. peaks.

Relations between afferent stretch discharges and reflex e.m.g. responses in contracting muscles. In experiments described in the preceding paragraphs (with the exception of 'falling-weight' tests), subjects were instructed to remain relaxed in wrist muscles exposed to the stretch stimuli. As exemplified in Figs. 2*A* and 5*A*, e.m.g. recordings usually confirmed that relaxation was complete. Occasionally, however, one or two small e.m.g. bursts appeared in response to the stretch stimuli; latency of the initial e.m.g. response seldom being shorter than 60–70 msec.

During contraction, segmentation of the neural responses was equally or even more prominent than during relaxation, with three or often four well-defined neural bursts occurring during stretch movements lasting 60–70 msec (Fig. 6*A*). Averaged e.m.g. responses were segmented similarly to afferent stretch discharges, successive e.m.g. peaks being delayed 20–25 msec after peaks in the neurogram. However, as illustrated in Fig. 6*A* and *B*, the e.m.g. response often contained one peak less than the neural

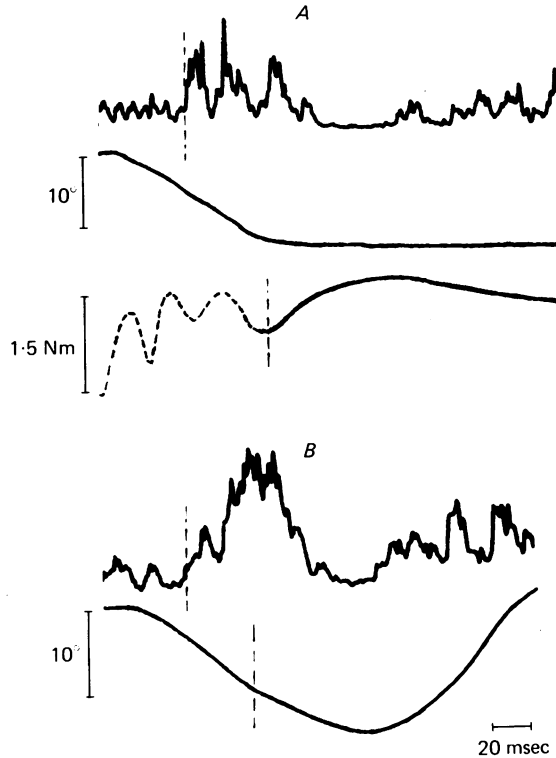


Fig. 8. Segmented e.m.g. responses of contracting wrist flexors to abrupt extensions, with accompanying reflex changes in torque (*A*) and wrist angle (*B*). *A*, extensions generated by hydraulic motor. Average of four events. Top to bottom: e.m.g. response, wrist angle, torque. Following initial torque oscillations during movement (dashed part of trace) the reflex-induced rise in torque starts 40 msec after start of e.m.g. response (dashed vertical lines). *B*, extensions generated by torque motor. Average of ten events. Top to bottom: e.m.g. response, wrist angle. Start of reflex-induced decelerations indicated by 'angle' in goniometer trace, appearing 40 msec after start of e.m.g. response (dashed lines).

response. The total duration of segmented e.m.g. responses during stretches of the type illustrated seldom exceeded 75 msec and following the last e.m.g. peak there was a period of motor subnormality, as indicated by the flat e.m.g. record.

Stretch movements of short duration also gave rise to segmented e.m.g. responses, provided neural bursts occurred after the end of the stretch (Fig. 7*A*). Small stretch stimuli of the type which did not produce more than one distinct neural burst were followed by only one distinct e.m.g. peak in the contracting muscle, a peak occurring 20–25 msec after the neural burst (Fig. 7*B*).

Relations between reflex e.m.g. responses and mechanical reflex events. For stretch movements of duration 60–70 msec, like those illustrated in Fig. 6*A*, the reflex mechanical response to the perturbation started at about the time the stretch movement was completed. For this type of wrist extension generated by the hydraulic machine, the strain gauge signalled reflex torque as an upward deflexion starting 60–80 msec following the start of the stretch movement and 40–60 msec following the beginning of the first e.m.g. peak (Fig. 8*A*). Following torque oscillations during the stretch movements (dashed in the Figure), the reflex torque rose to its peak within about 40 msec and then gradually declined. For wrist extensions generated by the torque motor, initiation of the mechanical reflex response could often be seen as a deflexion in the goniometer trace occurring 40–60 msec after the initiation of the first e.m.g. peak. This deflexion, representing the start of reflex resistance to the imposed movement, is shown in Fig. 8*B*, where the imposed torque lasted for about 120 msec, and the reflex then occurred in time to act as a decelerative force resisting the perturbation.

DISCUSSION

The present findings demonstrate that successive e.m.g. bursts appearing in response to brisk joint displacements may result from successive afferent volleys evoked by the displacement. However, our results also give rise to a series of questions concerning the genesis and impulse composition of the successive afferent volleys, questions which need consideration before more definite conclusions can be drawn concerning primary causes of the segmented e.m.g. response.

Genesis and impulse composition of the afferent bursts. The findings provide evidence that a single abrupt joint movement is sensed by intramuscular stretch receptors, not as one single mechanical event but as an event containing a series of mechanical stimuli. Alternative ways of explaining the segmentation of the multiunit stretch discharges are not easily found. Clearly, the burst intervals are far too long to be accounted for in terms of different conduction velocities in separate fibre populations. Even though many types of mechano-receptors are probably excited by the brisk stretch movements, it is unlikely that the successive neural peaks derive from different receptor populations recruited in a step-wise order during the stretch. It is also unlikely that individual units in a given receptor population would fire synchronously at intervals of 20–30 msec without the influence of any mechanical 'pace-maker'.

The torque, goniometer and accelerometer traces shown in previous studies often do not show 'notches' or 'angles' indicative of oscillatory variations in torque or speed of movement. As a rule, however, the mechano-transducers have been attached to a mechanical part of the moving system, and small variations in imposed joint movements might therefore be undetected. Some previous investigators of motor responses to brisk joint displacements have, during the movements, observed oscillations in torque, signalled by a strain gauge attached to the plate or handle moving the limb. No major attention was paid to these oscillations which were considered to result from mechanical interaction between soft subcutaneous tissues and the hard surface of the manipulandum (Tatton & Bawa, 1979). The rhythmical

torque and low-amplitude wrist goniometer deflexions observed in the present study deserve particular attention since they obviously represent mechanical events which can also be sensed by intramuscular stretch receptors.

The present experiments give no definite clues regarding the genesis of these mechanical oscillations. The initial acceleration and final deceleration generated by the motors may well produce action and reaction forces when compressible tissues of the hand react with the hand plate or handle. However, since oscillatory events were also sensed by the intramuscular receptors when no manipulandum was in contact with the hand (Figs. 3 and 4*B*), they cannot be wholly dependent on the viscoelastic characteristics of subcutaneous hand tissues. It is uncertain whether, for instance, non-linearities in joint friction during movement may contribute to the oscillatory tendencies or whether they are mainly due to mechanical characteristics inherent in the musculo-tendinous part of the system. As demonstrated by Joyce, Rack & Westbury (1969) and Nichols & Houk (1976), mechanical compliance of a contracting muscle produces marked non-linearities in mechanical resistance to ramp stretches. Lakie, Walsh & Wright (1980) have more recently demonstrated that the relaxed human wrist is much stiffer for small than for large movements, a fact attributed to 'thixotropic' properties of muscles. It remains uncertain whether or not transient high viscous resistance appearing during the initial phase of a fast stretch movement may result in damped intramuscular vibrations persisting during the remaining part of the stretch (cf. Pringle, 1977). Transient mechanical events occurring at different times in neighbouring forearm muscles exposed to the stretch may also contribute to successive mechanical fluctuations. Whatever components of the moving body parts are mainly responsible for the oscillations, these components seem to have an inherent resonant frequency of 40–60 Hz which increases with the speed of movement but is fairly independent of whether the muscles are relaxed or stiffened by voluntary contraction.

A second question concerns which intramuscular stretch receptors are sensitive enough to respond to the small rhythmical fluctuations and responsible for the successive impulse volleys detected by the micro-electrode in the muscle nerve. Several arguments can be presented in favour of the view that the end-organs mainly responsible are primary muscle spindle endings. (*a*) Multi-unit neural recordings involve a bias favouring detection of impulses in large group Ia afferents. (*b*) Similar temporal grouping of impulses (at intervals of about 20 msec) to those seen in multi-unit recordings was also seen in single unit recordings (Fig. 4), where the impulses certainly originated from group Ia afferent fibres. (*c*) In the cat, primary endings are characterized by high dynamic stretch sensitivity, much more pronounced for small than for large changes in muscle length (Matthews & Stein, 1969; Poppele & Bowman, 1970; Hassan & Houk, 1975). Furthermore there is evidence that the vibration sensitivity of human muscle spindle endings is optimal during ongoing passive stretch of the receptor-bearing muscle (Burke, Hagbarth, Löfstedt & Wallin, 1976). There is also evidence that primary spindle endings in isometrically contracting human muscle possess a very high dynamic sensitivity to minute perturbations (Hagbarth & Young, 1979).

Reflex effects of successive spindle bursts. As illustrated by the averaged records in Figs. 6 and 7, successive e.m.g. bursts resulting from wrist displacement are

time-locked to successive spindle afferent bursts. Each e.m.g. burst begins 20–25 msec after a corresponding afferent burst, a timing which suggests that mono- or oligo-synaptic segmental reflex paths are responsible not only for the first e.m.g. burst, as all investigators agree, but also for the second and third e.m.g. bursts. An alternative interpretation would be possible if segmentation of the neural response had been present only in those instances when there was background voluntary contraction and a segmented e.m.g. response to the stretch. It could then be argued that the neural bursts succeeding the initial one are not afferent stretch responses but afferent spindle bursts induced by fusimotor action accompanying the e.m.g. bursts. This interpretation is not tenable since segmented afferent responses were also evoked from relaxed muscles without motor responses to the stretch. It has been demonstrated that when a vibrator is applied to a contracting muscle the discharges from the firing motoneurone pool tend to become monosynaptically time-locked to the vibration waves (Homma, Kanda & Watanabe, 1971; Desmedt & Godaux, 1975; Hagbarth, Hellsing & Löfstedt, 1976). Similar vibration-induced synchronization of motor discharges seems to occur transiently whenever a contracting muscle in an intact limb is passively stretched by an abrupt joint movement of sufficient speed and amplitude. The fact that periods of relative neural silence (between bursts) often coincided with periods of high e.m.g. activity agrees with the view that the e.m.g. peaks are due to successive spinal stretch reflexes, not involving any fusimotor-induced co-activation of spindles (Burg, Szumski, Struppler & Velho, 1973; Hagbarth, Wallin, Löfstedt & Aquilonius, 1975).

As recently shown by Bawa & Tatton (1979), the successive e.m.g. peaks (M_1 , M_2 and M_3) do not merely represent synchronized oscillatory activity of alpha motoneurons: the M_1 peak seems to derive mainly from low-threshold, slow-twitch motor units and the M_2 peaks from high-threshold, fast-twitch motor units. If an initial afferent burst of spindle impulses predominantly activates the low-threshold alpha motoneurons a second afferent burst arriving 20 msec later may find these neurons in a postexcitatory subnormal state, whereas higher-threshold α -motoneurons, brought into the subliminal fringe by the first afferent volley, are now ready to respond.

It cannot be definitely inferred from the present experiments that the successive e.m.g. peaks are generated *entirely* segmentally by successive impulse bursts in Ia afferents. A contribution from other mechanoreceptors cannot be excluded. Also, as Phillips (1969), Evarts (1973) and others have demonstrated, there apparently are 'reflex' arcs or loops of varying length including transcortical ones, through which segmental afferent input can quickly reach cerebral structures and affect pyramidal tract discharges that may impinge on spinal motoneurons in advance of signals initiating reaction time movements. Such supraspinal actions are probably integrated with those brought about by segmental mechanisms. It should be noted, however, that in our experiments stimuli producing only one afferent burst evoked only one single short-latency e.m.g. burst (Fig. 7B). We agree with Ghez & Shinoda (1978) that 'the time of onset of long loop actions cannot be inferred from the peaks and troughs of the e.m.g. records'. The timing of these motor events is mainly determined by timing of the successive volleys in the spindle afferents.

The 'functional segmental stretch reflex'. As suggested by Hammond (1960) and later

reinforced by Phillips (1969) and Melvill-Jones & Watt (1971), the second e.m.g. peak is more potent than the first in generating force. One reason for this may be that, as judged by its higher amplitude, the second peak usually involves activity in a larger number of motor units, but it is also possible that the type of units participating in the second burst are more potent in generating twitch force (cf. Bawa & Tatton, 1979). In any case, the repetition rate of these successive e.m.g. bursts is high enough to produce fused reflex torque, which in contracting human wrist muscles starts 60–70 msec after initiation of the stretch movement and reaches its peak about 40 msec later (Fig. 8). Thus, the spindle unloading effect of the reflex contraction cannot account for neural segmentation which occurs during stretch movements like those illustrated in Fig. 6*A* and *B*. The reflex torque is 'functional' in the sense that it can oppose ongoing stretch movements, provided they last longer than 60–70 msec. It can also counteract unwanted irregularities in the speed of ongoing voluntary movements (Vallbo, 1973; Young & Hagbarth, 1980). Even if the perturbation is shorter, the reflex can still be 'functional' in the sense that it may compensate for sudden unwanted changes in position or trajectory (Cooke, 1979). For alternating flexion-extension movements, occurring at a rate of 7–9 Hz, the reflex torque resulting from each stretch movement will occur during the succeeding shortening phase and thus reinforce the ongoing alternating movements. This mechanism has been invoked to explain enhanced physiological tremor (Halliday & Redfearn, 1956; Hagbarth & Young, 1979; Young & Hagbarth, 1980).

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