

**OBSERVATIONS ON THE TIME COURSE OF THE  
ELECTROMYOGRAPHIC RESPONSE REFLEXLY ELICITED BY  
MUSCLE VIBRATION IN MAN**

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SUMMARY

1. Surface electromyography has been used to study the initial reflex response of various muscles to vibration, applied to their tendons, when the subject was already contracting them voluntarily.

2. The response at the onset of vibration was of a latency appropriate for Ia monosynaptic action and was always highly phasic with an initial wave rising far above any maintained increase in electromyogram (e.m.g.) activity; its duration was typically well below 20 ms in the rectified average. Thus, there is nothing peculiar, in this respect, about flexor pollicis longus for which such behaviour has already been described, and used to draw certain wide-ranging conclusions about the stretch reflex.

3. Theoretical considerations, developed in an Appendix, show that quite apart from the operation of any inhibitory mechanisms such a phasic response is to be expected from a population of tonically discharging motoneurons when there is a step increase in the level of their excitatory drive.

INTRODUCTION

On forcibly extending the thumb, the human flexor pollicis longus gives a distinctive long-latency reflex response, occurring well after any initial tendon-jerk-type activity. This was recently suggested to be a spinal reflex evoked by the spindle group II afferents with the additional delay occurring in the peripheral afferent fibres (Matthews, 1983*b*, 1984*a*). The evidence for this view was the new finding that muscle vibration, unlike stretch, elicits little or no long-latency response in accordance with its relatively weak action upon the group II afferents. This was so even when the Ia-dependent, short-latency action of vibration was similar to that of stretch. The various observations were held also to exclude the two main alternative hypotheses, both of which attribute the late stretch responses solely to Ia action although they disagree profoundly as to whether the reflex is mediated spinally or supraspinally (Marsden, Merton & Morton, 1976; Eklund, Hagbarth, Hägglund & Wallin, 1982). However, the remarkably phasic response which the flexor pollicis longus motoneurons gave at the onset of a period of vibration might be suggested to be peculiar to this muscle, arising for some unsuspected adventitious reason, and so providing an insecure basis for wide theorizing. The present observations on a range of muscles consolidate earlier findings (Matthews, 1983*a*) and show that

an initial phasic response to vibration is standard behaviour. Moreover, as outlined in the Appendix, this is indeed the way in which a population of motoneurons that are already discharging might be expected to respond to a step increase in the level of afferent excitation.

#### METHODS

Normal adult subjects were studied using methods which have already been described in detail (Matthews, 1984*a, b*). In brief, with the aid of a visual monitor, the subject contracted a particular muscle or muscle group so as to exert a steady voluntary force against an isometric transducer and muscle activity recorded by surface electromyography. The muscles studied were the long flexors of the big toe and of the thumb, biceps and triceps brachii, flexor carpi radialis, and rectus femoris. Each has been studied in at least four subjects (for flexor carpi, this includes observations made with Dr F. W. J. Cody and Dr H. C. R. Richardson who had already independently studied this muscle). The effect of vibration was investigated by rectifying the electromyograph (e.m.g.) and averaging the responses to a number of trials; this was done retrospectively from tape recordings.

The subject was asked to maintain a constant force between stimuli by exerting a constant effort throughout and to avoid responding voluntarily to the stimulation. Forces of 10–20 % of maximal voluntary contraction were used. Any small reflex changes in force occurred too rapidly to be tracked visually and the same results were obtained when such transients were removed from the visual display by low-pass filtering.

*Application of vibration.* For the thumb and big toe, the proximal phalanx was usually clamped and a large electromagnetic vibrator used to displace the distal phalanx at high frequency, thereby moving the interphalangeal joint and sending vibration along the tendon. For each of the four other muscles, the vibration was applied percutaneously to its tendon, close to the muscle, by a smaller electromagnetic vibrator which was pressed against the overlying skin with a constant force by means of a lever arrangement. For flexor pollicis longus, the two methods of application elicit similar responses (Matthews, 1984*a*). The frequency of the vibration was either 150 or 143 Hz and it was normally applied in bursts of 100–300 ms duration and repeated every 800 ms for a period of about 30 s. Both vibrators gave a dead-beat response with the vibration reaching virtually its full amplitude in the first cycle, and then ceasing after the last cycle without significant die-away oscillations. This was achieved by driving them with an appropriate sequence of pulses rather than with a sinusoidal signal. The desired performance was assured by continuously recording the movement of the shaft of each of the vibrators by a length transducer incorporated within the vibrator mounting. Usually, the movement was sinusoidal and made symmetrical about the initial position when it commenced with half a cycle of relaxation. Sometimes, however, a series of unidirectional pulses were applied, each starting from the initial position. Similar results were obtained with the two methods.

*Electromyography.* The e.m.g. was recorded with electrodes placed a few centimetres apart over the belly of the muscle being studied. As judged from observing the background discharge, the unitary potentials were usually di- or triphasic and lasted 5–10 ms. The recording bandpass was 10 Hz–1.25 kHz. The bin width used for averaging the rectified signal was normally 0.8 ms. No further filtering or smoothing was introduced so that from the instrumental point of view the temporal resolution was good to within 1 ms, but because of the finite duration of the unitary muscle potentials the present e.m.g. recordings inevitably provide a more highly smoothed indication of the time course of the discharge in the motor axons. On studying biceps and triceps, in addition to the e.m.g., the force reflexly produced at the wrist was recorded on a high gain and then averaged after automatically backing-off the steady component of force, as described elsewhere (Matthews & Muir, 1980).

#### RESULTS

*The phasic response at the onset of vibration.* Fig. 1 shows typical responses at the onset of vibration for each of the six muscles studied. The response of flexor pollicis longus (top centre) resembles in its essentials those published before (Matthews,

1984*a*), though settling relatively smoothly to a steady level after the initial peak without any further large waves, as sometimes found. The other five muscles can be seen to behave in much the same way; as here, they regularly showed only a single large initial wave. The beginning of the response occurs at a time appropriate for Ia monosynaptic excitation, as to be expected from the first cycle of vibration being

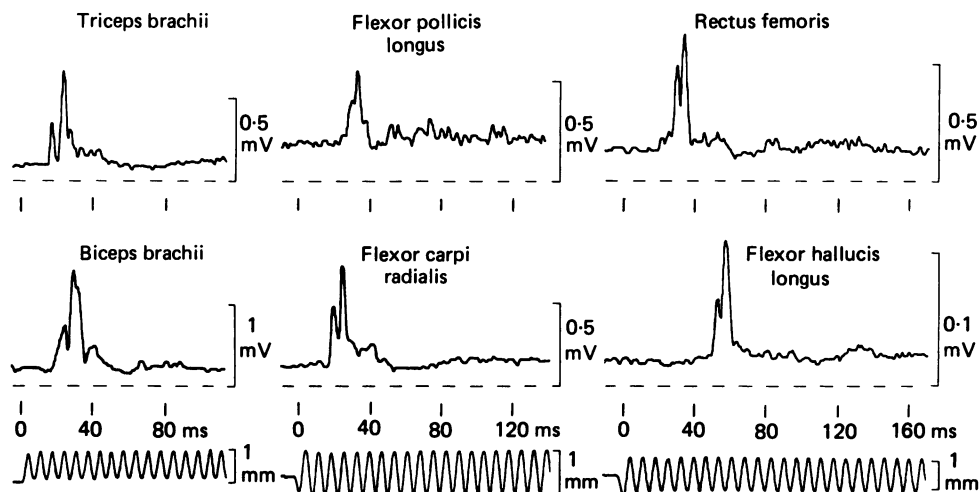


Fig. 1. The highly phasic reflex response occurring at the onset of vibration seen in the averaged rectified surface electromyogram. Results for six different muscles from five different subjects of varying size. The vibration signals at the bottom were obtained from a length transducer incorporated in the vibrator and were recorded at the same time as the e.m.g. responses lying immediately above; the wave form of the vibration used to elicit each of the top responses did not differ sufficiently to merit illustration and was of comparable amplitude. Upwards deflexion corresponds to stretching of the muscle. For biceps and triceps the vibration consisted of a series of unidirectional pulses. For the other muscles the sinusoidal movement was symmetrical about the initial position and began with a release; time zero has been taken as the beginning of the first stretching phase. The long flexors of the thumb and of the toe were vibrated by oscillating the whole digit to and fro at 143 Hz; the proximal phalanx of the toe was clamped, but that of the thumb was not (cf. Matthews, 1984*b*). For the other muscles the vibrator was pressed percutaneously upon their tendons. 64 or 128 individual responses averaged in each case; the vibration was repeated every 800 ms (400 ms for biceps in this example).

equivalent to a brief tap on the tendon. The latency is suitably greater for muscles further from the spinal cord. There was no indication that the initiation of the response depends upon temporal summation of the afferent input from successive cycles of vibration since, when tested, neither the latency nor the wave form of the response varied appreciably with the amplitude of vibration.

In every case, the initial response to vibration was highly phasic and consisted of a brief burst of motor activity followed by a sharp drop down to, or below, the pre-existing level. The duration of the initial wave showed considerable variation, but usually the rectified e.m.g. had fallen to 20% or less of its initial peak well within 20 ms. In the present limited series, no particular attention has been paid to the precise level then reached, whether it was just above or just below the pre-existing

value, and how far different muscles behaved differently; triceps, however, rather commonly showed a marked trough in the level of activity (Figs. 2 and 3). But in all cases, after the initial drop, the e.m.g. normally showed various smaller, more prolonged, waves (see also Fig. 5). Thus, the wave form of the response is always quite

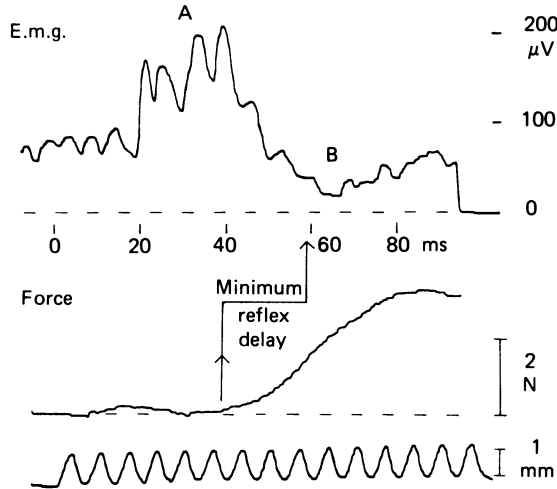


Fig. 2. Relation between the initial electrical and mechanical events on vibrating triceps brachii. Top, surface e.m.g. Bottom, force recorded at the wrist with an isometric transducer. The subject was exerting a steady extension force of 40 N. The force record has been filtered to remove small cyclical fluctuations at the vibration frequency (high-frequency cut at 50 Hz); this produced a lag of about 3 ms in the recordings, for which no correction has been made. The records are averages of the responses evoked by sixty-four applications of a 100 ms period of vibration at 1.25 Hz.

different from that of the stimulus, considering the latter as a maintained step of vibration. This ignores, of course, that the vibration is made up of a series of cycles, each of which will elicit a separate afferent volley; but staggered delays, occurring both peripherally and centrally, can be expected to smooth out much of this pulsatile activity and so prevent it appearing in the rectified average. In any case, the initial phasic drop cannot be equated with the interval between successive cycles of vibration since the relative timing is wrong, and the drop occurs at just the time that additional cyclically phased motor volleys should have been eliciting extra electromyographic activity (i.e. at 7, 14, 21 and 28 ms from the beginning of the reflex response). It may be noted that any splitting of the initial peak seems likely to be due at least as much to the shape of the unitary action potentials, as to the action of successive closely spaced motor discharges. Averaging the e.m.g. without prior rectification showed a large initial di- or triphasic response, lasting up to 15 ms, which on full-wave rectification would give a visibly notched response when the temporal resolution was good enough, as in the present experiments.

*Is spindle unloading responsible?* The soleus of the decerebrate cat may show an even more markedly phasic response at the onset of vibration (Matthews, 1966, Fig. 2) and this is probably partly due to its strong reflexly elicited contraction unloading

its muscle spindles and so reducing their response to the continuing vibration. Some such unloading presumably occurs also in normal man. But under the present conditions, with the muscle studied already contracting tonically, the effect seems likely to be small since the reflexly elicited contraction was never more than a small fraction of the pre-existing contraction (below 10 % when measured, as in Fig. 2). More crucially, because of the considerable conduction distances presently involved, any reduction in reflex activity due to such unloading would have occurred too late, at any rate for more distal muscles, to be held responsible for the present abrupt drop of the reflex discharge from its high initial level.

Fig. 2 develops the argument using data obtained on vibrating triceps brachii. In addition to the usual electromyographic response, the force produced at the wrist by the reflex contraction of triceps was recorded with an isometric transducer. Taking this as indicating the onset of contraction, then any unloading could not affect the e.m.g. until nearly 60 ms from the beginning of the vibration, since a further complete circuit of the reflex pathway is required to produce such an effect. In fact, the e.m.g. fell from its initial peak about 20 ms earlier suggesting that some quite different mechanism is involved. Similar results were regularly obtained for biceps and triceps brachii. However, due to various mechanical lags, it seems inevitable that the actual contraction of the muscle began appreciably before the first change in the recorded force. Indeed, jumping to an unlikely extreme, if there were no delay at all between the first e.m.g. response and the onset of contraction, then in the particular example of Fig. 2, the observed drop occurs at just about the right time to be explained by unloading. However, this was not invariably so even for the two most proximal muscles studied, namely biceps and triceps. For the more distal muscles investigated, by virtue of the much greater delays involved in peripheral conduction, the same argument gives a conclusive verdict against the unloading hypothesis as being uniquely responsible, and mechanical recording with its inevitable uncertainties becomes quite unnecessary. This can be readily seen in Fig. 1 for the recordings from flexor hallucis longus. Measured from the beginning of the vibration, the minimum possible latency of any unloading response has to be more than *twice* that of the first observable response in the e.m.g., whereas the actual fall in the e.m.g. occurred much earlier. However, the more proximal the muscle studied, the more possible it becomes for unloading to contribute to the early fall in the response and more particularly to any immediately ensuing trough; but whether it actually does so to a significant extent is quite another matter, and the mechanisms responsible for the effect for distal muscles can be expected to remain in action.

*Cessation of vibration.* On terminating a period of vibration, the Ia discharge can be expected to drop immediately to a much lower level. Such withdrawal of a component of the excitatory drive to the  $\alpha$ -motoneurons will temporarily reduce their discharge, and so also the level of electromyographic activity, as has been regularly observed. Fig. 3 illustrates such behaviour for the triceps brachii for two different short periods of vibration; this example also shows a marked 'inhibitory dip' (B) immediately after the initial peak. The trough D is demonstrated to be due to the termination of the vibratory train by virtue of the fact that it occurs with the same latency, from the end of the period of vibration, in the two cases; this can be seen most clearly on the right where the sweep has been triggered in synchrony with

the last pulse of vibration. The arrow indicates the expected time of onset of the reflex response to the last cycle of vibration, on the supposition that it will have the same latency as the response to the first cycle. The level of e.m.g. activity can be seen to fall very shortly thereafter, showing that these direct reflex pathways continue to

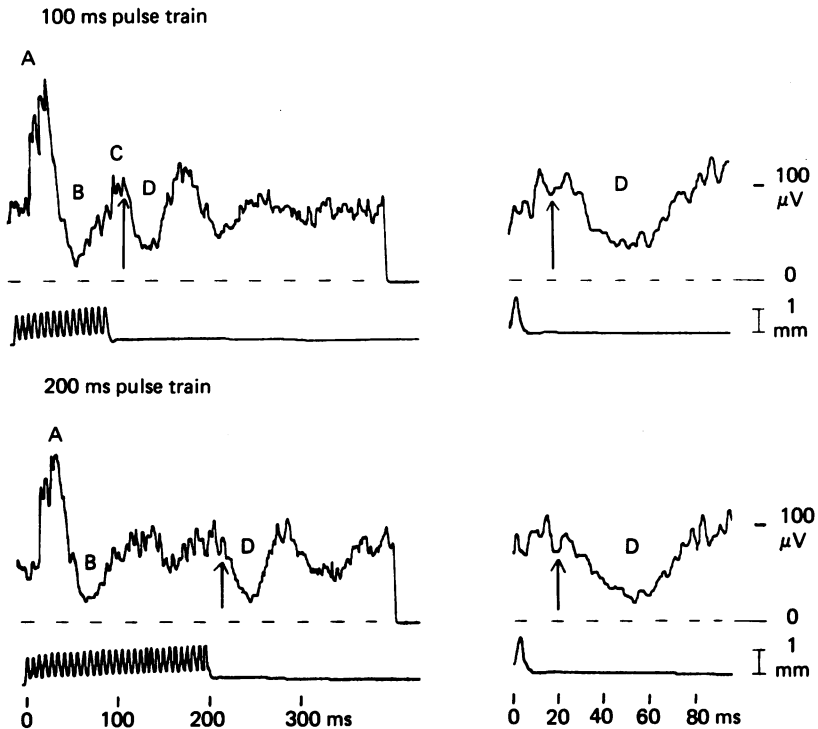


Fig. 3. The 'off' response (D) seen for two different periods of vibration applied to triceps brachii. Left, the responses throughout the whole period shown on a slow time scale, with time zero corresponding to the onset of vibration. Right, the responses on cessation of vibration on an expanded time scale, with time zero now corresponding to the beginning of the last cycle of vibration. The arrow indicates the start of the response to be expected from the last cycle of vibration. The complex series of waves in the e.m.g. have been arbitrarily labelled A-D. Same subject as in Fig. 2 with similar averaging.

contribute to the response throughout the vibration, whether or not longer latency pathways are also acting. On sporadic testing, similar findings were obtained whatever the duration of the vibratory train, though in absolute terms the 'off' response was smaller when it occurred immediately after the initial peak A.

As in Fig. 3, the 'off' response was normally of smaller amplitude though longer duration than the preceding 'on' response when the period of vibration was 100-300 ms. The difference in amplitude may be partly related to the fact that the 'off' response cannot fall below zero in any individual trial, whereas the size of the 'on' response is not limited in this way. No attempt has been made to compare quantitatively the relative areas of the 'on' and the 'off' responses elicited by a given period of vibration. On qualitative inspection, they were often broadly comparable, as in Fig. 3.

It deserves emphasis that on removal of the vibration the level of e.m.g. activity normally drops well below the level pre-existing before the application of vibration, and not just back to it. As outlined in the Appendix, this is to be expected from the known properties of motoneurons. The same thing would presumably also happen if the vibration was reduced in its stimulating efficacy rather than ceasing altogether. This means that a trough, like B, occurring immediately after the initial peak of response cannot be uniquely attributed to an active 'inhibitory' process, though such may well be occurring. A trough could equally be produced by a failure of the vibration to continue to excite the afferents as powerfully as it did in its first few cycles, whether from mechanical factors, partial refractoriness of the afferents, or any spindle unloading produced by the reflex contraction.

The complexity of the series of waves evoked by these short periods of vibration is also noteworthy. In particular, it is interesting on comparing the two sets of responses in Fig. 3 to see how an apparently clear-cut wave like C in the upper trace owes its prominence as much as anything to the immediate subsequent occurrence of trough D, dependent upon the cessation of the vibration. The same might well be true for some of the varied responses that may be elicited by stretch. Thus, as now widely recognized, the activation of a long-loop reflex provides only one out of several possibilities for the development of any later waves in the electromyographic response evoked by a given stimulus, especially when the temporal patterning of the causal afferent volleys is unknown.

#### DISCUSSION

For a variety of muscles, the motor discharge at the onset of a period of continued vibration has been found to show a large initial phasic surge, far above any immediately ensuing maintained increase in motor activity. This was so both when the vibration was applied percutaneously to the appropriate tendon and, for those cases in which it was mechanically appropriate, when the relevant joint was displaced sinusoidally at high frequency. The periods of vibration used have been deliberately short (100–300 ms) and the study has not been concerned with the complex slow responses that prolonged vibration may evoke over a time scale of many seconds.

The immediate question is whether the present phasic reflex responses simply reflect a similar phasic response on the part of the Ia afferents, or whether they depend more fundamentally upon a transformation of the pattern of activity by the spinal cord on its reflexly converting the afferent input into a motor output. The unitary recordings of others show that vibration evokes a large Ia input to the spinal cord and that this is well maintained with time (Burke, Hagbarth, Löfstedt & Wallin, 1976; Roll & Vedel, 1982). The details of the initial part of the afferent response, however, seem to have attracted rather little attention; this is perhaps partly because some vibrators (especially those employing an unbalanced electric motor) cannot be expected to produce a constant amplitude of movement from the very beginning. The vibrators employed in the present study do not have this limitation. It seems probable that on starting to vibrate, the sum total of Ia activity would show some degree of initial phasic response over and above the subsequent maintained level; some individual Ia afferents can be presumed to fail to be driven 1:1 by the vibration so

that after responding to the first cycle of vibration they would then fail to respond to one or more of the immediately ensuing cycles. But there seems little possibility that the whole population of Ia afferents could react in this way on a sufficient scale for the envelope of the afferent input to be at all close to that of the motor output as currently observed. Moreover, analysis of the time delays involved showed that any reduction of afferent discharge, caused by the reflex contraction itself mechanically unloading the muscle spindles, would often have occurred too late to be held responsible for the abrupt decline of the motor response from its initial peak.

The precise behaviour of the Ia afferents at the very beginning of vibration certainly merits further study. Nonetheless, it may be provisionally concluded that the patterning of the motor output differs appreciably from that of the afferent input with the spinal cord performing an operation akin to mathematical differentiation. Westbury (1970) has already advanced this view on the basis of studying the response of cat motoneurons to sinusoidal stretching, but not all other authors have felt similarly (Poppele & Terzuolo, 1968). The present effect might be suggested to be due to the excitation of inhibitory afferents with a slightly slower conduction velocity than the Ia afferents and which could then cut the motor discharge short in spite of a continued Ia excitatory bombardment of the motoneurons. If so, the relevant afferents need to be sought in muscle or its surrounds rather than skin or joint, since the phasic responses of flexor pollicis longus to vibratory movement of the terminal phalanx are still found after the thumb has been anaesthetized (Matthews, 1984*a*).

There is no shortage of known central mechanisms potentially capable of making the motor discharge so phasic. It is well known, for example, that the second of two closely spaced tendon jerks or H reflexes is much smaller than the first (Paillard, 1955), showing that the 'excitability' of the reflex centres is reduced immediately after they have been activated. In part, this can be presumed to occur because active inhibitory processes are brought into play by even a pure Ia input. The motoneurons receive a post-synaptic inhibition from the Renshaw cells which depends upon the amount of reflex discharge. The Ia fibres themselves receive presynaptic inhibition, via interneurons, which increases with the level of their own activity. Both can be expected to operate with a lag. But the knowledge that this and other inhibitory 'neural wiring' exists does not indicate how strongly it may act under the present circumstances nor the contribution that it makes to the observed responses; this could well vary from muscle to muscle and subject to subject.

*Motoneurone modelling.* A crucial part in determining the pattern of reflex response must also inevitably be played by the motoneurons themselves, considered individually, as a result of the way in which they generate rhythmic firing. In consequence of its relative refractoriness, when a given motoneurone has just discharged, whether spontaneously or in response to stimulation, it becomes relatively unavailable to any immediately ensuing input. Ter Haar Romeny (1983) has recently demonstrated such changes of responsiveness to tendon taps by recording from single motor units in the human biceps brachii. Such behaviour provides the essential basis of the motoneurone models used by Ashby & Zilm (1982) and by Fetz & Gustafsson (1983) to explain the relation between an underlying excitatory post-synaptic potential (e.p.s.p.) and the resulting change in the post-stimulus histogram of a tonically discharging motoneurone. As detailed in the Appendix, such a model also



predicts that the onset of a step increase in afferent input to a population of tonically discharging motoneurons will lead to a sudden but transitory increase in the over-all motor discharge. After an initial, more-or-less synchronized volley, the level of activity rapidly falls back to, and then temporarily oscillates about, a level only slightly above the pre-existing level, as occurs in practice. The initial phasic discharge will also receive a contribution from a number of motoneurons which were not discharging beforehand; some of these will be brought to threshold by the first of the Ia volleys initiated by vibration, and then need time to recover before firing again. Any Ia activation of motoneurons via polysynaptic pathways would, of course, tend to blur the initial phasic response, as would any excitatory contribution from slower afferents. An 'inhibitory dip' in which the level of activity immediately after the initial phasic response sometimes falls below the pre-existing level, might well sometimes be due to a frank inhibition. But this is not inevitable, since such a 'dip' could also occur as a result of any faltering in the Ia afferent discharge from the high level set by the first cycle of vibration; theory and experiment combine in showing that any reduction in Ia firing leads to an immediate reduction in the motor discharge, even though the central drive from higher centres is being maintained.

*Modelling and the stretch reflex.* It may be concluded that the experimentally observed phasic response to the onset of vibration has plenty of potential causes and so its occurrence occasions no surprise. Rather, on the basis of the present modelling alone, some special explanation would seem to be required for the more tonic response to a stretch of constant velocity, which over a period of some tens of milliseconds may approximate to a square wave or show a progressive increase (Matthews, 1984*a*, *b*). If such a response were to depend solely upon the Ia input evoked by a stretch, then the level of Ia firing would have to increase very considerably throughout the rising phase of the stretch so as to maintain, or even augment, the motor output in the face of the various factors making for its adaptive decay. But on the basis of animal and the limited human unitary recordings, the converse behaviour seems the more likely, with the Ia discharge to stretch immediately jumping up to a high level at the very beginning in an 'initial burst' and then falling back to an intermediate level before rising again, and then often only slowly (for a human example see Fig. 5, Roll & Vedel, 1982). The continued motor discharge seen with stretch suggests the arrival at the motoneurons of a yet more potent excitatory input than that provided monosynaptically by the Ia afferents so that new motoneurons are brought to fire, even though they failed to do so earlier in response to the initial Ia volley. Ia excitation mediated by polysynaptic pathways would not appear to be responsible, since this might be expected to be seen also with vibration. However, an entirely adequate explanation is provided by the hypothesis that the spindle group II afferents produce autogenetic excitation and so provide continued support for the Ia action. Such co-operation between the two types of spindle afferent in mediating the stretch reflex would ensure that the initial response was of high speed and high sensitivity, as provided by the spindle primary endings, but this would only be maintained to produce an appreciable over-all effect when the more sluggish spindle secondary endings signalled that muscle length had, in fact, undergone an appreciable perturbation.

## APPENDIX

*Response of a model motoneurone to a step input*

Fetz & Gustafsson (1983) recently analysed the effect of intercalating a brief e.p.s.p. on the response of a model motoneurone that was already discharging tonically. Fig. 4 shows an extension of their approach to cover the case of a maintained increase in

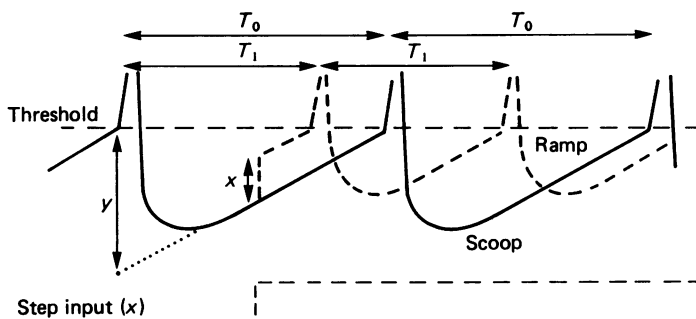


Fig. 4. Trajectory of membrane voltage of a model motoneurone that is discharging tonically and its modification by a step increase in afferent drive (shown dashed). See text for explanation.

afferent input, as opposed to a transitory one. The continuous line shows the behaviour of the noise-free model in the absence of the step input and simply reiterates the known membrane-potential trajectory of real motoneurones that are discharging rhythmically in response to a steady input (Schwindt & Calvin, 1972). After firing a spike, the membrane undergoes an after-hyperpolarization with an initial 'scoop' followed by a linear decay or 'ramp' until the firing threshold is reached and the motoneurone discharges again. The dotted line shows the effect of adding a step input of depolarization of size  $x$ , which is assumed to remain constant throughout the interspike interval thus making the scoop shallower without influencing the slope of the subsequent ramp, as occurs for real motoneurones on injecting additional current. The threshold depolarization at which the motoneurone discharges is also assumed to be constant. Real motoneurones, of course, do not always behave precisely like this simplified example, but Ashby & Zilm (1982) have shown that this does not greatly affect such modelling when the additional excitatory drive is relatively weak and can only bring the motoneurone to discharge towards the end of its normal recovery cycle.

The step input in Fig. 4 can be seen to cause the motoneurone to discharge its next spike at time  $T_1$  rather than at the normal  $T_0$ , and all succeeding interspike intervals will be similarly shortened for the duration of the stimulus. Thus, at equilibrium, all motoneurones will show an increase in their rate of firing by an amount that depends upon the size of the step; the geometry of similar triangles shows the proportional increase to be  $x/(y-x)$ , where  $y$  is the depth of the scoop at time 0 as given by backwards extrapolation of the ramp to the beginning of the preceding spike. In the absence of neural interactions this then is the amount by which the mean level of

motor activity, as seen in the rectified e.m.g., should increase when the stimulus has been maintained for an appreciable time.

At the onset of the step input, all motoneurons which have their membrane potential lying within  $x$  of the firing threshold will be abruptly brought up to it and discharge a spike. The proportion of motoneurons doing this, out of those that are

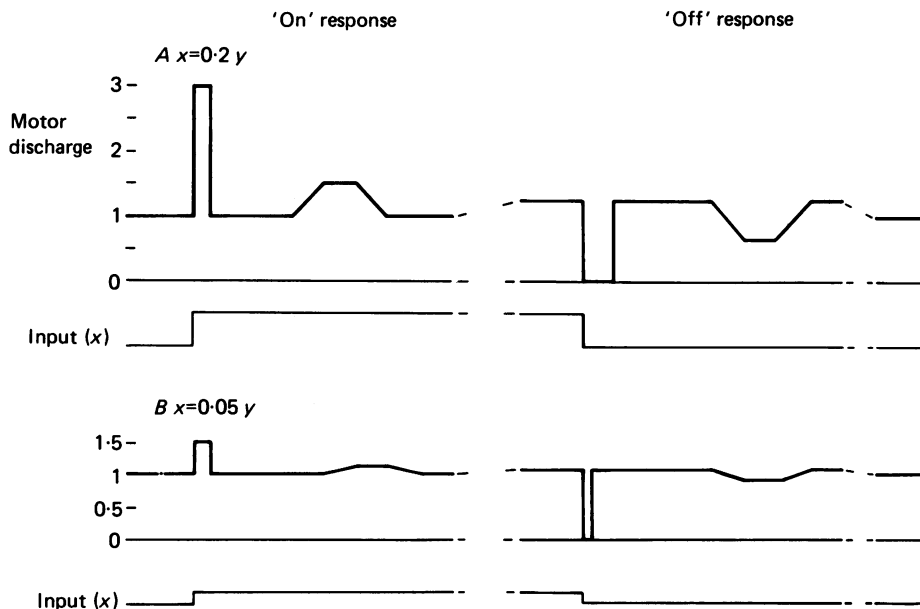


Fig. 5. Effect on the discharge of a pool of model motoneurons of first introducing and then withdrawing a maintained step increase in afferent drive of two different sizes (*A*, *B*). The ordinate may be seen equally, either as the probability of firing of a spike by any one of a number of motoneurons, or as the average level of the rectified electromyogram. The magnitude,  $x$ , of the depolarizing input is expressed in relation to the size,  $y$ , of the post-spike after-hyperpolarization (see Fig. 4). Further explanation in text.

already tonically active, is simply  $x/y$ . Suppose that this extra discharge occurs over a period of  $1/10$  of the normal cycle (say over 5 ms for neurones discharging at 20/s), then there will be a brief phasic motor discharge at the onset of the step of  $10 \cdot x/y$ , over and above the existing level taking this latter as unity. As illustrated in Fig. 5, if  $x$  is 20% of  $y$ , the phasic peak will rise above the ongoing level by 200%; if  $x$  is only 5% of  $y$ , the peak will still be 50% above the ongoing level, and so in real life probably still clearly detectable above the background noise. Any excitation of motoneurons that were not already tonically active would increase the peak yet further relative to the pre-existing background.

Immediately after the initial phasic discharge, the level of motor activity temporarily falls back to precisely the same level as before, as the remaining motoneurons are successively recruited by the enhanced input slightly earlier than they otherwise would have been, but in no greater numbers per unit time. At a time  $T_1$  after the beginning of the step input, those motoneurons which fired at its onset will fire once again to produce a second peak, but since different motoneurons will not in

fact fire at precisely the same rate this peak will be longer and lower than the first one though having the same area, as measured above the ongoing level. Further similar, but progressively more blurred, peaks will occur until the asynchrony of firing of the different units has stabilized the level of activity at a new steady level, which as noted above is only slightly above that seen before stimulation (by 25% and by 5% for the examples of Fig. 5). Slightly different assumptions and the introduction of additional complexity into the model would inevitably modify the numerical values given in Fig. 5. But the general pattern of behaviour could be expected to remain the same, namely that at the onset of a step input there is a transitory motor discharge which is surprisingly large in relation to the final maintained increase in motor activity. This new equilibrium, moreover, is only achieved after some oscillations at a frequency corresponding to that of the majority of the motoneurons.

*'Off' response.* The effects of a step decrease in afferent input can be treated very similarly. In Fig. 4 this corresponds to making the transition from the dotted line back to the continuous line. All motoneurons that would otherwise have fired in the period from  $T_1$  to  $T_0$  will now fail to do so, leading to a period of complete motor inactivity and electromyographic silence, as illustrated in Fig. 5. The duration of the silence will be given by  $x \cdot T_0/y$ , or  $x \cdot T_1/(y-x)$ . In the examples illustrated, this works out at 10 ms when  $x$  is 20% of  $y$ , and 2.5 ms when  $x$  is 5% of  $y$ . However, if a dispersion of 5 ms is introduced (as was done for the excitation, and for which numerous causes can be suggested) withdrawal of the larger step would lead to a nearly complete silence over a period of 15 ms and of the smaller step to a 50% decrease in the level of activity over 5 ms. If the withdrawn excitation had been even larger then the silence would have lasted yet longer. On the resumption of firing, the mean level of activity returns for a time to the higher value that it had during the application of the stimulus. This is followed by a series of troughs at the repeat frequency of the motoneurons until the discharge stabilizes at the original level, mirroring the behaviour at the beginning of the stimulus.

Because of the higher steady level of activity during stimulation, the deficit of activity in the first trough on withdrawing the stimulus is slightly greater, in terms of area, than the initial excess of activity seen on introducing the stimulus, namely by  $x/(y-x)$ . In addition, it is differently distributed in time. The excitatory peak at 'on' occurs more or less synchronously in all units involved, and has the same duration for inputs of different sizes. In contrast, the duration of the silence at 'off' increases with the magnitude of the stimulus that is being withdrawn; but when in the model it is studied on a fine enough time scale, the silence is always complete with all motor discharge ceasing for the period involved. In this last respect, however, the model is probably misleading since in real life there will inevitably be a number of factors making for temporal dispersion and so smoothing out the trough, though without altering its area. For example, on recording the e.m.g., the scatter of conduction velocities of different  $\alpha$ -motor fibres and the finite duration of the muscle action potential must inevitably prevent this indicator of motor activity falling to zero when the total cessation of motor discharge is sufficiently brief. The inevitable occurrence of neural noise will also tend to maintain some motor discharge throughout. Neural interactions can also be expected to distort the pattern of response in a number of ways. In particular, the occurrence of any autogenetically mediated presynaptic

inhibition would reduce the size of the 'off' response below that of the corresponding 'on' response, as has been suspected to occur for the short-latency response of flexor pollicis longus (Matthews, 1984a).

*Response to synchronized inputs.* Next, how will the model respond to the onset of a repetitive train of Ia impulses as set up by vibration, and so approximately synchronized in all afferents, rather than to a square-wave step? To begin with, the spread of conduction velocity of the various Ia afferents involved will slow the rising phase of the initial wave of depolarization and so delay the discharge of some motoneurons that would have responded instantaneously to a square-wave input. Thus, the initial motor discharge will be somewhat dispersed as already allowed for in the construction of Fig. 5. But as shown by Ashby & Zilm (1982) this will have little or no effect on its over-all size, expressed as an area, as in the present case. Thereafter there will be a series of ripples, at the vibration frequency, superimposed on the resulting depolarization of the motoneurone and this will have interesting but second-order consequences. It is assumed that the size of the Ia volleys elicited by vibration remains constant throughout. The depth of the ripples will depend upon a number of factors, such as the temporal dispersion of the afferent volley, the membrane time constant, and whether any of the excitation is conveyed to the motoneurons via polysynaptic pathways as well as monosynaptically.

If the falling slope of the ripple is steeper than the rising phase of the ramp recovery from the after-hyperpolarization, then for this period all motor discharge will cease. But any motoneurons that would then have fired if the stimulus had remained at its maximal value will instead discharge on the rising phase of the next ripple, along with those which would have discharged during this latter period if the stimulus had been held constant. The number then responding will, however, be appreciably below the number responding to the first cycle of vibration and represents a bunching of the spikes that would anyhow have been discharged in response to steady depolarization rather than the occurrence of extra ones as for the first cycle. (If the vibration frequency were 150 Hz and the neural firing rate 20 Hz, as in Fig. 5, then approximately twice as many spikes would fire in response to the first cycle of vibration as to the second for  $x = 0.2 y$ , where  $x$  is now the maximum depolarization produced by the vibration.) As the depth of the ripple is progressively decreased, the point will be reached when its falling phase no longer overwhelms the natural recovery and some spikes will begin to be discharged during this period, with a corresponding reduction in the number initiated during the rising phase of the next ripple; and eventually the discharge will become uniform again as with the square-wave input.

The precise effect observed from thus superimposing a ripple on a steady depolarization will depend very much upon the coarseness of the time scale employed for study. If the matter is examined on a sufficiently fine time scale, the motor output will be seen to be temporally quantized, with a partial or even a complete phase-locking of the motor discharge in relation to the vibratory input. But if it is examined on a coarser time scale, as by instrumental or computational smoothing or that provided in part by studying the e.m.g. rather than neural discharges, then this rhythmicity will be averaged out while the mean level is preserved. Moreover, this mean level is the same as that produced by a square-wave depolarization of the same magnitude as the peak depolarization produced by a pulsatile input. Some of the striking, but

essentially unimportant, effects of altering the bin width used for analysis of the responses to vibration have already been illustrated for motor units of the cat (Clark, Matthews & Muir, 1981, Fig. 2). But whatever the mode of analysis the response of the model to the onset of a maintained period of vibration would be expected to show much the same marked initial phasic response as that elicited by a completely square input step. Again, there would be rather little subsequent maintained response over and above the pre-existing level of response, though it would now tend to occur in bursts phase-locked to the vibration.

Finally, it is interesting that the above analysis indicates that a given mean level of afferent input will produce a greater excitatory action when it is mediated by grouped afferent volleys than it will when the various afferents are discharging asynchronously, since when a ripple is superimposed upon a depolarization, its excitatory action is determined by its peak value rather than by its average level. Over and above this, and less fundamentally, when it is the e.m.g. that is being studied, the same over-all amount of motor discharge may well produce a larger signal when it is partially synchronized in the various units involved, because the oppositely going phases of their di- or triphasic potentials will then no longer interfere with each other to the same extent as when they are occurring randomly. In contrast, an isolated brief phasic input leading to a typical short e.p.s.p. produces relatively little net excitatory effect on a pool of tonically discharging motoneurons provided their response is averaged over a period corresponding to an appreciable part of an interspike interval. This is because the motoneurons that respond are merely those which would in any case have discharged shortly thereafter; spikes are simply translocated from the falling to the rising phase of the e.p.s.p. Given the mechanical filtering properties of muscle, such a temporal shifting of perhaps 10 ms will have rather little effect on the level of ongoing muscular contraction (cf. Hammond, 1960). Any excitation of motoneurons that were not responding initially would, however, produce an obvious mechanical effect.

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