MECHANISM OF THE VIBRATION PARADOX: EXCITATORY AND INHIBITORY EFFECTS OF TENDON VIBRATION ON SINGLE SOLEUS MUSCLE MOTOR UNITS IN MAN

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SUMMARY

1. The parameters of presynaptic inhibition of the Ia spindle afferents from soleus muscle by vibration have been investigated. The inhibitory effects increase with the amplitude of vibration, but decrease when the vibration frequency is increased.

2. The monosynaptic reflex threshold of twenty-one single soleus motor units activated in the H (Hoffmann) reflex by a single electrical stimulus to the posterior tibial nerve was estimated quantitatively and expressed in relation to the size of the simultaneously recorded H reflex.

3. A parametric study of the effects of various Achilles tendon vibrations on the reflex threshold of the single soleus motor units indicated that their order of de-recruitment is concordant with their rank order for activation in the phasic reflexes of the soleus. The last recruited motoneurones are the most susceptible to being silenced by steady vibration.

4. Muscle vibration progressively recruits single motor units according to the motoneurone size principle through polysynaptic proprioceptive pathways. However the presynaptic inhibition of Ia spindle afferents simultaneously induced by the vibration works in reverse on the same rank order of motoneurones of the soleus spinal pool, thereby limiting the polysynaptic recruitment of units in the tonic vibration reflex while depressing the autogenic phasic proprioceptive reflexes. These mechanisms elucidate the so-called vibration paradox and extend the size principle of Henneman to presynaptic inhibitory effects.

INTRODUCTION

No adequate explanation has yet been provided for the vibration paradox in which sinusoidal vibration of the Achilles tendon in man elicits two opposed reflex effects in the soleus muscle: on the one hand the maintained vibration activates a tonic contraction which is known as the Tonic Vibration Reflex (TVR) both in man (DeGail, Lance & Neilson, 1966; Lance, DeGail & Neilson, 1966; Eklund & Hagbarth, 1966; Hagbarth, 1973; Lance, Burke & Andrews, 1973) and in the decerebrate cat (Matthews, 1966). On the other hand the vibration simultaneously inhibits the phasic reflexes such as the Achilles tendon reflex elicited in the soleus muscle by proprioceptive afferent volleys (DeGail *et al.* 1966; Lance *et al.* 1973).

The two effects are independent phenomena produced by the proprioceptive input

activated by vibration which rather selectively stimulates the primary Ia spindle afferents (Bianconi & Vandermeulen, 1963; Matthews, 1966) and which in man can also excite the group II spindle afferents (Burke, Hagbarth, Löfstedt & Wallin, 1976). The progressive recruitment of motoneurones in the human TVR and the abolition of the TVR by barbiturates or below a spinal transection suggest that it involves poly-synaptic spinal pathways (DeGail *et al.* 1966; Lance *et al.* 1973; Ashby, Verrier & Lightfoot, 1974). On the other hand the vibration-induced depression of soleus phasic proprioceptive reflexes is primarily related to a presynaptic inhibitory mechanism involving the depolarization of soleus Ia afferents (Gillies, Lance, Neilson & Tassinari, 1969; Barnes & Pompeiano, 1970; Delwaide, 1973). Contrary to the TVR, the vibration-induced inhibition of phasic reflexes is increased during spinal shock, but impaired in longer-standing patients developing spasticity after spinal transection (Ashby *et al.* 1974).

The present paper attempts to resolve the vibration paradox in which the tonic soleus response to autogenic proprioceptive input coexists with a presynaptic Ia inhibition of the soleus phasic reflexes. Several working hypotheses could be con-sidered. For example the TVR and the phasic reflexes might involve different (tonic or phasic) motoneurones of the soleus pool (DeGail *et al.* 1966), but this appears unlikely since the same motor units can participate in both types of reflexes (Lance *et al.* 1966; Ashworth, Grimby & Kugelberg, 1967). Another possibility is that the presynaptic inhibition might be unequally distributed among soleus Ia afferents so that the Ia excitatory pathway to certain soleus motoneurones would be more depressed. Alternatively the presynaptic inhibition could involve the monosynaptic Ia pathway mediating phasic reflexes but not the Ia polysynaptic pathway primarily involved in the TVR, as suggested by Delwaide (1973). None of these proposals has been substantiated by the present findings which lead to an alternative explanation extending the hierarchical rank organization of motoneurones in a pool (cf. Henne-man, Somjen & Carpenter, 1965; Henneman, Clamann, Gillies & Skinner, 1974) to the conditions of presynaptic Ia inhibition.

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METHODS

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Twenty-one single motor units were studied in detail in four normal subjects between 22 and 33 years old. The units were recorded from the soleus muscle with micro-electrodes made of 200 μm tungsten wire electrolytically sharpened to a tip of about 5 μm and covered with eight separate coats of varnish baked at 180 °C. The varnished tip was minimally exposed by the passage of an adequate DC current under binocular examination in saline. The electrode resis-tance was 2–5 MΩ as measured with 180 Hz sinusoidal current. The micro-electrode was inserted through a steel cannula into the soleus muscle, about 20 cm above the external malleolus. These electrodes had to be much more selective than those used before (Desmedt & Godaux, 1977) in order to isolate consistently a single motor unit potential in the strong discharge of maximal Hoffmann (H) reflexes. The recording conditions were very stable throughout the series of tests required to estimate the units' thresholds statistically, before and during various vibration conditions. The potentials were amplified by a 100 MΩ input impedance differential amplifier and displayed on Model 565 Tektronix and Model 1201 Hewlett Packard cathode ray oscillo-scopes. A circuit for Z modulation was used to intensify the fast vertical swings of the spot while recording on 35 mm film with a Grass C4 camera.

The electromyogram of the soleus muscle was recorded with small stainless steel subcutaneous needles inserted at 2 and 10 cm respectively below the insertion of the gastrocnemii on the Achilles tendon, as recommended by Hugon (1973) and by a recent committee on methodology

(Hugon, Delwaide, Pierrot Deseilligny & Desmedt, 1973). The subject was comfortably seated in a semi-reclining position, with the ankle at 90° and the knee at 120°, thereby relaxing the gastrocnemii which are inserted on the femur bone, while slightly stretching the soleus inserted on the tibia. The electrical stimulation with single square pulses of 1·0 msec duration was delivered by a Simon electrode on the skin of the popliteal fossa over the tibial nerve while the anode was placed above the patella (Hugon *et al.* 1973). The single stimuli were separated by intervals of at least 5 sec to avoid any cumulative depression of the H reflexes. The skin temperature was measured with a thermistor and maintained when necessary at 34–36 °C by infra-red heating. The vibrations were delivered to the Achilles tendon by a rotating motor with an eccentric load; their amplitudes were chosen between 0·2 and 2·0 mm and their frequency between 20 and 180/sec (cf. Desmedt & Godaux, 1975).

The experiments were very mild and carried no risk of harm. They were performed with the understanding and consent of each subject.

RESULTS

The estimation of the monosynaptic reflex threshold of single soleus motor units. Appropriate electrical stimuli of 1·0 msec duration delivered to the tibial nerve in the popliteal fossa elicit in the soleus a consistent monosynaptic reflex known as the Hoffmann or H reflex (Hoffmann, 1922; Magladery, Park, Porter & Teasdall, 1952; Hugon, 1973). Under standard conditions, a single shock of small intensity only stimulates the Ia spindle afferents of larger diameter, thereby eliciting a small H reflex with a latency of 30–35 msec; as the shock intensity is progressively increased the H reflex increases to a peak and then decreases while a direct M response appears with a shorter latency of 5–10 msec (Fig. 1*E*). The M response corresponds to the orthodromic excitation of the soleus alpha motor axones by the tibial nerve shock, and the progressive decrease of the H reflex with the stronger stimuli results from occlusion by the antidromic volley in the soleus motor axons (Hoffmann, 1922; Magladery *et al.* 1952).

The reflex threshold of single soleus motor units was estimated statistically on the basis of ten trials at each of a series of single shock intensities, and expressed as a function of the peak voltage of the H reflex that was simultaneously recorded with surface electrodes over the soleus muscle. The main technical problem in these experiments was to design very selective micro-electrodes which recorded one all-or-none single motor unit consistently, even during maximum H reflex stimulation throughout the series of tests (Fig. 1*A–D*). As a rule the unit fired insecurely at liminal intensities (Fig. 1*B*) and discharged one spike at the higher intensities eliciting larger H reflexes (*C*, *D*). The 50 % probability of firing of the motor unit was estimated by extrapolation as shown in Fig. 1*F* and expressed relative to the shock intensity eliciting a half maximum M response in order to obtain comparable scaling in different experiments. The unit's threshold was also related to the voltage of the corresponding H reflex (Fig. 1*E*), thereby allowing comparison of the thresholds of the same unit under conditions where the H reflex amplitude was changed, e.g. by vibration. The monosynaptic reflex thresholds of nineteen soleus units corresponded to a wide range of H reflex amplitudes (cf. Fig. 4) extending from very small to maximum H reflexes (0·2–4·7 mV). The two remaining soleus units only fired for tibial nerve shocks slightly exceeding the value which elicited a maximum H reflex (right side of Fig. 4*B*).

The effect of tendon vibration on the monosynaptic reflex threshold of a single motor

unit. The vibration-induced inhibition of the H reflex (DeGail *et al.* 1966; Lance *et al.* 1973) varies with the parameters of the steady vibration and this was systematically studied in preliminary experiments, in much the same way as we had examined the tonic vibration reflex in masseter motor units (Desmedt & Godaux, 1975). The inhibition of the soleus H reflex increased with the vibration amplitude at constant frequency (Fig. 2A–D), but it decreased with increasing vibration frequencies at the
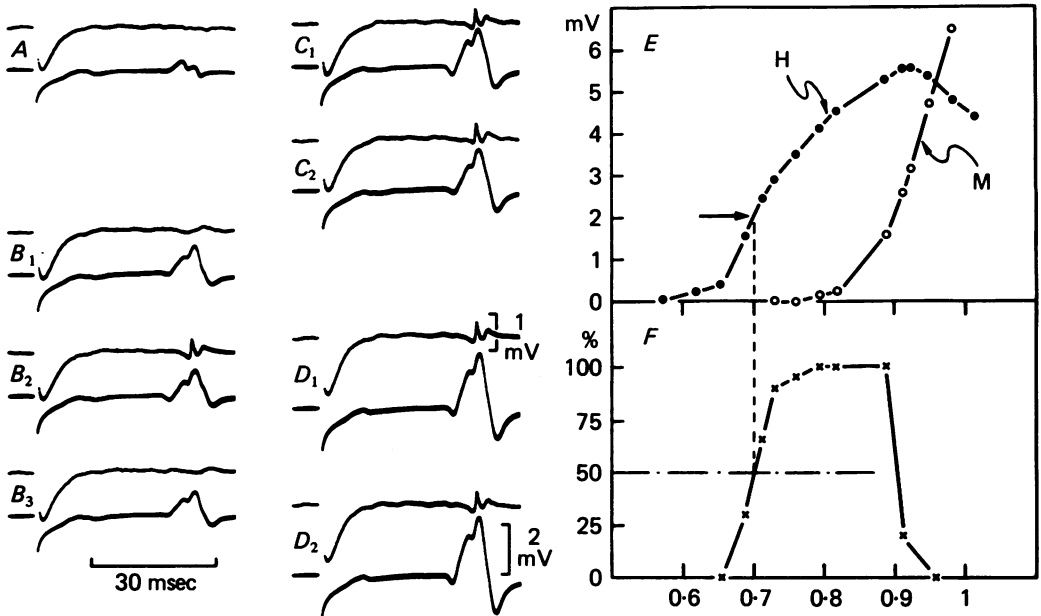

Fig. 1. Estimation of the threshold of a single soleus motor unit activated monosynaptically by an electrical stimulus to the tibial nerve in the popliteal fossa. A–D, simultaneously recorded oscillograms of the unit potential (upper trace) and of the belly-tendon soleus electrogram (lower trace) for single stimuli of 9·8 mA (A), 10·2 mA (B), 10·8 mA (C) and 11·4 mA (D). The motor unit fails to discharge in A and it fires all-or-none in one of the three trials shown for a somewhat higher intensity in B. Larger intensities in C and in D exceed the threshold of the unit. The voltage of the reflex H response increases from A to D. The stimulus intensities plotted in the abscissa of E and F are expressed relative to the intensity which elicits a half maximum direct M response in the soleus. The ordinate in E plots the mean voltage of ten belly-tendon H or M responses at any given intensity. The ordinate in F plots the motor unit threshold as a percentage of the number of trials in which the unit fired a spike at the stated stimulus intensity.

same amplitude (Fig. 2E–H). The results were used to titrate the vibration effects, and a complete parametric analysis of each soleus motor unit was carried out with at least five different vibration conditions. For example, the soleus unit of Fig. 3 reached its monosynaptic reflex threshold (that is 50 % probability of firing) when the tibial nerve shock was 0·79 in relative units (Fig. 3B, crosses) and the amplitude of the simultaneously recorded H reflex was 3·73 mV or 89 % of the maximum H reflex (Fig. 3A). The same unit did not fire when similar or even larger shocks were delivered during a strong tendon vibration (open circles) which reduced the maximum H reflex to 2·36 mV; the latter maximum H reflex was indeed much smaller than the

one corresponding to the unit's threshold recorded without vibration. For another series of trials with a moderate vibration that reduced the maximum H reflex to only 3·80 mV (filled circles), the same unit could be made to fire and its threshold corresponded to a shock intensity of 0·83 and to an H reflex amplitude of 3·57 mV. Throughout these tests the direct M response was not affected by the vibration.
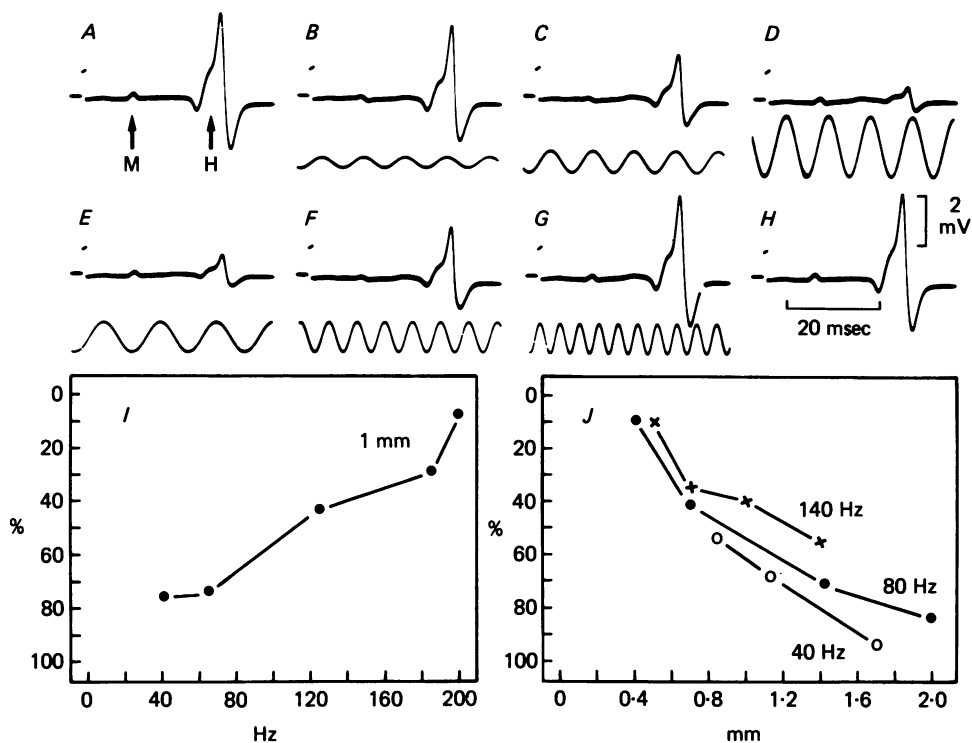

Fig. 2. Effect of vibration parameters on presynaptic inhibition of the H reflex. Recording of the global soleus electrogram. The single shock to the tibial nerve (see artifact 3 msec after initiation of the sweeps) has the same intensity throughout and it elicits near maximum H reflexes with a small direct M response. *A* and *H*, control H reflexes. *B*, *C* and *D*, steady vibration at 80 Hz with an amplitude of 0·4 (*B*), 0·7 (*C*) and 2·0 mm (*D*) respectively. *E*, *F* and *G*, steady vibration with 1 mm amplitude and frequencies of 65 (*E*), 125 (*F*) and 200 Hz (*G*) respectively. *I* and *J*, vibration-induced inhibition of the H reflex expressed as percentage (ordinate) as a function of the vibration frequency at constant 1 mm amplitude (abscissa in *I*) or of vibration amplitude (abscissa in *J*) at three chosen vibration frequencies.

De-recruitment order of soleus single motor units during vibration. Fig. 4*A* illustrates for nineteen soleus motor units the monosynaptic reflex thresholds expressed as the amplitude of the simultaneously recorded H reflex with or without vibration. The vibration parameters were of course chosen so as to avoid silencing the unit. The observed roughly linear relation with a slope close to unity indicates that vibration had little, if any, effect on the unit's monosynaptic threshold expressed in relation to the amplitude of the H reflex (which is reduced by vibration, see Fig. 5). Thus each

soleus unit was recruited by the monosynaptic volley when about the same fraction
of the soleus motoneurone pool had been made to fire, irrespective of the presence or
absence of vibration-induced inhibition.

If this is so, the low threshold units recruited for small H reflexes should require
stronger vibrations to be silenced. To examine this point the H reflex thresholds of
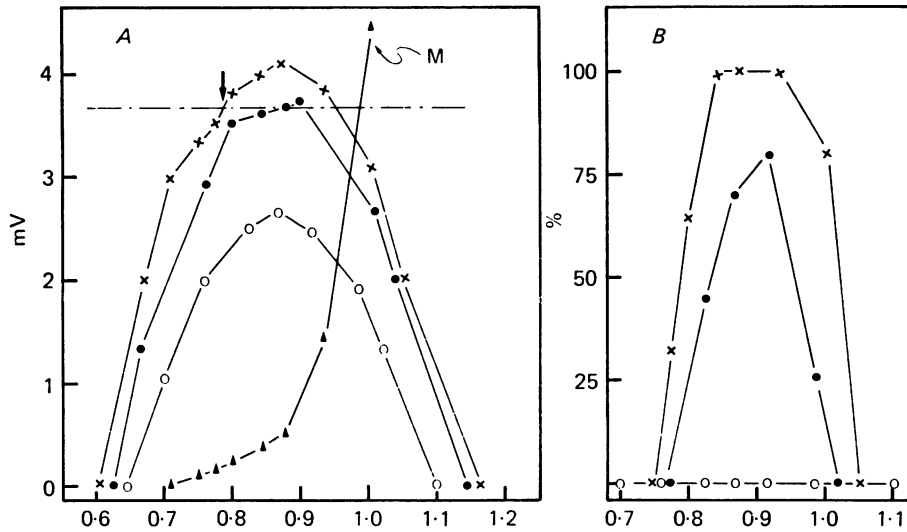the units were ranked on a scale in which the maximum H reflex was given the value

Fig. 3. Effect of vibration on the monosynaptic reflex threshold of a single soleus motor
unit. A, recruitment profile of the H reflex, expressed in the ordinate as peak-to-peak
voltage of the belly-tendon soleus response, without vibration (crosses) or with steady
vibration of 0·4 mm (filled circles) or 0·8 mm (open circles) amplitude at 80 Hz. The
horizontal interrupted line corresponds to the single motor unit's threshold without
vibration. Abscissa, intensity of the single shock to the tibial nerve in relative units
(cf. Fig. 1). The M response (triangles) is not affected by the vibration. B, probability of
firing of the single motor unit expressed as percentage on the basis of ten trials
(ordinate). Same abscissa as in A. Crosses, control without vibration. The unit was
silenced by the 0·8 mm vibration (open circles) and its probability of firing was reduced
by the 0·4 mm vibration (filled circles).

of 100 % (Fig. 4B). Under various vibration parameters the stronger vibration still
compatible with a given unit's monosynaptic response (filled circles) and the next
stronger vibration that completely suppressed the unit's response (open circle) were
determined. These data define a 'fork' of levels of H reflex vibration inhibition which
defines the inhibition susceptibility of the unit. The results are in line with the work-
ing hypothesis just stated.

Two single soleus motor units with different threshold could be recorded consis-
tently from the same micro-electrode site in two experiments. Fig. 5A–D shows the
sequential recruitment of units 1 and 2 for single tibial nerve shocks of increasing
intensity that elicit larger and larger H reflexes up to 4·7 mV. When shocks eliciting
such maximum H reflexes were delivered during tendon vibrations of increasing
amplitudes (Fig. 5F–H), the H reflex was more and more inhibited while the two single
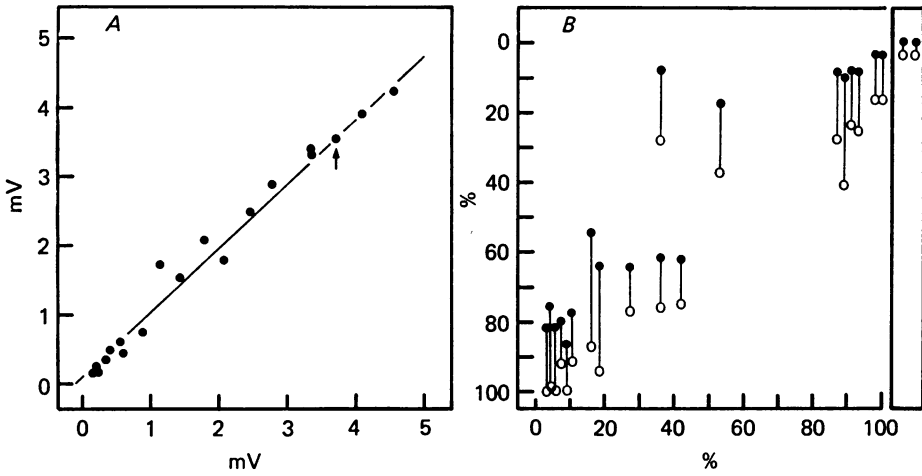motor units were de-recruited in reverse order.

Fig. 4. *A*, pooled data on the monosynaptic thresholds of nineteen single soleus motor units expressed as the size of the simultaneously recorded H reflex in the absence (abscissa) or in the presence of steady vibrations which were chosen so as to reduce the H reflex without silencing the motor unit response to the tibial nerve shock. The calculated linear regression was: $y = 0.93x + 0.10$ ($r^2 = 0.98$). *B*, susceptibility to vibration-induced inhibition in relation to the ranking order of soleus motor units recruited in the phasic H reflex. Abscissa, reflex thresholds of the twenty-one units studied, expressed as the size of the simultaneously recorded H reflex in the absence of vibration (expressed as percentage of the maximum H reflex). Ordinate, potency of the vibration inhibition of the H reflex that is required in order to suppress the reflex response of each unit (see text).
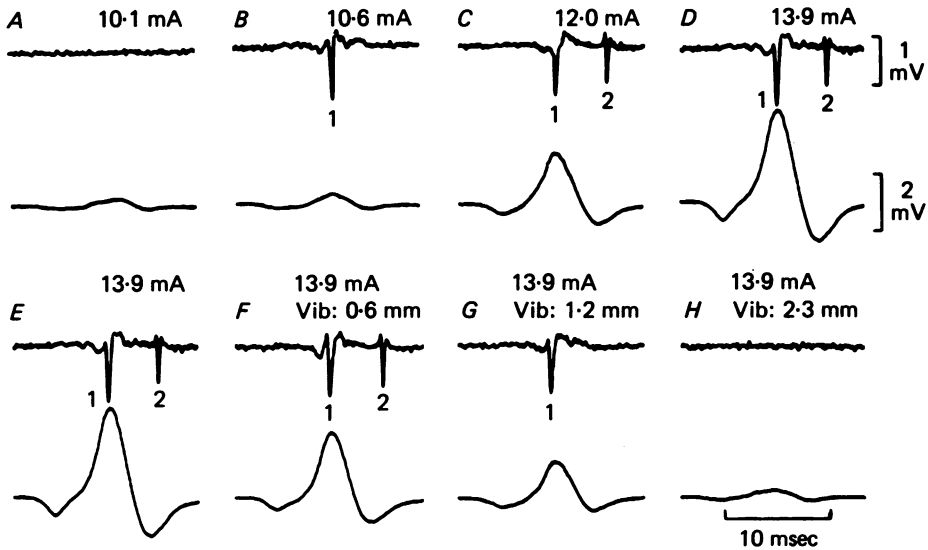

Fig. 5. *A–D*, recruitment order of two single motor units when the H reflex increases as a result of increasing the tibial nerve shock. The intensities of the stimuli are indicated in mA. *E*, same condition as in *D*. *F*, *G* and *H*, inhibition of the H reflex to a 13·9 mA stimulus by steady vibrations of various amplitudes at 80 Hz. The two units are inhibited in reverse order.

DISCUSSION

In spite of the current interest for the motor and perceptual effects of muscle vibration (Goodwin, McCloskey & Matthews, 1972; Hagbarth, 1973; Lance et al. 1973; Delwaide, 1973; Ashby et al. 1974), the actual mechanisms involved in the vibration paradox are still obscure. The depression of phasic proprioceptive reflexes by tendon vibration is primarily related to presynaptic inhibition of Ia afferents (Gillies et al. 1969). The possibility that the afferent volley of the phasic reflex (tendon percussion or electrical stimulation of the Ia afferents in the tibial nerve) might be reduced through occlusion or 'busy line effect' by the steady vibration-induced input (Burke & Ashby, 1972; Hagbarth, 1973) does not provide a sufficient explanation (Lance, Neilson & Tassinari, 1967) since the vibration depression is reduced or abolished in parallel with presynaptic inhibition in patients with spastic hemiplegia (DeGail et al. 1966; Burke & Ashby, 1972; Delwaide, 1973) or in cats after picrotoxine injection (Gillies et al. 1969), thus under conditions not affecting the afferent conduction. The vibration-induced inhibition is prominent in soleus and in other limb muscles (Lance et al. 1966) but it does not occur in jaw-closing muscles where chin vibration does not depress, but rather potentiates, the phasic proprioceptive reflexes like the masseter reflex (Godaux & Desmedt, 1975). The latter evidence points to a major difference in the functional organization of the brainstem pathways for jaw-closing muscles and indeed suggests a lack of presynaptic inhibitory mechanism for the corresponding proprioceptive primary afferents.

This peculiarity probably explains why the TVR of the masseter and temporal muscles is much stronger than that of limb muscles in man, and it also accounts for the closer temporal relation of single motor unit discharges to vibration cycles in the masseter TVR (Desmedt & Godaux, 1975; Godaux, Desmedt & Demaret, 1975). The slow onset of the TVR results from the progressive recruitment of motoneurones by polysynaptic proprioceptive pathways which play a major role in the generation of the TVR-induced motoneurone depolarization (Westbury, 1972). These polysynaptic Ia pathways are located in the spinal cord (Hultborn & Wigström, 1978) and receive facilitatory influence from the vestibulospinal and reticulospinal pathways (Gillies, Burke & Lance, 1971) which explains why the TVR is permanently abolished below a spinal transection (DeGail et al. 1966; Matthews, 1966; Ashby et al. 1974). The latter finding should not be taken to imply that the polysynaptic TVR pathway might actually travel up through the brainstem because in the acute spinal cat, the intravenous injection of L-3,4 dihydroxyphenylalanine (L-DOPA) can restore the TVR (Goodwin, McGrath & Matthews, 1973) by a temporary potentiation of monoaminergic synapses which mediate the supraspinal facilitation (Lundberg, 1967).

Progressive recruitment by polysynaptic proprioceptive pathways is also a feature of the human masseter TVR in which however the monosynaptic Ia excitation (supposed free from presynaptic inhibition) plays a significant additional role in determining the actual timing of the vibration-induced motoneurone firing (Desmedt & Godaux, 1975; Hagbarth, Hellsing & Löfstedt, 1976). By contrast, in limb muscles and for example in soleus, the monosynaptic Ia excitation modulating the motoneurone membrane potential with the vibration cycles is apparently reduced by presynaptic inhibition to such an extent that it fails to lock the discharge to any definite

phase of the vibration cycles (Godaux *et al.* 1975). The observation that the size of the TVR response is much smaller in human soleus than masseter muscle suggests that the presynaptic inhibitory effect also depresses the polysynaptic Ia excitation which is essential for TVR recruitment.

Because the depolarization of the presynaptic inhibition spreads electrotonically throughout the central arborization of the Ia primary afferents, it would indeed seem unlikely that the Ia terminals acting on the interneurones of the TVR polysynaptic pathway could be immune while the terminals of the same Ia fibre acting on the soleus motoneurones are inhibited, as postulated by Delwaide (1973). We rather propose that both the polysynaptic and the monosynaptic Ia excitatory pathways are depressed by vibration, and the present single motor units' analysis has been able to resolve the vibration paradox in line with this hypothesis.

Several requirements have been met in order to make the study possible: (1) use of micro-electrodes capable of isolating consistently the spike of a single soleus motor unit in strong synchronous discharges of the H reflex; (2) determination of vibration parameters allowing the presynaptic inhibitory effects to be graded (Fig. 2); (3) design of a procedure for estimating the monosynaptic reflex threshold of each motor unit in terms of the size of the simultaneously recorded H reflex (Figs. 1 and 3). The ranking order of motor units for recruitment in the phasic H reflex was found to be concordant with the order for de-recruitment of the same units when the H reflex was subsequently reduced through vibration-induced presynaptic inhibition (Figs. 4 and 5). Thus each unit ceased to respond when the simultaneously recorded H reflex had been reduced by an appropriate vibration to roughly the size at which the same unit had first been activated in the absence of vibration. The vibration inhibition works in reverse on the same rank order of the soleus motor units, the last recruited motoneurones being the most susceptible to being silenced (Fig. 5). This makes sense of the vibration paradox by showing that for any slight change of a given parametric set, either the next lowest threshold (still silent) motor unit is going to be recruited, or the highest threshold (already firing) unit will be silenced. On the other hand we have confirmed in the human soleus that the motor units are recruited in the TVR in the same order as in graded phasic reflexes or voluntary contractions (Desmedt & Godaux, 1975). The steady proprioceptive input during muscle vibration elicits a certain level of presynaptic Ia inhibition which simultaneously brakes the further recruitment of soleus motoneurones through the polysynaptic pathways of the TVR and reduces the phasic monosynaptic reflexes below their control level in the absence of vibration. These data extend for the presynaptic inhibition of primary afferents the motoneurone size principle already shown to apply for excitatory and for post-synaptic inhibitory effects (Henneman *et al.* 1974; Clamann, Gillies & Henneman, 1974).

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