THE RESPONSES OF HUMAN MUSCLE SPINDLE ENDINGS TO VIBRATION DURING ISOMETRIC CONTRACTION

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SUMMARY

1. In human subjects, vibration of amplitude 1·5 mm and frequency 20–220 Hz was applied to the tendons of muscles in the leg to examine the effects on the discharge of primary and secondary endings during manoeuvres designed to alter the level of fusimotor drive.

2. In four experiments, the peroneal nerve was completely blocked with lidocaine proximal to the recording site in order to de-efferent spindle endings temporarily. The responses to muscle stretch and vibration, as seen in multi-unit recordings and in single unit recordings, were similar during the block as in the relaxed state prior to the block. Thus, these experiments provided no evidence of a functionally effective resting fusimotor drive.

3. The responses to vibration of nine primary endings and four secondary endings were examined during isometric voluntary contractions of the receptor-bearing muscles. Providing that the endings were responding submaximally in the relaxed state, voluntary contraction enhanced the response to vibration, suggesting co-activation of the fusimotor system sufficient to compensate for mechanical unloading. Unloading effects were observed during contractions of neighbouring synergistic muscles, indicating a close spatial relationship between the co-activated skeletomotor and fusimotor outflows.

4. Recordings were obtained from ten primary endings and seven secondary endings during isometric reflex contractions resulting from the vibratory stimulus (TVR contractions). For twelve endings, the appearance of the tonic vibration reflex in the receptor-bearing muscle resulted in a significant decrease in the response to vibration, suggesting that the endings were unloaded by the extrafusal contraction. On voluntary

suppression of the reflex contraction spindle responses reverted to their previous levels.

5. These results suggest that the tonic vibration reflex, like the tendon jerk reflex, operates predominantly or exclusively on alpha motoneurones and that it does not utilize the same cortically originating efferent pathways as are used in the performance of voluntary contractions.

INTRODUCTION

In the previous report, it was shown that in the relaxed state, the responses of human muscle spindle endings to vibration can be altered by passive changes in length of the receptor-bearing muscles (Burke, Hagbarth, Löfstedt & Wallin, 1976). These effects were attributed to mechanically induced alterations in spindle responsiveness rather than to changes in sensitivity dependent on alterations in fusimotor tone. The present study was undertaken to examine the responses of human muscle spindle endings to vibration during manoeuvres designed to alter the level of fusimotor drive.

The major aims were to determine: (i) whether the responses of spindle endings in relaxed muscles can be altered by local anaesthetic agents infiltrated around the nerve to block the fusimotor innervation; (ii) whether voluntary contractions of the receptor-bearing muscle are accompanied not only by increased static spindle discharge (Hagbarth & Vallbo, 1968; Vallbo, 1970, 1971, 1974b) but also by heightened spindle responsiveness to vibration; (iii) whether changes occur in the spindle response following the development of a tonic vibration reflex (TVR), and whether these changes are analogous to those seen during sustained voluntary contractions. A preliminary account of some of the findings was presented at the symposium 'Understanding the Stretch Reflex' held in Tokyo, Japan, November 1975 (Hagbarth, Burke, Wallin & Löfstedt, 1976).

METHODS

Data were obtained from the same unit material presented in the preceding paper (Burke *et al.* 1976), and similar experimental procedures and analysis techniques were used. Care was necessary to ensure that all muscle contractions studied involved primarily the receptor-bearing muscle. This was done by visual inspection, palpation of the tendon of the receptor-bearing muscle, and careful placement of e.m.g. electrodes such that the activity of muscle fibres surrounding the appropriate receptor was monitored. With voluntary contractions subjects usually required training before they could activate the receptor-bearing muscle preferentially. This was particularly so with the complex movements produced by the peroneal muscles. The contractions studied were always of weak or moderate strength since stronger contractions engaged several muscles and also tended to dislodge the micro-electrode in the nerve. When studying the reflex contraction produced by the tonic vibration

reflex, subjects were instructed to remain passive and neither help nor hinder the development of any motor change which they might perceive. On the other hand, in tests involving voluntary suppression of the reflex the subjects were instructed to counteract actively any perceived motor change.

The local anaesthetic, lidocaine, was used to produce a reversible nerve block involving the fusimotor system, thus de-efferenting spindle endings temporarily. Lidocaine 1 % was infiltrated around the peroneal nerve 10 cm proximal to the recording site. In four experiments complete block of the peroneal nerve was verified by paralysis of innervated muscles and cutaneous anaesthesia in the distribution of the nerve. In one experiment a partial nerve block was induced to block preferentially the fusimotor system. This was verified by loss of the normal ability to accelerate a spindle ending during isometric voluntary contractions, in the presence of a preserved spindle response to stretch and retained ability to contract the extrafusal fibres.

In three nerve block experiments multi-unit recording sites were used. The recorded neural activity was integrated using a R-C low pass filter with a time constant of 0·1 s.

RESULTS

Spindle responsiveness before and during fusimotor block. In four experiments, complete block of the peroneal nerve with lidocaine produced no decrease in the responses to stretch or to vibration. In three experiments,
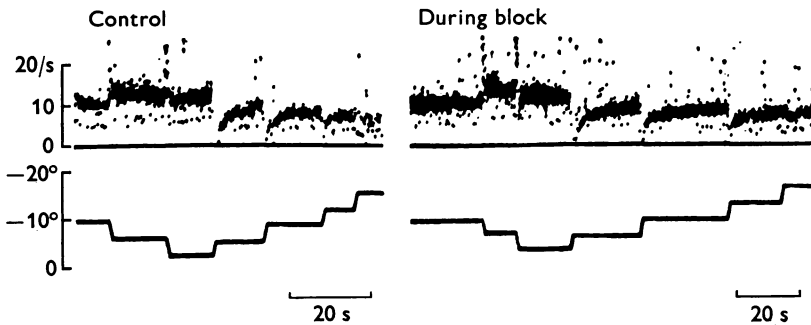

Fig. 1. The effect of de-efferentation on the response to stretch and shortening of a primary ending in the relaxed peroneus longus (PL) muscle. De-efferentation achieved by complete nerve block with lidocaine proximal to recording site. Upper trace: 'instantaneous' frequency plot. Lower trace: joint position. As in other Figures, a downward deflexion indicates stretch of the receptor-bearing muscle.

the micro-electrode was positioned such that multi-unit recordings with good signal-to-noise ratios were obtained from fascicles innervating tibialis anterior (TA). The responses to stretch were recorded in all three experiments, and the responses to vibration in two. In these latter experiments, the vibration frequencies were 30–100 Hz in one experiment and up to 180 Hz in the second. In all tests the integrated afferent responses were of

similar amplitude during the block as in the relaxed state prior to the injection of lidocaine.

In the fourth experiment single unit recordings were obtained from three primary endings in the peroneus longus muscle (PL). From one ending recordings were obtained before the block, during its development and when it was fully established, without any detectable change in the background discharge rate. Furthermore, no significant change could be detected in the responses to passive stretch and passive shortening (Fig. 1). When examined at a muscle length just short of that at which a tonic
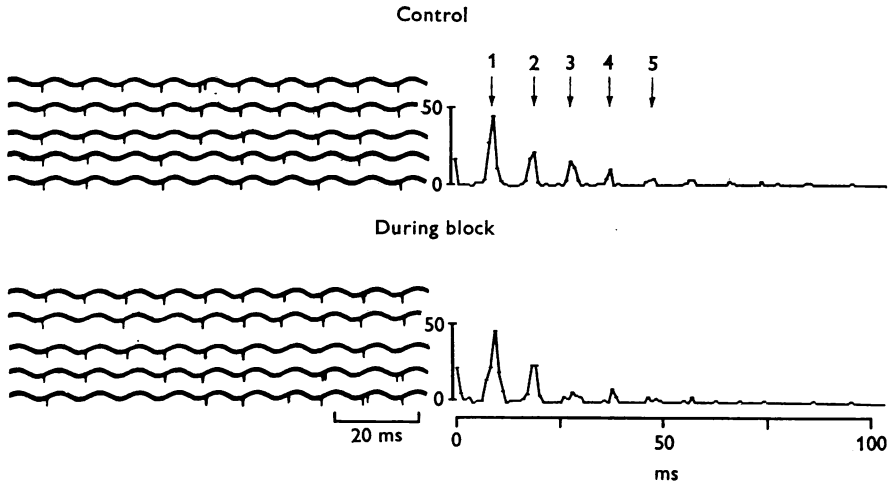

Fig. 2. The effect of de-efferentation on the response to vibration of a primary ending in PL. Same ending as in Fig. 1. Joint position: $-7°$. Vibration frequency: 105 Hz. To the left, individual sweeps with unit potentials transformed into standard pulses electronically added to the monitored vibration wave. To the right, interdischarge interval histograms, with the response of the ending occurring at latencies corresponding to the indicated multiples of the duration of the vibration cycle. Note in both histograms the very early peak due to occasional double discharges. Each histogram based on 256 potentials.

vibration reflex developed during control testing, the response to vibration at 105 Hz was also not altered by the block (Fig. 2). Indeed, when stretched further to a position at which a tonic vibration reflex had developed before the block, this functionally de-efferented ending was capable of discharging twice in many vibration cycles (cf. Fig. 9B).

Recordings were obtained from the other two primary endings during the stage of complete block. The responses to vibration of these de-efferented endings were sufficient to place them among the most responsive endings seen in the present studies (cf. Burke *et al.* 1976). Both

responded one-to-one to vibration of 120 Hz, even when the receptor-bearing muscle was short of the zero position (− 7° for both endings). One of the endings was capable of discharging twice per vibration cycle when subjected to further static stretch.

The outcome of these experiments is consistent with previous studies indicating that under normal conditions there is no functionally significant background fusimotor drive to relaxed muscles (Hagbarth, Hongell & Wallin, 1970; Vallbo, 1970, 1974a; Wallin, Hongell & Hagbarth, 1973; Hagbarth, Wallin & Löfstedt, 1975).
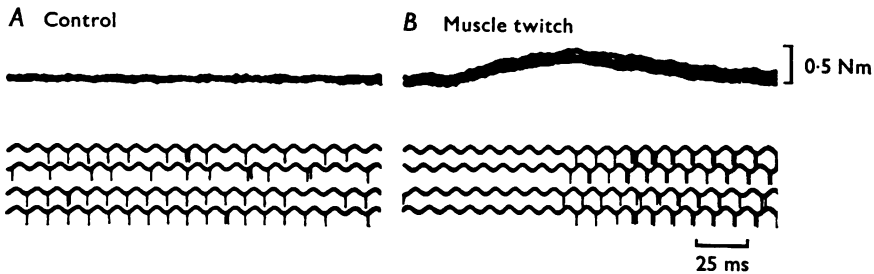
A Control   **B** Muscle twitch

] 0·5 Nm

⊢—————⊣
25 ms

Fig. 3. The effect of muscle twitch contraction on response to vibration of a primary ending in PL. Joint position: 0°. Vibration frequency: 95 Hz. Upper trace: torque. Lower traces: single sweeps formed as in Fig. 2, left.

Effects of electrically induced muscle twitches on the response to vibration. The responses to vibration of four primary endings in the TA and the PL were examined during twitch contractions of the receptor-bearing muscles. During the rising phase of twitch torque, all four endings ceased responding to the vibratory stimulus. During the falling phase of twitch torque, the responses to vibration were enhanced as evidenced by the appearance of double or triple discharges to individual vibration cycles (Fig. 3). The spindle responses remained locked to the vibration wave, the multiple discharges being confined to the same phase of the cycle.

One Golgi tendon organ (in TA) was subjected to combined vibration and muscle twitch. As expected, this ending responded best as twitch torque increased.

Effects of isometric voluntary contractions on the response to vibration. The effects of voluntary contractions were studied under isometric conditions on thirteen spindle endings (nine primary, four secondary) located in the extensor digitorum longus (EDL), TA and PL. In control tests in the absence of vibration it was ensured firstly that the subject could activate the receptor-bearing muscle with a reasonable degree of selectivity, and secondly that in such contractions the fusimotor co-activation was capable of increasing spindle discharge in the face of the spindle unloading

caused by the extrafusal shortening. The e.m.g. control to ensure that the contraction occurred in the 'correct' muscle was crucial since it was frequently observed that contractions restricted to neighbouring synergistic muscles produced pure spindle unloading (cf. Vallbo, 1970; Hagbarth, Wallin & Löfstedt, 1975). In Fig. 4, a secondary ending in EDL increased its discharge rate on preferential contraction of the receptor-bearing muscle (*A*),
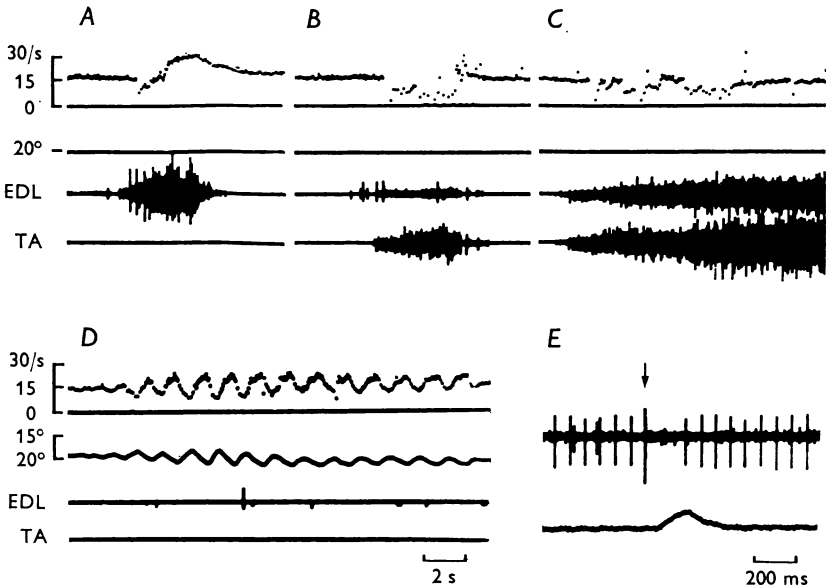

Fig. 4. The effects of isometric voluntary contractions on basal discharge rate of secondary ending in EDL. In *A*, *B*, *C* and *D*, traces are: instantaneous frequency; joint angle; e.m.g. of EDL; e.m.g. of TA. In *E*, an electrically induced twitch delivered at the arrow produces a twitch contraction, recorded by the myograph (lower trace), and a typical pause in spindle discharge, seen in the original neurogram (upper trace). In *D*, the close parallelism between imposed joint movement and discharge rate suggests that the ending is a secondary ending. In *A*, contraction of EDL accelerates the spindle (after a brief unloading). In *B*, contraction of predominantly TA decreases discharge rate. In *C*, contraction of both muscles, the opposing effects largely cancelling out.

but the discharge rate decreased when the contraction involved predominantly the neighbouring TA (*B*). Simultaneous contraction of both muscles produced a complex interaction which ultimately resulted in a discharge rate similar to that during relaxation (*C*).

Isometric voluntary contraction of the receptor-bearing muscle increased the response of all spindle endings to vibration providing that the ending was responding submaximally prior to the contraction. In Fig. 5, a primary

spindle ending in the relaxed TA muscle was activated only at subharmonics of the vibration frequency of 175 Hz, the histogram showing that discharges occurred at intervals of 6–12 vibration cycles. With isometric voluntary contraction, higher firing rates were obtained, with discharges every 2–5 cycles. If a spindle ending was responding one-to-one to vibration, voluntary contraction usually produced no change in discharge rate, or occasionally, an irregularity of response to vibration attributable to concomitant activation of synergistic muscles.
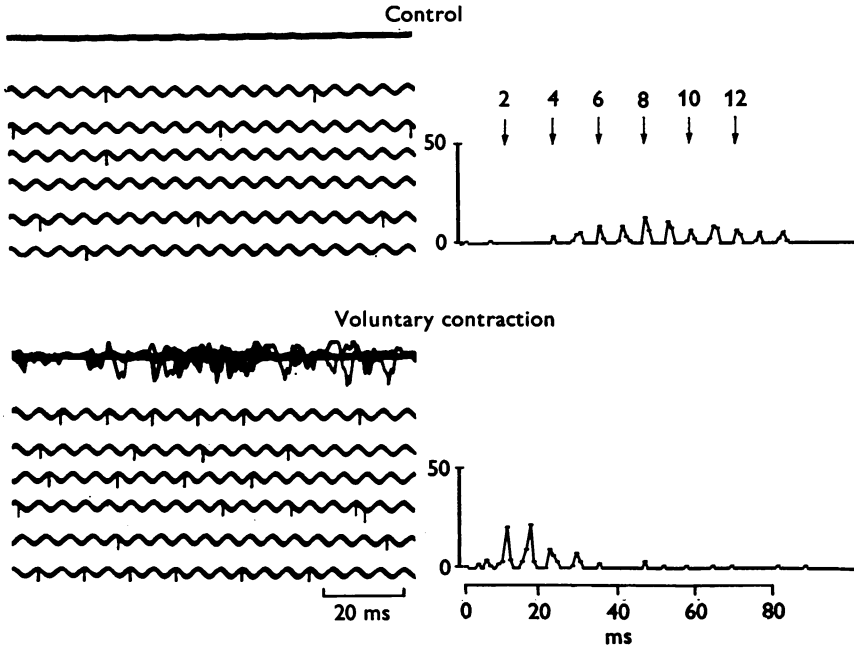

Fig. 5. The effect of isometric voluntary contraction on response to vibration of a primary ending in TA. Joint angle: 0°. Vibration frequency: 175 Hz. To the left, upper trace is e.m.g. of TA (six superimposed sweeps). Lower traces are the corresponding six sweeps containing unit discharges superimposed on vibration wave, as in Fig. 2, left. To the right, interdischarge interval histograms as in Fig. 2, right. Each histogram based on 128 potentials.

Fig. 6*A* presents another example of increased spindle response to vibration during contraction of the receptor-bearing muscle. However, in Fig. 6*B*, it can be seen that the response to vibration of the same ending was reduced by contraction of a synergistic muscle, an unloading effect similar to that illustrated in Fig. 4*B*.

Isometric voluntary contraction also increased the response to vibration

of two Golgi tendon organs, the discharge of both receptors remaining locked to the vibration cycle (Fig. 7A).

The effect of the tonic vibration reflex on the response to vibration. With seventeen spindle endings (ten primary, seven secondary), an involuntary tonic reflex contraction developed at some stage during vibration of the receptor-bearing muscle. These reflex contractions had all the character-
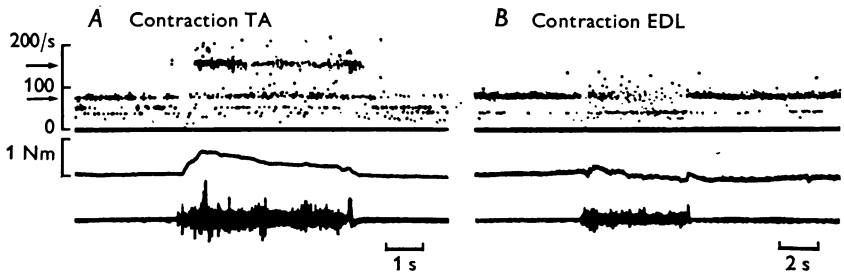

Fig. 6. The effect of isometric voluntary contraction on response to vibration of another primary ending in TA. Joint position: 8°. Vibration throughout each sequence at 150 Hz in A, 75 Hz in B, as indicated by horizontal arrows on the frequency scale. Upper trace: instantaneous frequency of ending. Middle trace: torque produced by contraction. Lower trace: e.m.g. A, contraction of receptor-bearing muscle (TA). B, contraction of synergist (EDL).
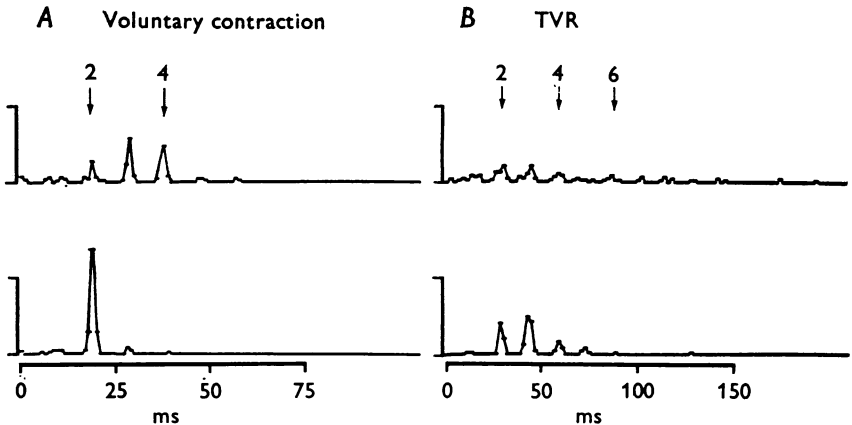

Fig. 7. The effect of contraction on response to vibration of a Golgi tendon organ in TA. Interdischarge interval histograms, each based on 128 discharges of the ending. Vertical calibrations: 50 potentials. Upper histograms: controls. Lower histograms: during contractions. A, the effect of voluntary contraction. Joint angle: 22°. Vibration frequency: 110 Hz. B, the effect of a tonic vibration reflex (TVR) contraction. Joint angle: 18°. Vibration frequency: 70 Hz.

istic features of the tonic vibration reflex of normal man, including gradual onset and decline, and susceptibility to voluntary suppression (cf. Hagbarth, 1973; Lance, Burke & Andrews, 1973).

For twelve spindle endings the appearance of a tonic vibration reflex resulted in a significant decrease in response to vibration, the discharge remaining locked to the vibration cycle. For the remaining five endings the appearance of a tonic vibration reflex produced either no detectable change or insignificant changes in discharge rate. For none of the seventeen spindle endings was an increased response to vibration seen. The reduction in spindle response occurred as frequently with secondary endings as with
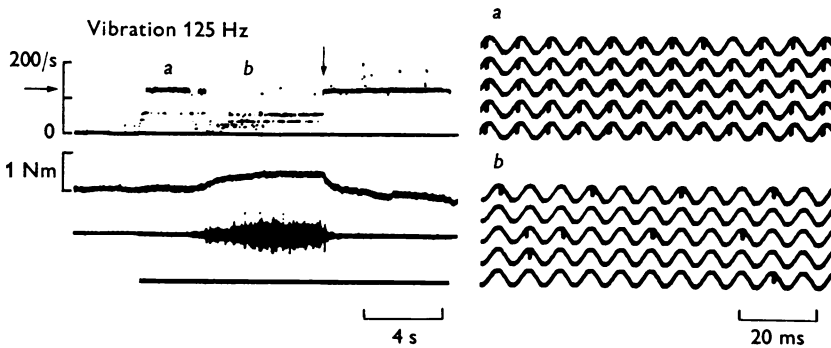

Fig. 8. The effect of the tonic vibration reflex on the response to vibration of a primary ending in TA. Joint angle: 12°. Vibration at 125 Hz indicated by bar. To the left, upper trace: instantaneous frequency plot, showing one-to-one response prior to development of a tonic vibration reflex and after its voluntary control (indicated by vertical arrow); middle trace: torque; lower trace: e.m.g. of TA (note the slight thickening of e.m.g. record before development of the vibration reflex due to vibration artifact). To the right, single sweeps as in Fig. 2, left, obtained from positions *a* and *b* on the frequency plot.

primary endings, and was not dependent on vibration frequency. To be certain that this phenomenon was not an unloading response to contraction of synergistic muscles, care was taken to ensure that the reflex contraction involved mainly the receptor-bearing muscle. Fig. 8 illustrates the phenomenon for a primary ending in TA. The development of the reflex contraction resulted in a decrease in discharge of the ending from the one-to-one response seen before the appearance of the tonic vibration reflex to a 1 : 3 or 1 : 4 response. As seen in Fig. 8, a partial recovery of the vibration responsiveness of primary endings often occurred with prolonged vibration.

With the primary ending studied before and during complete nerve block, the appearance of a tonic vibration reflex reduced the response to

vibration. As illustrated in Fig. 9*A*, such a reflex developed before the block when the receptor-bearing muscle was at − 4°, and the contraction increased when the muscle was stretched to − 1°. Coinciding with the tonic vibration reflex, and most clearly seen at − 1°, the spindle response to vibration was *reduced* to subharmonics of the vibration frequency.
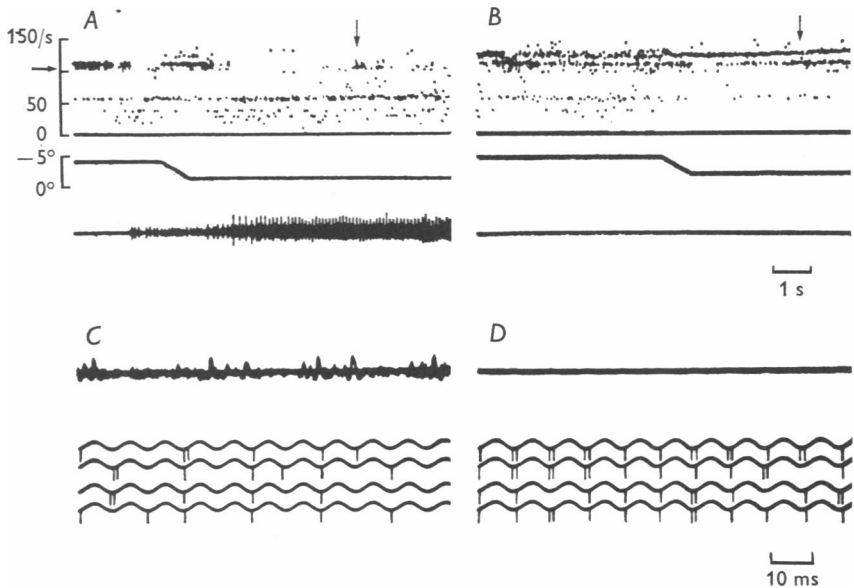

Fig. 9. The effect of de-efferentation on response of a primary ending in PL to vibration at length at which the tonic vibration reflex developed. Same ending as in Figs. 1 and 2. Vibration throughout *A* and *B* at 105 Hz. *A*, and *B*, upper traces: instantaneous frequency plots, showing unloading and a subharmonic response at the more stretched position of − 1° in *A*, but better response in *B* with the normal facilitatory effect of muscle stretch. In the frequency plots, the second line at a slightly higher frequency than that of the vibrator is present only during muscle stretch in *A*, but is more consistently present in *B*, particularly at − 1°. This line indicates the occurrence of double discharges (cf. Methods section in Burke *et al*. 1976). Middle traces: joint position showing stretch from − 4 to − 1°. Lower traces: e.m.g. of PL. *C*, and *D*, successive sweeps of ending discharges superimposed on vibration wave (as in Fig. 2, left) obtained at the vertical arrows in *A* and *B* respectively, the upper traces being the corresponding four e.m.g. sweeps.

However, after de-efferentation, when for obvious reasons no tonic vibration reflex developed, muscle stretch from − 4 to − 1° *enhanced* the response to vibration, the ending discharging twice in many vibration cycles (Fig. 9*B*).

A tonic vibration reflex developed during recordings from one of three

Golgi tendon organs. This ending became more securely driven by the vibration wave during the reflex (Fig. 7*B*).

Voluntary suppression of the tonic vibration reflex. When the reflex contraction was suppressed voluntarily by the subject (indicated by the arrow in Fig. 8), the spindle discharge reverted to the level it had before the reflex developed. Thus, voluntary suppression of the tonic vibration reflex is not mediated by a withdrawal of background fusimotor tone since it is accompanied by changes in spindle response which are the opposite of those to be expected from such a withdrawal.
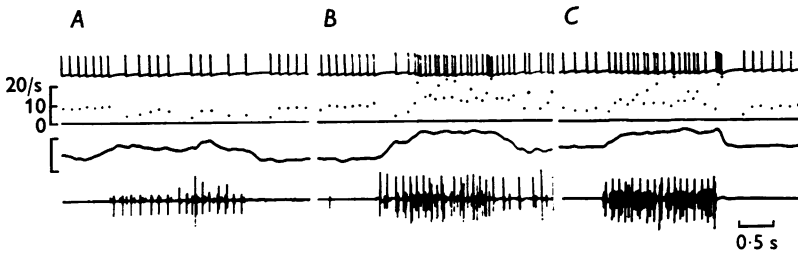

Fig. 10. The effect of partial nerve block on the response of a primary ending in TA to isometric voluntary contraction of TA. Joint angle: 8° in *A* and *B*; 0° in *C*. Upper traces: fibre potentials transformed into standard pulses. Second traces: instantaneous frequency plots. Third traces: torque (calibration equals 0·4 Nm for *A* and *B*, 1 Nm for *C*). Lower traces: e.m.g. of TA. *A*, partial nerve block. Voluntary contraction reduces spindle discharge rate. *B*, partial recovery. *C*, complete recovery. Note that in *A* and *B* the basal discharge frequencies before the contractions are identical.

Simultaneous recordings of e.m.g. activity from antagonistic muscles showed that the voluntary suppression of the tonic vibration reflex was only occasionally accompanied by activation of the antagonistic muscles. When the antagonist was activated, the e.m.g. activity occurred up to 200 msec after the tonic vibration reflex had been suppressed, suggesting that the suppression was not mediated by a process involving activation of the antagonist. This view was further supported by recordings from a TA primary ending during vibration of the Achilles tendon. Voluntary suppression of the tonic vibration reflex of triceps surae was not accompanied by activation of the TA spindle ending.

The effect of preferential block of fusimotor innervation on the spindle response during voluntary contractions. Recordings were obtained from a primary ending in TA during a partial local anaesthetic nerve block and during the gradual recovery from the block. Even at the height of the block the subject retained the ability to contract TA, but was unable to activate intrafusal muscle fibres and thus produce the usual spindle acceleration. At this stage of the block, voluntary contractions of TA decreased

the discharge rate of the spindle ending (Fig. 10*A*). This unloading response was replaced by spindle acceleration as recovery from the block occurred (Fig. 10*B* and *C*), the response returning to that usually seen on voluntary contraction of a receptor-bearing muscle.

The basal discharge frequency of this ending immediately before voluntary contraction was the same in Fig. 10*A* when the ending was de-efferented as in Fig. 10*B*, when at least partial recovery of fusimotor innervation had occurred. This finding reinforces the earlier results suggesting that there is no functionally effective background fusimotor tone in relaxed muscles. The recording in Fig. 10*C* was obtained at a shorter muscle length, so the basal discharge frequency is not comparable with those in Fig. 10*A* and *B*.

<div align="center">DISCUSSION</div>

In agreement with previous findings in the cat (Brown, Engberg & Matthews, 1967), the present results show that electrically induced muscle contractions are capable of reducing the response of human muscle spindle endings to vibration. That this does not normally occur in isometric voluntary contractions of the receptor-bearing muscle may be attributed to co-activation of the fusimotor system by the descending corticospinal pathways. The degree of fusimotor co-activation is sufficiently strong not only to maintain the previous response to vibration, but also, under certain conditions, to increase it. These results are thus compatible with earlier studies in man in which the effects of voluntary contraction on the basal discharge of human spindle endings were studied (Hagbarth & Vallbo, 1968; Vallbo, 1970, 1971, 1974*b*; Hagbarth, Wallin & Löfstedt, 1975), and also with studies in which it was shown that the fusimotor system could increase the response of feline spindle endings to vibration (Granit & Henatsch, 1956; Crowe & Matthews, 1964; Brown *et al.* 1967; Homma, Mizote, Nakajima & Watanabe, 1972; McGrath & Matthews, 1973).

By contrast, the reduced spindle response to vibration during contractions of the tonic vibration reflex suggests that this tonic autogenetic reflex does not involve fusimotor co-activation sufficient to overcome the spindle unloading effects of extrafusal contraction and, in this respect, in man is similar to the tendon jerk, which, as judged from the pauses in spindle discharge, is also of the 'alpha-type' (Szumski, Burg, Struppler & Velho, 1974; Hagbarth, Wallin, Löfstedt & Aquilonius, 1975). The finding that voluntary contractions produce spindle unloading during partial block of the muscle nerve supports the conclusion that the principal difference between voluntary and tonic vibration reflex contractions is the fusimotor co-activation in the former. Although changes in the contractile

state of the muscle may have altered the transmission of the vibration wave through the tissues, such phenomena cannot explain the opposite effects of reflex and voluntary contraction on the spindle response.

The findings during the partial nerve block also provide evidence that weak and moderate voluntary contractions can be initiated and maintained even when transmission through the gamma loop has been interrupted, results incompatible with the original concept of the servo control of movement (Merton, 1953).

Vibration induced reflex inhibition of fusimotor activity? In the decerebrate cat, muscle vibration sufficient to excite only primary endings can cause reflex alterations in background fusimotor tone (Brown, Lawrence & Matthews, 1968). For individual fusimotor fibres the autogenetic effects of vibration may be facilitatory, inhibitory or absent (Fromm & Noth, 1974, 1976; Trott, 1976). In the lightly anaesthetized cat, muscle vibration can produce an inhibitory effect on fusimotor outflow to synergistic muscles (Proske & Lewis, 1972). The question may therefore be raised whether reflex inhibition of fusimotor tone may contribute to the decreased spindle responsiveness to vibration observed to occur in the tonic vibration reflex in the human.

This seems unlikely. Firstly the outcome of the nerve block experiments suggests that in relaxed muscles there is little or no background fusimotor activity to be inhibited (cf. also Hagbarth *et al.* 1970; Vallbo, 1970, 1974*a*; Wallin *et al.* 1973; Hagbarth, Wallin & Löfstedt, 1975). Secondly, the better response to vibration obtained after functional de-efferentation indicates that the diminished response during the tonic vibration reflex could not have been due primarily to suppression of fusimotor tone but rather to the unloading effect of the extrafusal contraction (cf. Fig. 9).

The tonic vibration reflex – a variant of the classical segmental stretch reflex or a cortically relaying reflex? In the monkey, the corticospinal commands governing purposive movements are adapted in strength to the opposing external loads (Evarts, 1973), and it has been hypothesized that in man cortically relaying 'stretch reflexes' may play an important role in load-compensation (Marsden, Merton & Morton, 1973; cf. Phillips, 1969). Even though functional connexions between ascending proprioceptive information and corticospinal commands are now quite well established (Lucier, Rüegg & Wiesendanger, 1975; Murphy, Wong & Kwan, 1975) it is still uncertain how these 'long loop reflexes' operate under normal conditions and how they are integrated with segmental proprioceptive reflexes.

The tonic vibration reflex is easily elicited in the decerebrate cat (Matthews, 1966), and an apparently identical reflex can be recorded in spinalized animals after the intravenous administration of DOPA (Goodwin, McGrath & Matthews, 1973). Thus, there are no compelling reasons for

postulating that the tonic vibration reflex of normal man requires a cortically relaying pathway. Furthermore, the present results provide indirect evidence against a cortically relaying long loop reflex path for the human tonic vibration reflex. Since activation of corticospinal pathways in voluntary contractions produces demonstrable evidence of alpha-gamma co-activation, the failure to find such evidence in the human vibration reflex suggests that it does not use these pathways.

The fact that the tonic vibration reflex, like the tendon jerk, produces spindle unloading favours the view that both are variants of the classical segmental stretch reflex. Indeed, for the gamma loop to provide load-compensating servo assistance during voluntary contractions (von Euler, 1966; Granit, 1970; Matthews, 1972), the stretch reflex should activate predominantly the alpha motoneurones of the stretched muscle. As judged from the present results, the tonic stretch reflex of man fulfils this requirement.

Skeleto-fusimotor innervation of human spindles? Skeleto-fusimotor (beta) innervation of muscle spindles (Emonet-Dénand, Jami & Laporte, 1975; Emonet-Dénand & Laporte, 1975; McWilliam, 1975) cannot fully account for spindle co-activation during voluntary contraction in man since beta fibres innervate nuclear bag fibres almost exclusively (Barker, Emonet-Dénand, Harker, Jami & Laporte, 1975) and have a dynamic fusimotor function (Emonet-Dénand *et al.* 1975; Emonet-Dénand & Laporte, 1975; McWilliam, 1975). In human studies, the increase in basal discharge frequency and the activation of secondary endings (cf. Fig. 4) suggest that, no matter what the level of activity in dynamic fusimotor fibres, the fusimotor co-activation involves static fusimotor fibres (Vallbo, 1970, 1974b). Furthermore, the unloading of primary endings produced by the tonic vibration reflex and the phasic stretch reflex and the effects of the partial nerve block experiments are difficult to explain in terms of beta fibre activity.

Functional implications of spindle unloading during contraction of synergistic muscles. The present results confirm earlier conclusions of a close spatial relationship between the co-activated skeletomotor and fusimotor outflows in voluntary motor acts (Vallbo, 1970; Hagbarth, Wallin & Löfstedt, 1975). Increased spindle discharge rate and heightened responsiveness to vibration were seen only when the voluntary contraction involved the receptor-bearing muscle. Contractions of neighbouring muscles tended to unload spindle endings. These findings emphasize the necessity for identification of the precise site of a spindle ending under study and for careful monitoring of the e.m.g. activity not only of the receptor-bearing muscle, but in some instances of synergistic muscles as well. More important, however, the unloading effects from contraction of surrounding muscles

illustrate the potency of the mechanical interactions which can occur between muscles acting isometrically as synergists on the same joint, interactions which cannot be observed in experiments on extensively denervated animal preparations. The interactions are such that selective activation of a muscle in a finely graded task will result in a type of 'surround inhibition' involving the afferent activity of neighbouring muscles. This would tend to sharpen the contrast in the afferent feedback and thus in turn help to direct the autogenetic reflex support to the particular muscle or muscle portion which is most actively engaged in the load-bearing task.

Voluntary suppression of the tonic vibration reflex. The present results confirm the suggestion made by Marsden, Meadows & Hodgson (1969) that voluntary suppression of the tonic vibration reflex cannot be due to a reduction of the fusimotor drive to the vibrated muscle. Indeed, instead of a decrease in the afferent inflow, the spindle response increases when the reflex contraction is voluntarily suppressed. Marsden *et al.* (1969) also demonstrated that effective voluntary suppression of the tonic reflex was not accompanied by suppression of the monosynaptic H-reflex, indicating that the inhibitory process did not operate on the monosynaptic reflex path or at motoneurone level. The absence of any significant effect on the skeletomotor and fusimotor systems of the antagonist makes unlikely the possibility of some reciprocal action involving the antagonist. Thus, the results are consistent with the belief that volitional suppression of the tonic vibration reflex is mediated by descending pathways altering transmission in the polysynaptic arc of the reflex (Granit, 1970; Hagbarth, 1973; Lance *et al.* 1973).

Recently it has been shown that, in relaxed muscles, reflex reinforcement of tendon reflexes produced by the Jendrassik manoeuvre is attributable not to an increased afferent volley but presumably to altered reflex transmission within the spinal cord (Hagbarth, Wallin, Burke & Löfstedt, 1975). In the previous paper it was argued that the intense Ia afferent response which could be produced by vibration in normal subjects without producing the typical features of spasticity indicates that human spasticity is not a syndrome resulting predominantly from an excessive group Ia input due to exaggerated fusimotor drive (Burke *et al.* 1976). The consistent theme behind these suggestions is that the control and lack of control of stretch reflexes in health and disease are probably determined more by changes in reflex transmission than by selective involvement of the fusimotor system.

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