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THE RESPONSES OF HUMAN MUSCLE SPINDLE ENDINGS TO VIBRATION OF NON-CONTRACTING MUSCLES

BY DAVID BURKE,* KARL-ERIK HAGBARTH,
LARS LÖFSTEDT AND B. GUNNAR WALLIN

From the Department of Clinical Neurophysiology, Academic Hospital, Uppsala, Sweden

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SUMMARY

1. In micro-electrode recordings from the human peroneal and tibial nerves, the responses of thirty-two primary spindle endings, thirteen secondary spindle endings and three Golgi tendon organs were studied during vibration of the tendons of the receptor-bearing muscles in the leg. The amplitude of the applied vibration was 1·5 mm and the frequency was varied from 20 to 220 Hz. As checked with e.m.g. and torque measurements, the muscles of the leg were relaxed during the sequences analysed.

2. Providing that the vibrator was accurately applied, all endings responded with discharges phase-locked to the vibration cycles, the discharge rates being at the vibration frequency or at subharmonics of that frequency. The response to vibration was of abrupt onset and offset, was maintained for the duration of vibration, and was not subject to fluctuation with changes in attention or with remote muscle contraction.

3. The maximal discharge rate that could be achieved varied from one ending to the next, and increased with the length of the receptor-bearing muscle. For endings driven at their maximal rate an increase in vibration frequency produced a decrease in discharge rate as the ending changed to a subharmonic pattern of response. The converse occurred on decreasing vibration frequency.

4. For any given muscle length, primary endings could generally be driven to higher rates than secondary endings but there was a wide range of responsiveness within each group and a significant overlap between the groups. At medium muscle length, the most responsive primary endings could be driven up to 220 Hz but secondary endings did not reach discharge rates higher than 100 Hz.

5. With combined vibration and passive movements, primary endings

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* C. J. Martin Travelling Fellow of the National Health and Medical Research Council of Australia.

exhibited maximal vibration responsiveness during the stretching phases, sometimes firing twice per vibration cycle. During the shortening phases, however, they usually ceased responding to the vibratory stimulus. The vibration responsiveness of secondary endings was not potentiated to the same extent by on-going muscle stretch or reduced to the same extent by on-going muscle shortening. Thus, during shortening, secondary endings may be more responsive than primary endings.

6. The responses of primary endings to tendon taps were reduced during muscle vibration, a reduction which probably contributes to vibration-induced suppression of tendon jerks. Additionally, as the muscle shortened after tendon percussion, there was a transient pause in the response to vibration.

INTRODUCTION

In man, vibration of limb muscles is capable of producing complex motor and perceptual phenomena which have been the object of extensive study (cf. Delwaide, 1971; Goodwin, McCloskey & Matthews, 1972; Hagbarth, 1973; Homma, 1973; Lance, Burke & Andrews, 1973). To date, however, only limited data have been available for the human subject concerning the vibration-induced afferent inflow underlying these phenomena (Hagbarth & Vallbo, 1968; Vallbo, 1970), so that their interpretation has been based largely on data derived from the cat.

The tonic vibration reflex of human subjects is generally believed to result from the vibration-induced inflow from primary spindle endings, receptors which in the cat are known to be highly sensitive to vibration, the sensitivity increasing with passive muscle stretch and with increasing static and dynamic fusimotor drive (Granit & Henatsch, 1956; Bianconi & Van der Meulen, 1963; Crowe & Matthews, 1964; Brown, Engberg & Matthews, 1967; Homma, Mizote, Nakajima & Watanabe, 1972). However, other motor and perceptual events induced in man by vibration have been attributed by some authors to vibration-induced activity of secondary spindle endings (Eklund, 1971, 1972; cf. Hagbarth, 1973; Homma, 1973), receptors which in the cat are markedly less sensitive to vibration than the primary endings (Bianconi & Van der Meulen, 1963; Brown *et al.* 1967).

The present series of investigations was undertaken to define for the human subject the responsiveness of different muscle stretch receptors to vibration applied to the tendon of the receptor-bearing muscle, with particular attention to the comparative responsiveness of primary and of secondary endings and the changes in response induced by passive alterations in muscle length. The responses from receptors in non-contracting muscles form the basis of this paper, while the accompanying paper deals with the changes in vibration responsiveness induced by various types of muscle contraction (Burke, Hagbarth, Löfstedt & Wallin, 1976). 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

Material. Data were obtained from twenty-three experiments in eighteen healthy subjects, aged 17–48 years, all of whom gave informed consent to the experimental procedure. In these experiments, forty-five spindle endings and three Golgi tendon organs were subjected to vibration while recordings were made from their afferent fibres. Recordings were usually made from the peroneal nerve at the level of the fibular head, but in three experiments the tibial nerve in the popliteal fossa was used. The receptors were located in the tibialis anterior (twenty units), the peroneus longus and brevis (twenty-one units), the extensor digitorum longus (two units), and the gastrocnemii (five units).

Unit identification. Criteria for identification have been discussed previously (Vallbo, 1970; Hagbarth, Wallin & Löfstedt, 1975). All but five of the forty-eight units were subjected to an electrical twitch test, and were classified as spindle endings or Golgi tendon organs by their pattern of response (silence during the rising phase of torque with discharge on the falling phase for spindle endings, cf. Fig. 1*A*; discharge during the rising phase of torque for tendon organs, cf. Fig. 10*D*). The other five units were classified as probable spindle endings solely on the basis of their discharge characteristics and sensitivity to passive stretch. On the dynamic responses to ramp movements (cf. Fig. 1*B*) and alternating movements (cf. Fig. 1*C*), spindle endings were further classified as probable primary endings (thirty-two units) and probable secondary endings (thirteen units). However, it should be emphasized that some spindle endings did not fall clearly into one of two groups, and the classification of eight spindle endings (seven primary, one secondary) must be regarded as tentative in the absence of more definitive criteria such as conduction velocity. The response to vibration was not used as a criterion for the classification of endings.

Recording technique. Details of electrodes, equipment and recording procedures have been fully described (cf. Vallbo, 1970, 1971; Hagbarth, Hongell, Hallin & Torebjörk, 1970; Hagbarth, Wallin & Löfstedt, 1975). In brief, insulated tungsten micro-electrodes tapered to a tip of 1–5 μm were inserted manually through the skin into the appropriate nerve trunk and guided into an appropriate fascicle with the help of electrical shocks delivered through the micro-electrode. Once inside a fascicle minute electrode adjustments were made until the recording was dominated by the activity of a single fibre, the receptor of which was then located and identified. The reference electrode was a similar electrode bared of insulation for 3–5 mm from the tip and inserted 2–5 cm from the active electrode. The electrodes were connected to a pre-amplifier with a FET input stage and a fixed gain of 1000 and then to an amplifier of gain 20 or 50. After amplification the neural signals were stored on an eight channel Precision Instruments PI-6200 tape recorder together with other variables (see below).

The subjects lay on one side on a comfortable bed, with knee extended and foot fixed to the rotating plate of a hydraulic device with which the ankle joint could be subjected to passive movements of variable speed and amplitude (cf. Hagbarth, Wallin & Löfstedt, 1975; L. Löfstedt, in preparation). The ankle joint was centred over the axis of rotation and a goniometer recorded *ankle joint position*. The position of 90° at the ankle joint was taken as the zero position for each muscle. A strain gauge bridge was mounted in the foot-plate to measure the *torque* produced by contraction of the muscles acting on the ankle joint.

Electromyographic activity (e.m.g.) was recorded with needle electrodes identical to the reference electrode. These were inserted into the receptor-bearing muscle close to and in the same longitudinal plane as the receptor. They also served as

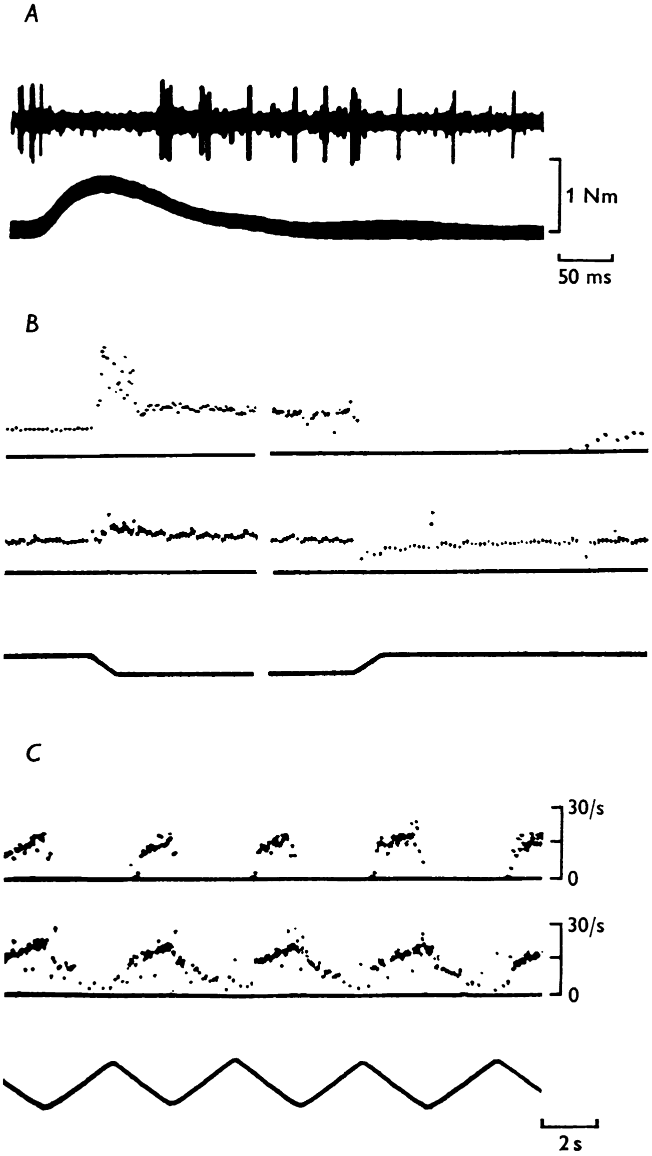

Fig. 1. For legend see facing page.

stimulating electrodes for the twitch contractions used in receptor identification. Occasionally similar e.m.g. recordings were obtained from other muscles in addition to the receptor-bearing muscle.

Vibrators. Vibration was applied to the tendon of the receptor-bearing muscle using one of three vibrators, all of which were adjusted so that the amplitude of vibration was approximately 1·5 mm. These vibrators were: (i) a commercially-available electric vibrator ('TVR Vibrator' – Heiwa Electronic Industrial Co., Osaka, Japan) of variable frequency, up to 185 Hz; (ii) a pneumatic vibrator powered by compressed air, and capable of frequencies up to 100 Hz; and (iii) a modified pneumatic drill to which an eccentric weight of suitable size had been attached to produce vibration of appropriate amplitude and of frequency up to 220 Hz. The third vibrator was used for twenty-six endings and each of the others for eleven endings. The frequency of vibration was derived from an Endevco 2222A accelerometer attached to the vibrator.

The vibrators were held manually with a constant force of application, found in control experiments to be 2–2·5 kg. The area of contact between skin and vibrator was approximately 1 cm^2. Manual application was superior to strapping the vibrator to the limb because both the site and the force of application could be better controlled. Additionally, the strap appeared to facilitate the spread of vibration to other muscles.

Analysis. Neural activity and other variables were monitored on an oscilloscope and a loudspeaker during the experiment, but all analysis was performed subsequently. Most of the analysis procedures have been described previously (Hagbarth, Hongell, Hallin & Torebjörk, 1970; Vallbo, 1971; Hagbarth, Wallin & Löfstedt, 1975). Except when checking potential shape for identification purposes, the band width of the neural signals was limited usually to between 700 and 2000 Hz since this gave optimal signal-to-noise ratio and effectively eliminated any vibration artifact. An amplitude discriminator (cf. Hagbarth, Hongell, Hallin & Torebjörk, 1970) was used to reduce the remaining noise. Unit frequency was calculated using an instantaneous frequency meter with a range of up to 500 Hz (Hagbarth, Wallin & Löfstedt, 1975). At times this range was insufficient to display the second discharge when a unit responded more than once per vibration cycle. However, usually this did not occur with every cycle of vibration so that the display from the frequency meter then showed two horizontal lines near the vibration frequency, one corresponding exactly to the vibration frequency, when the unit was responding 1 : 1, and

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Fig. 1. Identification of spindle endings. *A*, electrical twitch test showing afferent potentials in the original neurogram (upper trace) and the torque produced by contraction of the receptor-bearing muscle (lower trace). Five superimposed sweeps. Note that an early discharge occurs before torque starts to rise. Spindle discharge pauses as torque rises. *B*, 'instantaneous' frequency plots of spindle responses to ramp stretch and shortening of 3–4° at 7·5°/s for a primary ending (upper trace) and a secondary ending (middle trace). Calibrations as in *C*. *C*, 'instantaneous' frequency plots of responses to alternating movements at 7·5°/s for primary ending (upper trace) and secondary ending (middle trace). In both *B* and *C*, the movement of the ankle joint is shown in the lower trace, but for simplicity, the goniometer record for the primary ending has been omitted. The imposed movements for the two endings in *C* were very similar, but not quite identical in amplitude, so that occasionally the discharge of the primary ending appears slightly out of phase. As in subsequent figures, a downward deflexion represents stretch of the receptor-bearing muscle.

one at a slightly higher frequency corresponding to the slightly shorter interval between the second discharge in a cycle and the first discharge in the next (cf. Fig. 7*A* in present paper and Fig. 9 in Burke *et al.* 1976).

To illustrate the timing of receptor discharge in the vibration cycle, the recorded afferent potentials were transformed into pulses of standard amplitude and electronically added to the accelerometer signal (cf. Figs. 4*A*, 6, 7*A*, 9 and 10*C*). An Ortec 4620/4621 Time Histogram Analyzer was used for plotting interdischarge interval histograms and histograms of the 'jitter' of spindle discharge within the vibration cycle. For input to the analyser the unit potentials were represented by standard pulses derived from the frequency-meter and used normally for *Z*-axis modulation, so that it could be ensured that the histogram corresponded exactly to the desired segment of a frequency plot. To obtain the 'jitter' histograms the variability in latency between the unit pulses and the vibration wave (as monitored by the accelerometer) was calculated using the 'A–B interval' mode. To determine how much of the apparent 'jitter' was due to technical factors the 'jitter' of the vibration wave itself was determined routinely for the same sequence, using the 'A interval' mode.

It should be noted that the monitored 'vibration wave' was a measure of the acceleration of the applied stimulus, not of the resultant change in length of the receptor-bearing muscle. Thus no comment can be made on the precise latency of spindle discharge relative to the sinusoidal length change.

RESULTS

When vibration was applied to the tendon of the non-contracting receptor-bearing muscle, both primary and secondary spindle endings responded with repetitive discharges which were synchronized to the vibration wave even if they did not always follow the vibration frequency. As long as the receptor-bearing muscle was relaxed and at constant length, the response of a given ending remained constant for the duration of vibration and was reproducible on repeated testing. Changes in spindle response were not seen with alterations in the subject's attentive state or with reinforcement manoeuvres, such as contraction of distant muscles. The onset of the spindle response to vibration was abrupt, and on removal of the vibrator the response ceased as abruptly.

The frequency of vibration. For a given degree of muscle stretch, most spindle endings had a limiting discharge rate to which they could be driven by vibration, responding to each vibration cycle with only occasional 'drop-outs'. When the vibration frequency exceeded this level, the one-to-one driving was replaced by a response to every second vibration cycle. With further increases in vibration frequency, the ending's discharge rate again reached a limiting level, resulting in a drop in discharge rate as 2 : 1 firing was replaced by response to every third vibration cycle. Thus, with gradually increasing vibration frequency, the gradual increase of the spindle discharge rate was interrupted periodically by more or less sudden downward shifts as the ending changed its pattern of firing. Conversely, with gradually decreasing vibration frequency, the gradual fall in discharge rate was periodically interrupted by more or less sudden upward shifts as the ending changed its subharmonic pattern of firing (Figs. 2 and 3). The response at any given vibration frequency was often irregular in the sense that, in an apparently random fashion, some cycles failed to generate a spindle discharge, thus resulting in a frequency plot which contained a mixture of subharmonics. However, the interdischarge intervals always remained multiples of the vibration cycle; random discharges unrelated to the vibration wave did not occur.

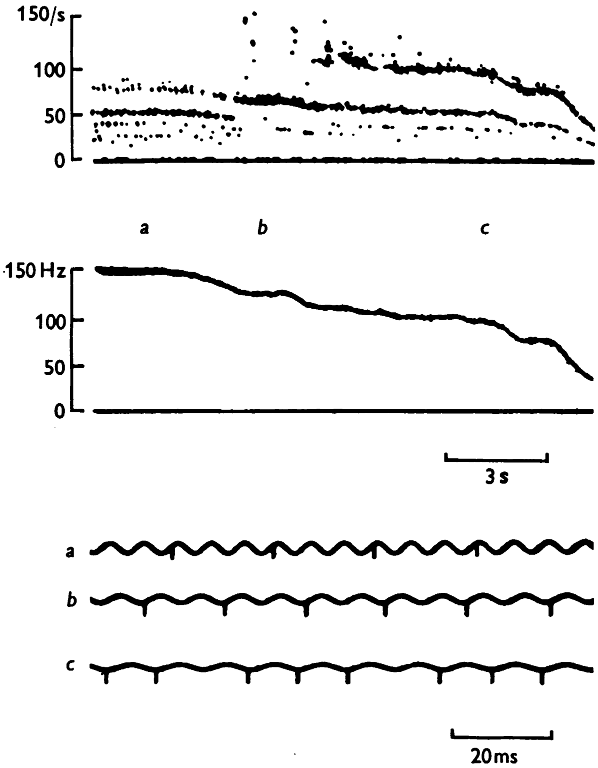

Fig. 2. Effects of changing vibration frequency on discharge of a tibialis anterior primary ending, with ankle joint stretched to +9°. Amplitude of applied vibration: 1·5 mm throughout entire sequence. Upper trace: instantaneous frequency plot of spindle discharge. Middle trace: instantaneous frequency of vibration. Lower traces: three sweeps showing superimposed vibration wave and ending discharges, sweeps *a*, *b*, *c* being obtained at the positions indicated on the frequency plots.

Since the limiting discharge rate for any particular ending changed with muscle length (see below), the position of the ankle joint had to be taken into account when comparing the responses to vibration of different endings. With the ankle joint at about the zero position, all primary endings but one had a limiting discharge rate of over 50 Hz, the most sensitive following vibration frequencies of up to 220 Hz (the maximum tested). By contrast, five of the thirteen secondary endings were unable to follow vibration of 50 Hz one-to-one, even when stretched past the zero position (0–16°, mean 9°). Nevertheless, even when responding at subharmonics of the vibration frequency, the mean frequency of discharge of secondary endings usually represented a significant increase over the basal firing rate. The best response obtained from a secondary ending was a one-to-one response at 130 Hz but this was recorded during a stretching movement and could not be sustained during subsequent maintained stretch.

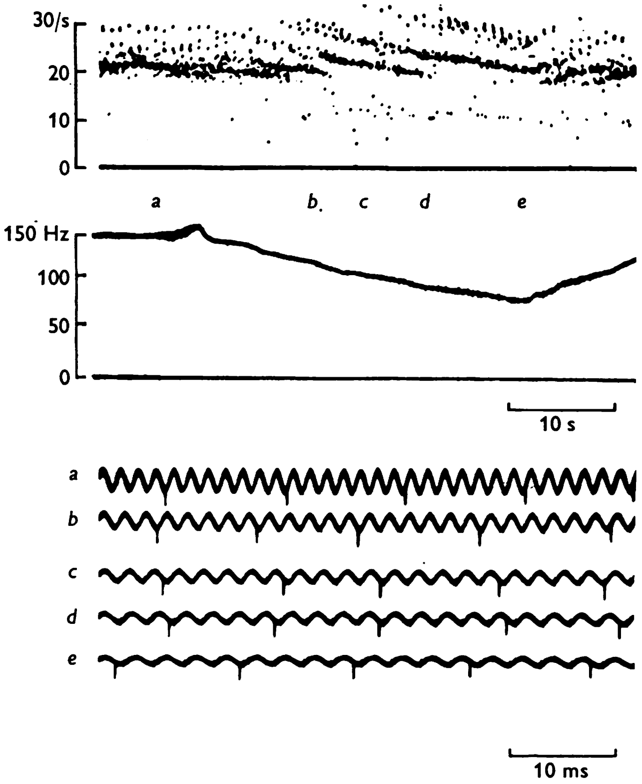

Fig. 3. Effects of changing vibration frequency on discharge of a tibialis anterior secondary ending with ankle joint stretched to +18°. Amplitude of applied vibration: 1·5 mm throughout entire sequence. Upper trace: instantaneous discharge frequency of ending. Middle trace: instantaneous frequency of vibration. Lower traces: single sweeps as in Fig. 2, obtained at *a*, *b*, *c*, *d* and *e* on the frequency plots.

On some occasions, spindle endings discharged twice per vibration cycle, and on four occasions three discharges were recorded for some vibration cycles (Fig. 4). More than one discharge per cycle was recorded only with primary spindle endings, only with vibration frequencies around or below 100 Hz, and usually only with combined vibration and passive stretch. The shortest interval between discharges in the same cycle of vibration was 1·2 ms, representing an instantaneous frequency for the second impulse of over 800 Hz.

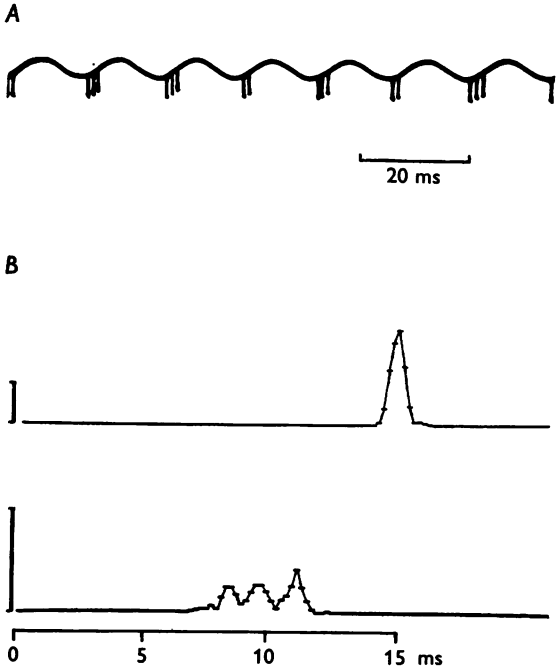

Fig. 4. Multiple discharges from a peroneus primary ending in response to vibration at 70 Hz, during the stretching phases of an alternating movement. *A*, vibration wave with superimposed pulses of standard amplitude, each representing a spindle discharge. *B*, histogram of the 'jitter' of spindle discharge relative to the vibration wave (lower trace). In this experiment the 'jitter' of spindle discharge was not significantly greater than the 'technical jitter' (upper trace). In the lower trace, 256 spindle discharges were counted, taken from only the stretching phases of the alternating movement. Vertical calibration: 100 discharges.

The precise timing of spindle discharge within the vibration cycle varied with the vibration frequency (cf. Figs. 2 and 3). However, for any given frequency, the potentials were triggered at a constant site with only a small 'jitter'. For the primary ending of Fig. 4, the 'jitter' of the potentials generated by vibration at 70 Hz during on-going stretch was not significantly greater than the 'technical jitter'. With less responsive endings, the 'jitter' was larger, being within the range 0·1–1·0 ms during vibration at 100 Hz, and increasing as the muscle was shortened (Fig. 5*B*).

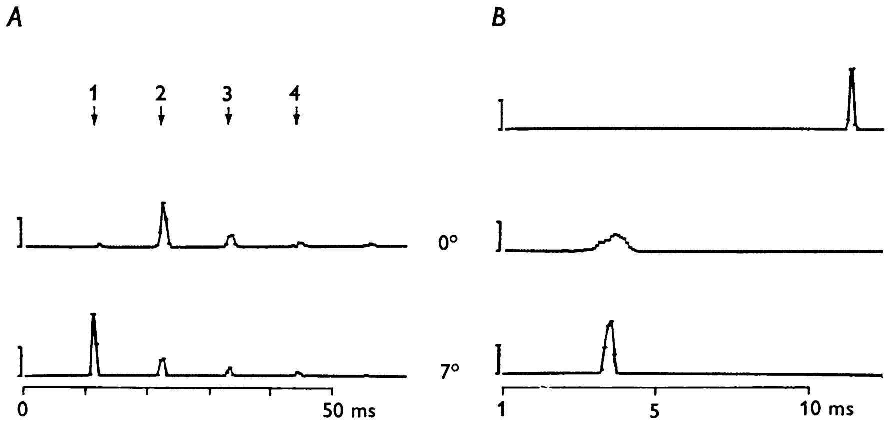

Fig. 5. The effect of static stretch from 0° to 7° on the discharge of a peroneus primary ending during vibration at 90 Hz. *A*, interdischarge interval histogram. Discharges occur every second, third or fourth vibration cycle at 0°, but at 7° the ending discharges in response to almost every cycle. *B*, histograms of the 'jitter' of spindle discharge at 0° (middle trace) and at 7° (lower trace). The upper histogram shows the 'technical jitter'. The positioning of the peak represents duration of the vibration cycle (11 ms) and the width of the peak the amount by which technical factors contribute to the 'jitter' of spindle discharge in the other two traces. In both *A* and *B*, 256 spindle potentials were used in each histogram. The vertical calibrations represent 100 discharges.

The site of application of the vibrator. Optimal spindle activation was obtained only when the vibrator was accurately applied to the appropriate muscle tendon or to the muscle belly in the vicinity of the receptor. Vibration applied to neighbouring or antagonistic muscles activated sensitive spindle endings, but only at subharmonics of the vibration frequency. The tibialis anterior primary ending illustrated in Fig. 6 was one of the endings most readily activated by distant vibration: it discharged to every third, fourth or fifth cycle when vibration of 115 Hz was applied to the Achilles tendon. On the other hand, the discharge of less responsive endings such as the secondary ending in Fig. 3 could be modified only by careful application of the vibrator to the tendon of the receptor-bearing muscle. The vibrator was usually not applied over the belly of the receptor-bearing muscle because although this effectively activated spindle endings, it generated more artifact and the micro-electrode was dislodged more easily.

The effects of passive changes in muscle length. In relaxed muscles, the discharge rate of both primary and secondary endings rarely exceeded 20–30 Hz in response to *maintained static stretch* alone. Different endings had different threshold lengths for static discharge, most being incapable of sustained activity until the muscle was stretched past the zero position (cf. Hagbarth, Wallin & Löfstedt, 1973; Vallbo, 1974*a*). Increasing muscle length increased the responses of both primary and secondary endings to vibration (Fig. 5), unless the response was already one-to-one. Just as the sensitivity to static stretch alone differed from one primary ending to the next and from one secondary ending to the next, so did different endings require different degrees of static stretch to achieve comparable responses to vibration (cf. Figs. 5 and 7*B*).

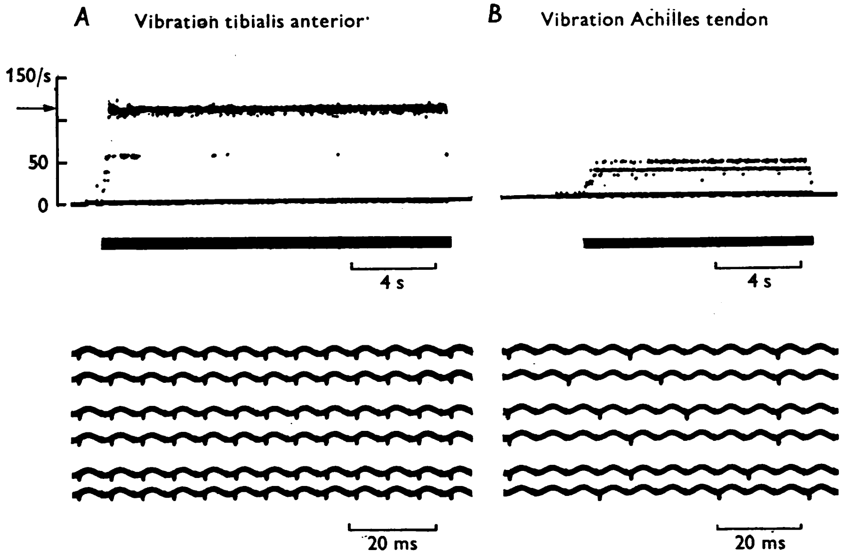

Fig. 6. Efficiency of spread of vibration. Vibration at 115 Hz of a tibialis anterior primary ending with ankle joint at + 9°. *A*, vibration applied to tendon of receptor-bearing muscle, showing 1 : 1 response in instantaneous frequency plot (upper trace) and in individual vibration cycles (lower sweeps). *B*, vibration applied to Achilles tendon activates the ending but at the third, fourth and fifth subharmonics. As in subsequent Figures, the vibration frequency is indicated by the arrow on the frequency scale.

The response to *ramp stretching and shortening movements* at velocities of up to 7·5°/s were criteria for the differentiation of primary and secondary endings, the primary endings being characterized by maximal discharge during the stretching movement and a pause in discharge on shortening

(Fig. 1). This dynamic behaviour was reflected in the response to vibration during ramp movements. During stretch, double and occasionally triple discharges could be generated by individual vibration cycles (Figs. 4 and 7*A*), and during shortening a pause in the response usually occurred, the discharge rate then slowly recovering to that appropriate for the new muscle length (Fig. 7*B*).

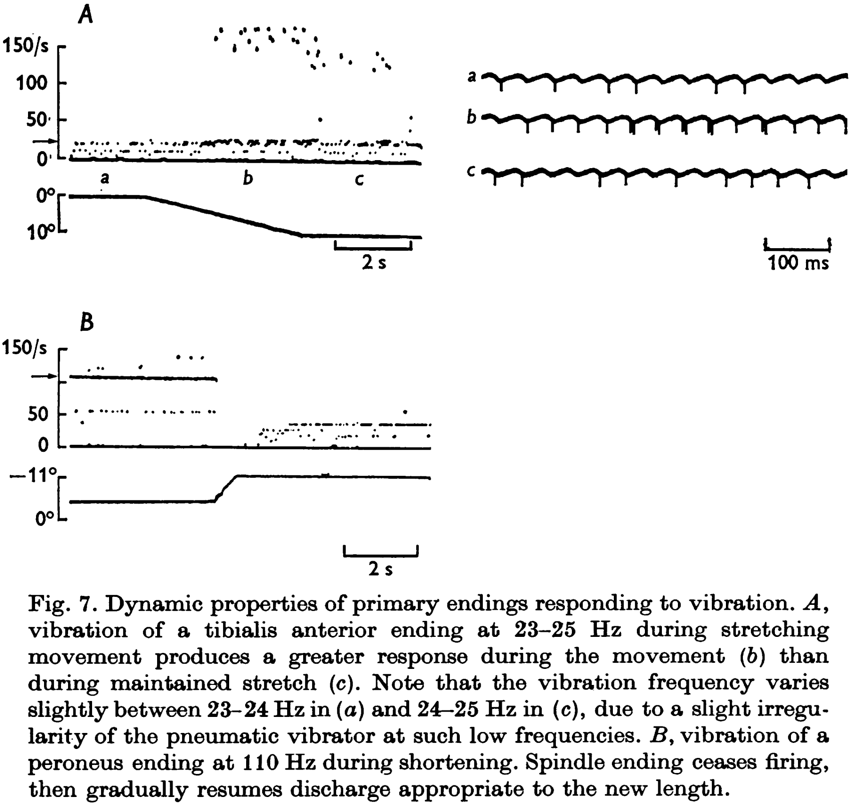

Fig. 7. Dynamic properties of primary endings responding to vibration. *A*, vibration of a tibialis anterior ending at 23–25 Hz during stretching movement produces a greater response during the movement (*b*) than during maintained stretch (*c*). Note that the vibration frequency varies slightly between 23–24 Hz in (*a*) and 24–25 Hz in (*c*), due to a slight irregularity of the pneumatic vibrator at such low frequencies. *B*, vibration of a peroneus ending at 110 Hz during shortening. Spindle ending ceases firing, then gradually resumes discharge appropriate to the new length.

With vibration at around 100 Hz, *passive alternating movements* at velocities of up to 7·5°/s generally produced one-to-one driving of primary endings during the stretching phases and almost complete silence during the shortening phases (Fig. 8*A*). For most secondary endings the contrast between stretch and shortening was not as prominent, discharge remaining at subharmonic frequencies during the stretching phase and not ceasing altogether during the shortening phase (Fig. 8*B*). For both types of endings, the increasing response with muscle stretch and the decreasing response with muscle shortening passed through successive subharmonics of the vibration frequency.

Fast stretch stimuli such as *tendon taps* generated brief bursts of impulses from primary spindle endings (Fig. 9). When delivered during vibration such stimuli produced smaller responses. Two factors seemed to contribute to this phenomenon. The randomly delivered taps were sometimes delivered during the unloading phase of the vibration cycle when the spindle ending was unresponsive, and, when delivered during the discharge phase of the cycle, occlusion between the tap and vibratory stimulus seemed to occur. Additionally, as shown in Fig. 9, spindle endings commonly became temporarily unresponsive to vibration as the force of percussion subsided and the muscle shortened after the transient tap-induced stretch.

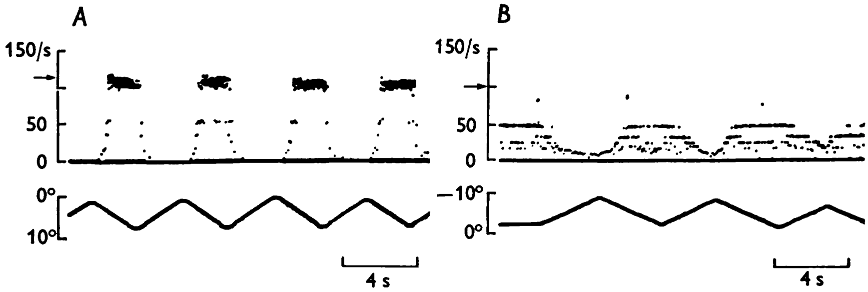

Fig. 8. Alternating movements. *A*, vibration of a tibialis anterior primary ending at 120 Hz produces a 1 : 1 response during the stretch phases and silence during the shortening phases. *B*, vibration of a peroneus secondary ending at 100 Hz. Response increases more gradually through subharmonics during the stretching phase to 1 : 2. With shortening the response gradually decreases again through subharmonics.

Other endings. Three *Golgi tendon organs* could each be activated by tendon vibration (Fig. 10). Two responded only at subharmonics of the vibration frequency, but, when the receptor-bearing muscle was stretched to + 18°, the third tendon organ could respond to every, or every other, vibration cycle at all frequencies tested, up to 120 Hz. It should be emphasized that, as with the spindle endings, these responses were obtained with passive receptor-bearing muscles, there being no evidence in the e.m.g. and torque recordings of reflex or voluntary contractions.

Five endings, provisionally identified as *Pacinian corpuscles* on the basis of their extreme sensitivity to dynamic stimuli, absence of response to maintained static stimuli and their wide receptive fields have been subjected to vibration. Irrespective of muscle length such endings were capable of following vibration frequencies up to 200 Hz one-to-one, and were activated equally well by vibration applied over antagonists.

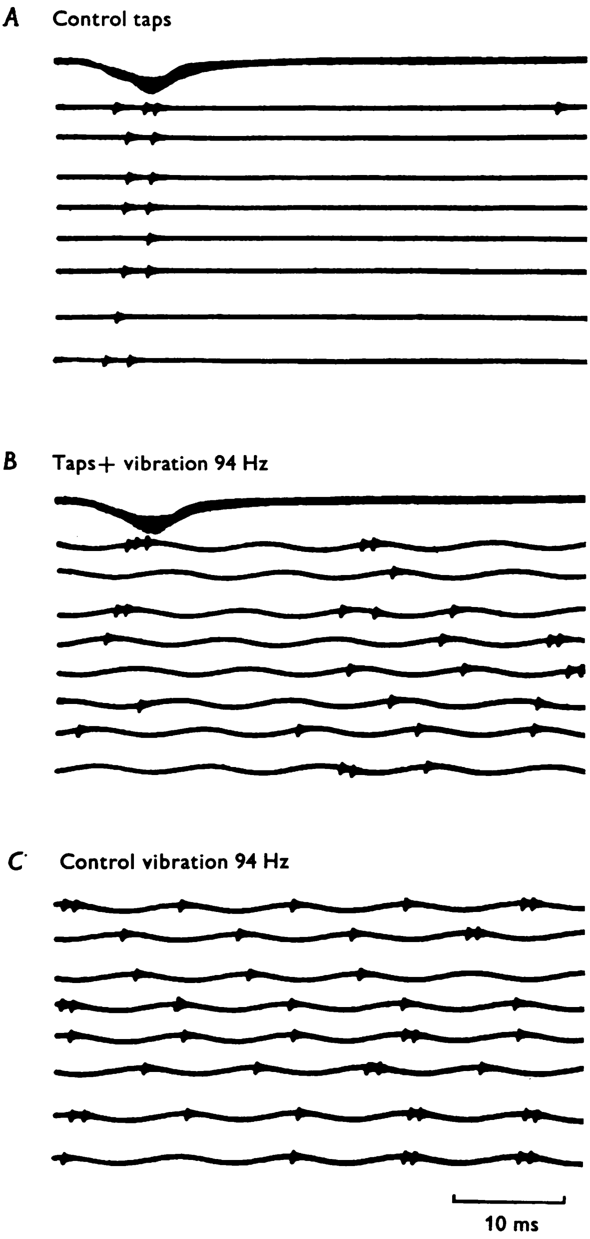

Fig. 9. For legend see facing page.

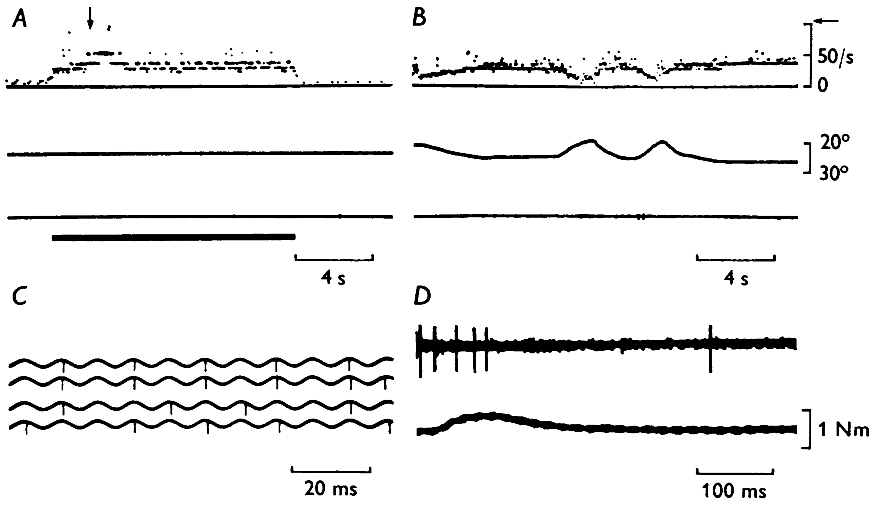

Fig. 10. Vibration at 110 Hz of a Golgi tendon organ in tibialis anterior. *A*, responses to vibration at constant muscle length and *B*, during alternating movements. Upper traces: frequency plots. Middle traces: ankle position. Lower traces: e.m.g. of tibialis anterior. Vibration indicated by bar in *A*, but is constant throughout the sweep in *B*. *C*, individual vibration cycles taken from the position indicated by the arrow in *A*. *D*, electrical twitch test. Three superimposed sweeps, showing discharge of the ending (upper trace) during the rising phase of torque (lower trace). Contrast with Fig. 1*A* for spindle behaviour during twitch test.

DISCUSSION

The present results demonstrate that in man primary and secondary spindle endings and Golgi tendon organs all respond to vibration of non-contracting muscles and that their capacity to follow high vibration frequencies increases with muscle stretch. Vibration locks receptor discharge to the vibration wave so that the excitation of the receptor produces

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Fig. 9. Tendon percussion and vibration at 94 Hz of a peroneus primary ending. *A*, eight control taps (tap torque superimposed in top trace) produce 1, 2, or 3 discharges during the rising phase of tap torque, the eight responses shown below each other. *B*, taps delivered when ending is responding to vibration produce no response if delivered at an 'insensitive' part of the vibration cycle (shortening phase) and if delivered at a 'sensitive' part of the cycle (stretching phase) they appear to elicit no more than three discharges, although they may alter the phase of discharge slightly. As tap torque subsides the spindle response to vibration is briefly suppressed. *C*, control vibration in the absence of tendon percussion. Ending responds mostly 1 : 1 or 2 : 1 although occasional cycles may be missed. In *B* and *C* vibration wave and unit discharge are superimposed as in Fig. 4*A*.

discharges at the vibration frequency or at subharmonics of that frequency. On the whole, primary endings can follow higher vibration frequencies than secondary endings, but within each group there is a wide range of responsiveness for different endings, a finding which may be partly related to the different geographical positions of the spindle receptors in the muscle (cf. Meyer-Lohmann, Riebold & Robrecht, 1974).

Responsiveness of spindle secondary endings. The greater vibration-responsiveness of human primary endings agrees with previous findings in the cat (Bianconi & Van der Meulen, 1963; Brown *et al.* 1967), but the extent to which human secondary endings respond to vibration applied to the muscle tendon could not have been anticipated from these earlier studies. Differences in technique may account for much of the discrepancy. In man the effective amplitude of vibration is unknown and the mode of application is probably less efficient than directly attaching a severed tendon to the vibrator. Nevertheless, the conclusion of Brown *et al.* (1967) that 'In man, vibration applied to a tendon in the absence of muscle contraction can be presumed to be a specific stimulus for the primary endings' is not supported by the present findings.

Of the two studies, that of Bianconi & Van der Meulen (1963) is more comparable with the present since they applied vibration by a stylus to the muscle overlying the appropriate ending or to the muscle tendon. Bianconi & Van der Meulen (1963) describe two types of response: 'either an ending was capable of following the vibrator, or an ending would maintain its background discharge independent of the vibrator phase and frequency'. However, in their published examples of 'non-responsive' endings (e.g. their Figs. 1*C* and *D*, 5*B*) they have not differentiated between endings that are truly unresponsive to vibration and those which although unable to follow the vibration frequency one-to-one are capable of subharmonic activation. Indeed in their Fig. 5*B*, a 'non-responsive' slowly conducting fibre appears to more than double its firing rate with increase in vibration frequency from 60 to 150 Hz.

Subharmonic activation of secondary endings was recognized by Brown *et al.* (1967), and also by McGrath & Matthews (1973), but with the higher vibration frequencies and lower amplitudes which they used they considered such activation minor compared with the extreme sensitivity of primary endings. Some of their endings appeared unresponsive to vibration, at least in terms of discharge rate. However, as illustrated in Fig. 3 of the present study it can occasionally be difficult to appreciate that an ending has responded to vibration if only changes in mean discharge rate are considered. These difficulties would be aggravated by a high background discharge rate (25–50 impulses/sec for de-efferented feline secondary endings in the study of Brown *et al.* 1967, cf. their Fig. 8).

It could be argued that high (static) fusimotor tone contributed to the sensitivity of secondary endings in the present study, since fusimotor activation will increase spindle sensitivity to vibration (Granit & Henatsch, 1956; Crowe & Matthews, 1964; Brown *et al.* 1967; Homma *et al.* 1972; McGrath & Matthews, 1973; Burke *et al.* 1976). However, previous studies revealed no evidence of resting fusimotor tone in relaxed normal human subjects (Hagbarth, Hongell & Wallin, 1970; Wallin, Hongell & Hagbarth, 1973; Hagbarth, Wallin, Burke & Löfstedt, 1975; cf. however Burg, Szumski, Struppler & Velho, 1974), and in the present study the spindle response to vibration was stable and reproducible unless changes occurred in the active or passive state of the receptor-bearing muscle. Furthermore, in the accompanying paper the properties of spindle endings de-efferented by complete local anaesthetic nerve block proximal to the recording site were similar to those reported in the present study (Burke *et al.* 1976). Together, all these findings suggest that, in accordance with the principle of alpha-gamma co-activation (Granit, 1970, 1975), when the skeletomotor system is silent, so is the fusimotor system.

The present results thus provide a credible basis for earlier studies which suggested that some motor and perceptual phenomena induced by vibration may result from activation of spindle secondary endings. Eklund (1971) observed that high frequency low amplitude vibration of the muscle tendon is an efficient means of producing a tonic vibration reflex but that a shift towards inhibitory phenomena can be produced in antigravity muscles by applying vibration of higher amplitude and lower frequency to the muscle belly, measures which might be expected to bias the spindle input in favour of the secondary ending. Similarly, vibration-induced positional illusions, considered to result from a distortion of position sense due to the vibration-induced afferent input (Goodwin *et al.* 1972; Eklund, 1972), may now be assessed in the light of the present demonstration that, in man, vibration of the muscle tendon can be a significant stimulus for endings other than the primary ending.

Effects of stretch and shortening on vibration sensitivity. Of previous studies in the cat, only Granit & Henatsch (1956) and Brown *et al.* (1967) have systematically examined the effects of static muscle stretch on spindle responsiveness to vibration. In the former study, increasing stretch (monitored as passive tension) resulted in a spindle response which passed through successive subharmonics until one-to-one driving was achieved. In the latter study, muscle stretch decreased the amplitude of vibration required to produce one-to-one driving. The present results in man are in full accord with these earlier findings. In man, once a one-to-one response has been achieved further increases in stretch appear to produce more secure driving by decreasing the 'jitter' of the spindle discharge. Thus, measurements of the 'jitter' probably reflect phenomena equivalent to the threshold amplitude for one-to-one driving used by Brown *et al.* (1967).

The response to vibration during an on-going stretching movement was found to reflect the dynamic sensitivity of the spindle ending. Thus, under appropriate conditions, primary endings may respond better during, and shortly after, the movement than they do when maintained in a stretched position but the response of secondary endings parallels the imposed length change more closely. Enhanced responses to vibration during a stretching movement were also seen on occasions with feline primary endings by McGrath & Matthews (1973). There appears to be no previous data on vibration-responsiveness during muscle shortening. The present study shows that a shift in relative sensitivity occurs in favour of the secondary ending during shortening. Thus, in man, not only is the secondary ending activated by vibration but under certain circumstances it may be better activated by vibration than the primary ending.

Implications for the stretch reflex. These data from relaxed muscles allow a number of inferences to be drawn concerning the tonic vibration reflex and the tonic stretch reflex. Since the spindle response to vibration starts and stops abruptly, the long latency, gradual build up and gradual decline of the tonic vibration reflex are difficult to explain purely on spindle mechanisms, and presumably result from central processes. That the tonic vibration reflex is a load-compensating reflex, capable of resisting externally imposed displacements has been well established in human experiments (Eklund & Hagbarth, 1966; Hagbarth & Eklund, 1966). Although changes in the contractile properties of muscle may account for some load-compensation, the major factor is likely to be greater reflex activity due to an increased afferent response with increasing muscle length.

Clearly the intensity of group Ia afferent activity induced by high frequency vibration is greater than that elicited by either sustained muscle stretch or a voluntary contraction of moderate strength (Hagbarth *et al.* 1973; Vallbo, 1974*a*, *b*). In fact, it is doubtful whether under normal conditions there ever occurs such an intense sustained group Ia inflow as that which can be induced artificially by vibration. Considering the alleged autogenetic excitatory role of group Ia afferents in the tonic vibration reflex, it is of interest that in none of the recording sequences used in the present study did a reflex develop. This does not imply that such contractions did not occur (cf. Burke *et al.* 1976) but that it was possible to select sequences which were not associated with reflex contractions. Nevertheless, the fact that the contraction of the tonic vibration reflex may be absent in healthy subjects instructed to remain passive and relaxed is not a sign of low spindle sensitivity but suggests, instead, that in the relaxed state the central gain of the tonic stretch reflex may be quite low. Furthermore, in the group Ia impulse showers produced by combined vibration and stretch, instantaneous discharge rates reached 800 Hz, rates which far exceed those so far recorded in spastic subjects in response to stretch alone, even in clonus (Hagbarth *et al.* 1973; Szumski, Burg, Struppler & Velho, 1974; Hagbarth, Wallin, Löfstedt & Aquilonius, 1975). Thus it is hard to see an excessive group Ia input as the sole or even the major factor responsible for the enhanced stretch reflexes of clinical spasticity. However, it should be recalled that, in man, vibration is not a selective stimulus for the primary endings, and autogenetic inhibitory effects from other endings could counteract or conceal the excitatory effects.

The spindle afferent activity induced by muscle stretch and by voluntary contraction is asynchronous, but with vibration the afferent activity is synchronized to the vibration wave. There is growing evidence that, whereas this afferent synchronization can influence the precise timing of motor impulses through the monosynaptic path (cf. Homma & Kanda, 1973; Desmedt & Godaux, 1975; Matthews, 1975; Burke & Schiller, 1976; Hagbarth, Hellsing & Löfstedt, 1976), the tonic vibration reflex is not critically dependent on this path or on the pulsatile nature of the spindle inflow (Matthews, 1975; Burke & Schiller, 1976; Hagbarth, Hellsing & Löfstedt, 1976). Nevertheless, the ability of the monosynaptic pathway to regulate the timing of motor discharge illustrates the efficiency of phasic reflex mechanisms in compensating for transient variations in external load (cf. Vallbo, 1974*b*).

Restraining effect of vibration on spindle discharge. In addition to the more obvious spindle excitation vibration also has a restraining influence on spindles in that they can respond only within a limited phase of the vibration cycle. Additional stretching stimuli such as tendon taps delivered 'out of phase' with the vibration cycle may find the ending unresponsive and will thus generate a smaller response than when delivered in the absence of vibration.

Furthermore, for some spindle endings, 'occlusion' occurs when the tendon is percussed 'in phase' with the vibration cycle: the spindle response to the combined stimuli being smaller than the sum of the responses to the two stimuli delivered separately. Thus, whether delivered 'out of phase' or 'in phase', tendon percussion may generate a smaller afferent volley, at least from some of the spindle endings in the muscle. The ability of vibration to suppress tendon reflexes in man has been the subject of much study and speculation (Delwaide, 1971; Hagbarth, 1973; Lance *et al.* 1973). Irrespective of other established mechanisms, such a finding can be expected solely on the basis of these restraining influences of vibration on spindle discharge.

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