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EVIDENCE THAT THE SECONDARY AS WELL AS THE PRIMARY ENDINGS OF THE MUSCLE SPINDLES MAY BE RESPONSIBLE FOR THE TONIC STRETCH REFLEX OF THE DECEREBRATE CAT

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SUMMARY

1. The size of the tonic stretch reflex of the soleus or gastrocnemius muscle of the decerebrate cat has been compared with the size of the reflex contraction elicited in the same muscle by high-frequency vibration applied to its tendon.

2. On the assumption that vibration preferentially excites the primary endings of the muscle spindles it may be used to estimate the relation between the reflex response and the frequency of the Ia input to the spinal cord. On this basis, the increase in tension evoked by increasing extension is too great to be explained by the increase in Ia input with extension previously found on single fibre recording in comparable preparations.

3. When vibration was superimposed on stretch reflexes elicited by different extensions, the size of the additional contraction elicited by the vibration remained approximately constant. If the stretch and vibration reflexes both depended entirely upon the Ia pathway, then occlusion between them would have been expected instead of the simple summation which was found.

4. The absence of occlusion was not due to variation of the contractile strength of the muscle with its extension. This was shown by finding that the reflex contraction of soleus produced by stimulating the medial gastrocnemius nerve also remained the same size when elicited at different lengths of the muscle.

5. The reflex effects were studied of superimposing alternate stretches and releases of 0·2 mm, on extensions of several mm. The small stretches elicited responses which were larger than expected from the response to large stretches, and which were approximately the same size at different mean lengths of the muscle.

6. It is concluded that the tonic stretch reflex of the decerebrate cat

cannot readily be explained solely by the increase in Ia discharge produced by stretching, as usually believed. Instead, it is suggested that the group II afferent fibres from the secondary endings of the muscle spindle also play an important part in its production.

INTRODUCTION

In the classical stretch reflex of the decerebrate cat, forcible elongation of an extensor muscle causes it to contract for as long as the extension is maintained (Liddell & Sherrington, 1924, 1925). The receptors responsible for the reflex were originally quite uncertain, but more recently several lines of evidence have shown that activity in the group Ia fibres from the primary endings of muscle spindles leads to excitation of the α motoneurones of their own muscle (autogenetic excitation, Ruch & Patton, 1965). The Golgi tendon organs and the secondary endings of the muscle spindles are also excited by muscle stretch, but those in extensor muscles are generally believed to produce only autogenetic inhibition (Granit, 1955; Hunt & Perl, 1960; Ruch & Patton, 1965). Excitation of the spindle primary endings is therefore usually assumed to be entirely responsible for the excitatory component of both the phasic and the tonic parts of the stretch reflex. The present experiments cast doubt on this assumption by comparing the size of the tonic reflex elicited by muscle stretch with that of the maintained reflex contraction elicited in the same muscle by high-frequency vibration. Vibration powerfully excites the spindle primary endings, while having little or no effect on the secondary endings and the Golgi tendon organs (Granit & Henatsch, 1956; Bianconi & Van der Meulen, 1963; Brown, Engberg & Matthews, 1967). The present results show that the stretch reflex is relatively much stronger than would be expected from measurements on the response to vibration, and that the reflex responses to stretch and vibration do not occlude each other in the way which would be expected if they both depended solely upon the Ia pathway from the primary endings. It is suggested that the group II fibres from the secondary endings of the muscle spindle, as well as the Ia fibres, are responsible for the maintained stretch reflex of the decerebrate preparation (Matthews, 1969). The pre-existing evidence against this suggestion is reviewed in the Discussion, but is not felt to invalidate it.

METHODS

Preparation. The experiments were performed on cats decerebrated by intercollicular section of the mid-brain while under Fluothane (I.C.I.) anaesthesia. Sometimes a portion of cerebellum was also removed to increase the rigidity of the preparation. The main results were obtained using the soleus muscle in six cats with large stable stretch reflexes. Additional results were obtained in a further nine cats using the gastrocnemius and soleus muscles together. When soleus was studied alone the nerves to gastrocnemius were cut. In all experiments the hind limb and hip were, as far as possible, denervated except for the muscle studied (nerves cut given in Matthews, 1966). The skin of the back of the leg was elevated to form a pool containing liquid paraffin over soleus and its nerve; gastrocnemius was left covered with skin when it was studied.

The passive tension developed in the muscle by different amounts of stretching was determined at the end of each experiment after sectioning the muscle nerve. For soleus, the passive tension was also determined at various times in the course of the experiment by inhibiting any reflex contraction in it by repetitively stimulating the lateral popliteal nerve (Matthews, 1959*a*, 1966). All measurements of the size of the stretch reflex were determined by subtracting the passive tension produced by the same stretch from the myographically recorded tension. The largest stretches used extended the muscles up to approximately the maximum length that it could take up in the body with the ankle fully dorsiflexed. The initial length at which the muscle was left between stretches was usually 9 mm less than this. Stretches lasting 5–10 sec were repeated 2–4 times a minute. They were usually applied at 10 mm/sec.

Mechanical arrangements. The tibia was rigidly fixed by pins in either end. The Achilles tendon with a flake of bone was attached directly to an isometric myograph which was mounted on the end of a 'stretcher'. The stretcher consisted of a large electromagnet (Pye-Ling, V 50) controlled by position and velocity feedback to form a positional servomechanism. With it the muscle could be extended at a constant velocity by amounts up to 10 mm, and could also be vibrated longitudinally at frequencies of 50–300 Hz with a peak-to-peak amplitude of up to at least 200 μ. The compliance of the moving element of the stretcher was 0·2 mm/kg, which is small enough for the system to be considered isometric (Buller & Lewis, 1965, found the compliance of soleus tendon to be about 0·5 mm/kg). The myographe employed a silicon strain gauge, and its compliance was about 0·07 mm/kg. Its high-frequency response was deliberately restricted so that vibration of the muscle did not produce too large an oscillatory output in the tension record; this was otherwise liable to occur even when the myograph was not attached to the muscle. The restriction was produced electronically by a high-frequency filter with a corner frequency (3db attenuation) of 37 Hz. This frequency limitation should not have affected the recording of the relatively steady contractions which are the subject of the present work. The frequency of vibration was controlled by an oscillator. The amplitude of vibration was controlled by an attenuator which had been previously calibrated by microscopic observation. The stated amplitudes of vibration are accurate to within about 10 %, except that at 50 Hz they are about 20 % too high (cf. Fig. 1); this has not seemed worthy of further mention as it does not affect the results. The small amplitude sudden stretches (Fig. 8) were produced by supplying the stretcher circuit with slightly rounded square waves which rose and fell exponentially with a time constant of 33 msec. The present apparatus is significantly more isometric than that used in an earlier study (Matthews, 1966) and in addition, being under servo control, it allowed the muscle to be controllably stretched to a number of different lengths.

Electrical recording. In all the experiments on soleus its gross electromyographic activity was recorded with a pair of silver electrodes, separated by about 2 cm and placed on the belly of the muscle. This provided a continuous check on the presence of a stretch reflex, and could confirm that the stimulus used to inhibit the stretch reflex (see above) was completely effective. In three experiments on gastrocnemius and soleus combined, efferent nervous activity was recorded from a fine branch to gastrocnemius. The potentials were amplified with a capacity coupled amplifier

(Tektronix 122, frequency band set to 80 Hz–1 kHz) and displayed on an oscilloscope. The amplified potentials were also fed to an 'integrating' circuit constructed from monolithic operational amplifiers. This circuit first 'clipped' the spike record at an adjustable level so that only the top 80 % or so of each spike was transmitted, and the noise rejected. Next the transmitted portions of the spikes were summed by putting a charge proportional to the area of each into a condenser with a resistive leak, arranged so that any potential on the condenser decayed with a time constant of 0·1 sec. The resulting summed potential was smoothed by a low-pass filter with a cut-off frequency of 17 Hz. Thus this circuit gave a continuous, reasonably smooth, record of the average efferent discharge which could be recorded on slowly moving paper; but it was never used without also recording the spikes which were being summed.

RESULTS

Comparison of the reflex response to increasing extension with that to increasing frequency of vibration

Figure 1 shows the response of a single muscle to two different extensions and to two different frequencies of vibration. Nearly all of the tension produced by the stretching was due to an active reflex contraction of soleus, for very little increase in tension was produced when the same extensions were applied after cutting the nerve or on inhibiting the stretch reflex (see Methods). After a small initial fall in tension on completion of the dynamic phase of stretching, the stretch reflex is seen to remain at an approximately constant level throughout the 6 sec the extension was maintained. This is the tonic stretch reflex as originally described by Liddell & Sherrington (1924) and which should not be equated with the tendon-jerk which reaction they considered as 'only a fractional manifestation' of the 'more comprehensive stretch reflex'. The amplitude of the vibration applied in the lower records was 150 μ (peak-to-peak) and this also is seen to elicit a maintained reflex response. Altering the amplitude of vibration between 100 and 200 μ while keeping the frequency constant produced no appreciable change in the size of the resulting reflex response (see also Matthews, 1966, Fig. 9). It may be presumed that this was because the vibration was then sufficiently powerful to force every primary ending in soleus to fire an impulse on each cycle of the vibration as has been observed to occur experimentally by recording from single afferent fibres (Brown *et al.* 1967); altering the amplitudes of vibration can then produce no change in the Ia input to the spinal cord.

Figure 2 shows more fully the effect on the strength of the reflexly induced contractions of altering the parameters of stimulation. The measurements were made 2 sec after the stretch or vibration had been maintained and so give the more or less steady 'tonic' response. The tension plotted for the stretch reflex is the 'active' tension left after subtracting the 'passive' tension produced by the same extensions in the absence of reflex.

The tension plotted for the vibration response is the increase in tension above that occurring immediately before each period of vibration. The stretch reflex of Fig. 2*A* increased approximately linearly with the extension (Granit, 1958; Matthews, 1959*a*), with a slope (stiffness) of 90 g/mm, which is a very typical figure for a preparation with good rigidity. The

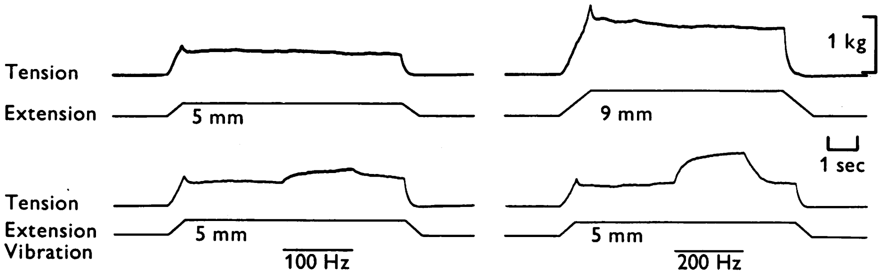

Fig. 1. Myographic records of the reflex responses of soleus to stretch and to vibration. Above, tension developed on simple stretching; below, on stretching and then vibrating. The passive tension developed by the stretching was a relatively small proportion of the whole (10 g for 5 mm extension, and 120 g for 9 mm). The extension and vibration markers are diagrammatic. The peak-to-peak amplitude of vibration was 150 μ, which produced a maximal response to vibration. (Decerebrate cat without cerebellectomy, and with no appreciable 'spontaneous' contraction of the muscle at the initial length.)

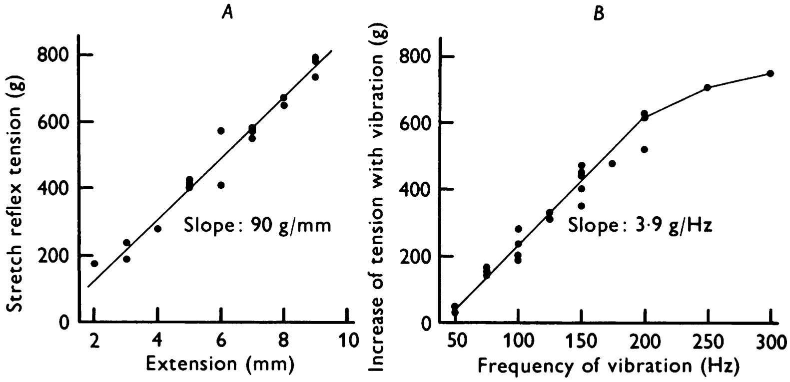

Fig. 2. Graphical comparison of the reflex responses to stretch and to vibration. *A*, the relation between the active tension developed in the tonic stretch reflex, and the extension applied to the muscle. *B*, the relation between the increase in tension, above that due to stretch alone, and the frequency of vibration. (The vibration was applied at an extension of 5 mm which elicited a stretch reflex of approximately 400 g. The stretch reflex was measured 2 sec after the final length of the muscle had been reached. The 'increase of tension with vibration' is the tension measured during the vibration 2 sec from its beginning, less the tension occurring immediately beforehand. Amplitude of vibration, 150 μ. Same experiment as Fig. 1).

vibration response of Fig. 2*B* increased approximately linearly with the frequency of vibration over the range 50–200 Hz. The slope of the linear portion of the graph is 3·9 g/Hz, which is slightly larger than the values found before (Matthews, 1966). Assuming that the vibration was powerful enough to drive every Ia fibre of soleus at the frequency of vibration and was not appreciably exciting other kinds of receptor (see Discussion), this figure may be transmuted into 3·9 g of reflex per impulse/sec average increase in Ia firing for each of the muscle spindles of soleus (i.e. 3·9 g per maximal Ia volley per second). The data of Fig. 2*B* may thus be used to estimate the increase in Ia firing required to produce a stretch reflex of the stiffness observed in Fig. 2*A*. This works out at 23 impulses/sec increase in the discharge of each Ia fibre for each mm of extension (i.e. 90/3·9). In other words, 23 impulses/sec/mm multiplied by the reflex responsiveness of 3·9 g/Hz gives the observed reflex stiffness of 90 g/mm. Table 1 shows the values similarly obtained in a number of different preparations, and using different combinations of the ankle extensors. The values of Ia sensitivity to extension required to produce stretch reflexes of the observed

TABLE 1. Comparison of the stiffness of the stretch reflex with the vibration responsiveness for a number of preparations. The 'required' Ia sensitivity is the increase of Ia firing/mm of extension needed to explain the stretch reflex solely in terms of increasing Ia discharge with extension. C, after the muscle, indicates that the observations were made after partial cerebellectomy. In two experiments observations were made both before and after cerebellectomy; the serial numbers of these are 3 and 7, and 4 and 6

Serial no. of observation	Muscle	Stretch reflex stiffness g/mm	Vibration responsiveness g/Hz	Required Ia sensitivity impulses/sec/mm
1	Soleus	81	2·4	34
2	Soleus	82	4·3	19
3	Soleus	100	8·5	12
4	Soleus	90	3·9	23
5	Soleus (C)	104	2·4	42
6	Soleus (C)	132	1·4	95
7	Soleus (C)	137	1·5	91
8	Soleus (C)	162	3·6	45
9	Medial gastrocnemius	150	1·9	79
10	Medial gastrocnemius	155	1·6	97
11	Gastrocnemius soleus	210	2·1	100
12	Gastrocnemius soleus	232	6·2	37
13	Gastrocnemius soleus (C)	485	14·2	34
14	Gastrocnemius soleus	535	4·9	110
15	Gastrocnemius soleus	278	3·9	71
16	Gastrocnemius plantaris soleus	365	3·1	118
17	Gastrocnemius plantaris soleus	602	3·5	172

stiffnesses range from 12 to 172 impulses/sec/mm, with a modal value of 71 impulses/sec/mm.

At first sight many of the values of the Ia firing required to produce the observed stretch reflex do not appear unreasonable, particularly if attention is restricted to the results for soleus which are all below 100 impulses/sec/mm. The soleus muscle is both structurally and functionally a simpler unit for the purpose of the above estimates than the combination of several ankle extensors, and the results obtained with it are therefore less open to equivocal interpretations. In fact, however, the 'required' values of Ia firing in Table 1 are considerably greater than those that have been found experimentally in comparable preparations. Granit (1958) found an average of 3·5 impulses/sec/mm for twenty 'soleus spindles' (presumably Ia afferents) in the decerebrate cat with intact ventral roots and partly intact dorsal roots. Matthews & Stein (1969), using the same preparation with identified Ia fibres and severed dorsal roots, found values ranging from 2 to 5 impulses/sec/mm (the published measurements were made 30 sec after completion of stretching, but similar values were obtained when the measurements were made after 1–2 sec). Individual Ia afferents in the decerebrate sometimes have sensitivities of slightly over 10 impulses/sec/mm (Eldred, Granit & Merton, 1953; Fig. 15; Jansen, J. K. S. & Matthews, P. B. C., unpublished), but even if such values applied to all Ia fibres in the present preparations their stretch reflexes would still not be explicable solely in terms of Ia excitation. A possible explanation for the contradiction is that the tonic stretch reflex depends not only upon the Ia fibres, but also upon some other group of fibres which are excited by the stretching but which are not excited by the vibration; the stretch reflex would then obviously be rather more powerful than expected from combining the present results with vibration and the previous results on the Ia sensitivity to extension. The only such afferents known are the group II fibres from the secondary endings of the muscle spindles. Contrariwise, if these group II fibres were to have had their conventional flexor reflex action in the present preparations, the stretch reflex should have been weaker than expected from the results with vibration.

Further details of measurements. In the preparations without cerebellectomy there was usually no 'spontaneous' contraction of the muscle at the initial length used, and the stretch reflex appeared at some threshold extension (cf. Matthews, 1959*b*). This limited the range over which the stiffness of the stretch reflex was determined; all the values given in Table 1 were determined over at least 3 mm of extension. After cerebellectomy the soleus was usually contracting at the initial length, and the reflex stiffness could be determined over a wide range. The larger the initial stretch reflex contraction the lower appeared to be the frequency at which the vibration response ceased to increase proportionally with the frequency of vibration (cf. Fig. 1). The origin of this saturation was not investigated, but it was possibly in the efferentdischarge or in the muscle, as the active tension due to the combined stretch and vibration was then often appreciably over half that which soleus could develop on tetanic activation at the same length on stimulation at 30/sec. The values of vibration responsiveness given in Table 1 were determined over a range of at least 100 Hz. The amplitude of vibration used for these determinations was usually 150 μ, and it was repeatedly checked that the amplitude was sufficient to cause a maximal reflex response (i.e. the response did not vary by more than about 10 % on altering the amplitude of vibration by ± 50 μ). This checking was done both subsequently by measurement of records, and also more effectively in the course of the experiment by observing the myographic responses to successive stimuli superimposed on a cathode ray tube with a long after-glow.

The determination of 'active' tension by subtraction of 'passive' tension from the total myographically recorded tension may be open to doubt when the active tension is only a small proportion of the whole. In none of the experiments was the active tension less than half the total myographically recorded tension, and often it comprised over 80 % (cf. Figs. 1 and 6), so any slight failure of the assumed simple compounding of active and passive tensions would not have significantly influenced the results.

Time course of responses. Regular differences were seen in the forms of myographically recorded responses to stretch and to vibration (Fig. 1). On stretching, there was an abrupt initial fall in tension immediately on completion of the dynamic phase of stretching, followed by a variable slower fall occurring over several sec and sometimes preceded by a slight rise (Liddell & Sherrington, 1924; Matthews, 1959*a*; Takano, 1966). In contrast, on starting a period of vibration the tension rose over about 1 sec to an approximate plateau value which was maintained for many sec, though sometimes with a slight upwards creep. The final tension reached in the plateau was approximately the same as that reached when the vibration started before the stretch and continued throughout its application. In previous experiments (Matthews, 1966), about 1 sec from the beginning of vibration the tension sometimes overshot its final equilibrium value. This has not been observed in the present experiments and was probably an indirect result of excessive compliance in the earlier stretcher (0·8 compared with 0·2 mm/kg). The relatively slow build up of tension at the beginning of vibration probably depends largely upon the way in which muscle responds to a constant low-frequency efferent discharge, for on recording from single α fibres in the ventral roots the discharge tends to adapt, rather than to augment, during a period of vibration (Brown, Lawrence & Matthews, 1968; Anastasijević, Anojčić, Todorović & Vučo, 1968). In some preparations the stretch reflex decayed rather markedly over the first few sec (i.e. as in Fig. 11*d* of Matthews, 1959*a*), while the vibration response kept its usual form. This suggests that the decay of the stretch reflex was more likely to have been due to receptor adaptation than to any central change. On release of extension the tension falls much more rapidly than on cessation of vibration, but this throws no light on the central reflex mechanisms, because when a muscle is shortening it develops considerably less tension than it does under isometric conditions with the same degree of efferent activation.

Absence of occlusion between the reflex responses to stretch and vibration

Taken alone, the discrepancy between the experimentally determined Ia sensitivities to extension and those required to explain the stretch reflex might not be judged an adequate reason for discarding a belief in a unique excitatory role for the Ia fibres in the stretch reflex. This is particularly so as the two sets of figures were obtained in different experiments. More compelling evidence was obtained on studying the interactions between the reflex effects of stretch and vibration. If both reflex responses depended solely upon the Ia pathway a rather simple form of occlusion should be found between them, for they would be the same reflex. Such occlusion, however, did not occur. This is illustrated in Fig. 3. On the left, the muscle was vibrated at 200 Hz after extending it by 4 mm. During the combined stimuli of stretch and vibration the muscle developed 750 g active tension. The amplitude of vibration was adequate to cause a maximal reflex response, and so the reflex response to an input of 200/sec in each of the Ia fibres of soleus is shown to develop about 750 g tension. On the right, is shown the response to an extension of 9 mm, which on its own elicited a stretch reflex developing 740 g. If the Ia fibres were the sole origin of the stretch reflex one would conclude that the larger extension by itself excited the Ia fibres to fire at about 200/sec. In that case, vibration at 200 Hz would produce no appreciable further increase in the afferent input, but would merely synchronize the discharge on to the vibration as has been observed experimentally (Brown *et al.* 1967); little or no increase in reflex output would then be expected. In fact, the records show that the vibration produced a slightly larger reflex response at the longer length than at the shorter. As rather little passive tension was produced by the stretching this surprising result is readily apparent on direct inspection of the records without the need for measurement. It cannot be attributed to any difference between the reflex responses to synchronized and to unsynchronized afferent volleys, since the total active tension is much greater during vibration at the longer than at the shorter length, yet in both cases the Ia afferent input should have consisted of synchronized volleys at 200/sec. The present finding would, however, be quite unremarkable if much of the tonic stretch reflex were due to a spindle group II input. The increase in Ia firing with extension could then be comparatively modest, as found experimentally (i.e. 3 impulses/sec/mm), and so the increase in Ia firing produced by vibration would be rather little different at the two extensions. The reflex effects of stretch and vibration might then be expected to summate

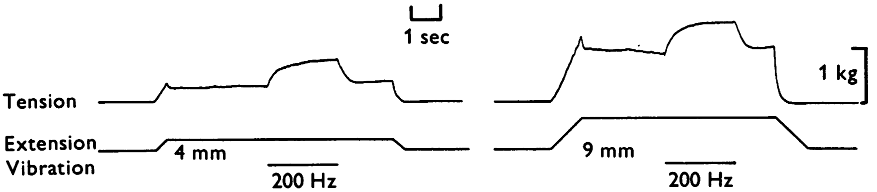

Fig. 3. Myographic records showing the effect of applying the same vibration at two different lengths of the muscle. (Same experiment as Figs. 1 and 2. Amplitude of vibration 150 μ.)

without obvious gross occlusion, as seen in Fig. 3 (i.e. the initial frequencies of firing might have been about 35 and 50 impulses/sec at the two lengths, whereas the frequency of vibration was 200 Hz). The slight increase in the vibration response at the greater extension could well be due to secondary factors such as an increase in the strength of the muscle with extension (see later), which might also mask the slight degree of occlusion which would still be expected.

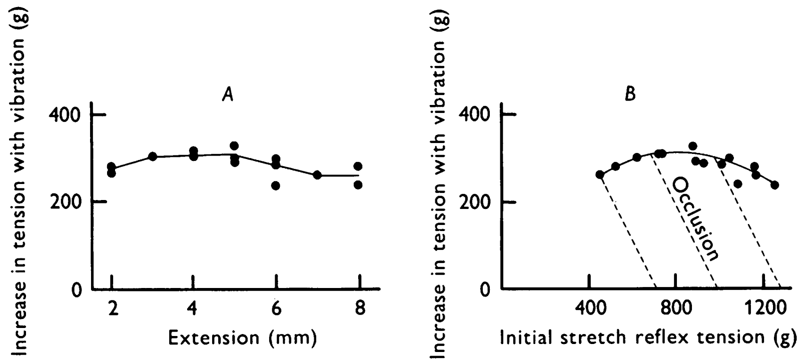

Fig. 4. The absence of occlusion between the reflex responses to stretch and to vibration. *A*, the response to vibration of 150 μ amplitude at 200 Hz plotted against the extension applied to the muscle. *B*, the same responses plotted against the initial stretch reflexes elicited by the various extensions. The continuous lines are drawn through the points to show their general arrangement. The dashed lines labelled 'occlusion' show what would happen, on taking three different places as the starting point, if a given increase in the stretch reflex led to an equivalent decrease in the response to vibration. (Same experiment as Figs. 1, 2 and 3 but after ablation of the cerebellum, which caused an increase in 'tone' and a contraction of the muscle at its initial length developing about 200 g.)

Figure 4*A* shows a more systematic demonstration of the constancy at different muscle lengths of the additional reflex contraction elicited by vibration. This data was obtained from the same preparation as that illustrated in Fig. 3, but after the stretch reflex had become larger following ablation of part of the cerebellum. Fig. 4*B* shows the same results replotted against the initial stretch reflex in order to emphasize the absence of occlusion. On any hypothesis, an increase in Ia discharge produced by increasing extension must lead to a decrease in the additional Ia input produced by vibration of a fixed frequency. On the classical hypothesis in which the stretch reflex output simply reflects the Ia input, any increase in the stretch with extension should lead to equivalent decrease in the vibration response, when this is measured above the pre-existing stretch reflex tension. In other words the vibration response should be 100% occluded by the stretch reflex as shown by the dashed lines in Fig. 4*B*, which for the sake of arbitrary illustration take different places as their starting point. The experimentally observed response to vibration is clearly not occluded in this manner, thus suggesting that the hypothesis which predicted such occlusion is false. Such results were typical, and were obtained in preparations both with and without 'spontaneous' contraction at the initial length, and on using the combined gastrocnemius and soleus muscles as well as with the soleus alone.

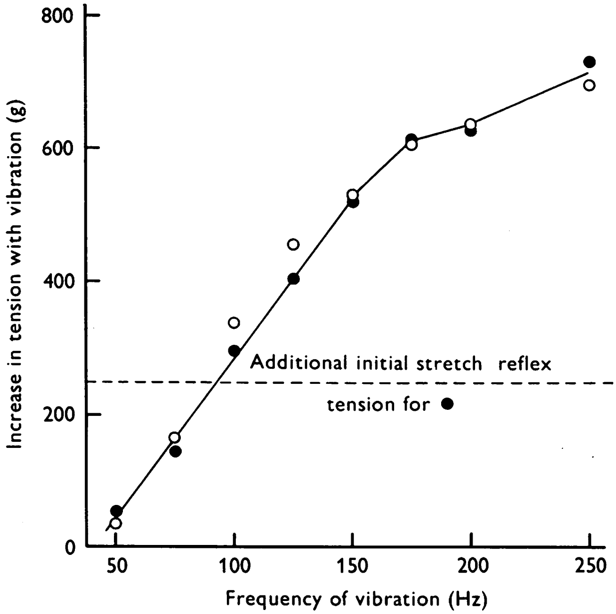

Fig. 5. The relation between the reflex response and the frequency of vibration determined at two different extensions of the soleus muscle. ○, determined during an extension of 6 mm which elicited a stretch reflex of 100 g. ●, determined during an extension of 9 mm which elicited a stretch reflex of 350 g. The dashed line shows the amount by which the stretch reflex elicited by the larger extension exceeded that elicited by the smaller extension. (Decerebrate cat without cerebellectomy, and without contraction of the muscle at the initial length.)

The absence of occlusion between the reflex responses to stretch and vibration did not depend upon any particular choice of vibration frequency. This is illustrated in Fig. 5, which shows the relation between the frequency of vibration and the resulting reflex response determined at two different lengths of the muscle. The dashed line shows the additional initial stretch reflex tension elicited by the larger extension. On the classical hypothesis, the points obtained at the larger extension (●) would be expected to be displaced downwards by approximately this amount, whereas in fact they do not differ systematically from those obtained at the lesser extension (○). This again, however, is very much what would be expected if much of the tonic stretch reflex is due to the spindle group II fibres. The two reflexes could then combine with relatively little occlusion, as found when other reflexes are combined with the stretch reflex (Matthews, 1959*b*). This was also found in the present experiments when the vibration was applied to a soleus which was contracting by different amounts in response to squeezing the opposite foot.

Comparison of the vibration response with that due to stimulation of the medial gastrocnemius nerve

Increasing extension of soleus leads to an increase in its contractile strength, particularly when it is contracting in an unfused tetanus (Granit, 1958; Matthews, 1959*a*; Rack & Westbury, 1969). It might be suggested that this had somehow concealed an occlusion between the responses to stretch and vibration, because they were assessed by means of the tension developed in the muscle rather than by direct measurement of the efferent discharge. For example, an efferent output elicited by vibration and which decreased with extension might conceivably be compensated by an appropriate increase in muscular strength, so that the additional tension produced by the vibration remained the same in spite of an increasing initial stretch reflex tension. It would be surprising, however, if this could cause exact cancellation of occlusion over a range of frequencies and lengths. Significantly increasing muscle strength with extension would be expected to manifest itself as an increase in the slope of curves of reflex response against the frequency of vibration, which did not occur (Fig. 5). More direct evidence against this theoretical possibility was obtained by comparing the response to vibration with that elicited by repetitive stimulation of the nerve to the medial head of gastrocnemius. This provided an afferent input which was independent of the extension applied to the soleus.

Figure 6 illustrates the results of comparing the two reflexes at three different extensions. The nerve stimulation evoked a maintained reflex contraction (Alvord & Fuortes, 1953; Matthews, 1959*b*), probably by exciting Ia fibres. The vibration frequency was chosen so that the two kinds of reflex were approximately the same size when the extension was 5 mm. The records show that they still remained about the same as each other at the other two extensions. In this experiment the stretch reflex was large, and so on the classical hypothesis the vibration response should have been completely occluded at the larger extensions. If the occlusion had somehow been concealed by increasing muscle strength with extension, the response to nerve stimulation should have increased with the extension, since its afferent input remains constant; but it did not.

Figure 7 shows a similar result from a different preparation in which there was no 'spontaneous' contraction of the muscle at the initial length. Figure 7*A* demonstrates the similarity in size of the two reflexes over a range of extensions. Figure 7*B* shows the absence of occlusion for either reflex using the same presentation as in Fig. 4*B*. Similar results were obtained in all five experiments on soleus in which nerve stimulation was used. These findings permit two linked conclusions. First, any variation of muscular strength with extension does not manifest itself under the present conditions, and in the range of lengths studied. A gross occlusion between the reflex effects of stretch and vibration is therefore

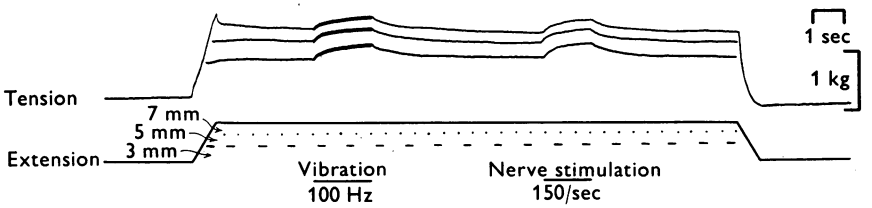

Fig. 6. Myographic records comparing the reflex responses of soleus to its vibration with those to electrical stimulation of the nerve to the medial head of gastrocnemius. Separate records were obtained for extensions of 3, 5 and 7 mm and subsequently superimposed. The passive tensions produced by the extensions were small (25, 50 and 90 g for extensions of 3, 5 and 7 mm respectively. Decerebrate cat with cerebellectomy. Muscle developed approximately 200 g wt. tension 'spontaneously' at the initial length. Amplitude of vibration 150 μ).

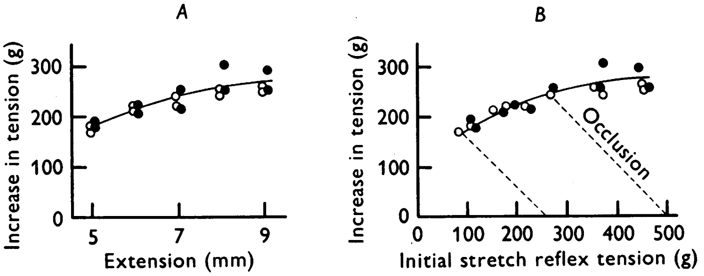

Fig. 7. The similarity of behaviour on increasing extension, and the absence of occlusion, shown graphically for the responses to vibration and to nerve stimulation in another preparation (no cerebellectomy, no contraction at the initial length). ○, reflex response of soleus to vibration of 150 μ at 95 Hz, ●, response to stimulation of the nerve to the medial head of gastrocnemius at 250/sec. *A*, reflex plotted against the extension. *B*, reflexes plotted against the pre-existing stretch reflex elicited by the various extensions. As in Fig. 4, the dashed lines show the decrease in the reflexes which would occur if they were quantitatively occluded by the stretch reflex.

unlikely to have been concealed by depending upon myographically recorded responses. Secondly, the additional afferent input produced by vibration is likely to have been approximately the same at different extensions, for the vibration response behaved in the same way as the response to nerve stimulation, when the afferent input was certainly constant with extension. This supports the suggestion that in the present experiments the Ia discharge only increased slightly with muscle extension, as found by recording from single fibres in earlier experiments (Granit, 1958).

The various responses were normally studied with the soleus close to the maximum length which it can take up in the body. Its contractile strength is then approximately constant with small variations of length for a wide range of frequencies of activation (Rack & Westbury, 1969), and so the above results are not surprising. When vibration and gastrocnemius nerve stimulation were applied with the muscle at shorter lengths (i.e. more than about 7 mm below physiological maximum) the reflexly elicited contractions usually became much less powerful, and the slope of the relation between tension and the frequency of vibration was smaller. This reduction in reflex response seems likely to have been due to a decrease in the contractile strength of the muscle. In addition, the Ia fibres may have been less effectively excited by the vibration when the muscle was short. At the other extreme, when vibration and nerve stimulation were applied at lengths at which there was already a large initial stretch reflex they might be slightly smaller than at shorter lengths. This may have been an occlusion resulting from the limited total strength of the muscle. Sometimes, however, this occlusion was slightly greater for the response to vibration than to nerve stimulation, suggesting that there had also been some significant occlusion on the afferent side of the reflex arc.

The nerve to the medial head of gastrocnemius was stimulated at 100–250/sec with shocks of the order of strength needed to excite the Ia fibres (100 mV, 100 μsec square waves). The excitatory effect on soleus of this nerve stimulation had a definite threshold, increased to a maximum for stimuli of 1·2–1·5 times threshold and then decreased with further increase of stimulus intensity to be replaced by an inhibition. An increase in the amount of excitation on increasing the stimulus strength above 2 × threshold (i.e. group II threshold; Eccles, R. M. & Lundberg, 1959*a*) did not occur in any of the five preparations studied. The excitatory effect with weak stimuli was presumably mediated by group Ia fibres, but even the weakest stimuli may also have excited fibres with an inhibitory action on the soleus α motoneurones (i.e. Ib fibres orthodromically and α motor fibres antidromically). The time course of the reflex contraction elicited by the nerve stimulation was usually similar to that of the vibration, as it was in Fig. 6.

The response to small sudden stretches

Another way of testing the importance of any variation of muscle strength with length is to alternately stretch and release the muscle by a small amount at different mean extensions. Single fibre recording has shown that in the decerebrate cat with intact motor outflow such stretching usually produces an approximately constant change in Ia firing when applied at different lengths of the muscle (Matthews & Stein, 1969).

Figure 8 shows that such small amplitude stretching and releasing produced a change in the reflex tension which was also virtually independent of the mean length of the muscle (the passive tension produced by the stretching may be ignored; see legend). Similar results were obtained in four out of the six preparations in which the matter was studied, and further supports the idea that any variation of muscle strength with muscle length is unimportant in the interpretation of the findings described earlier.

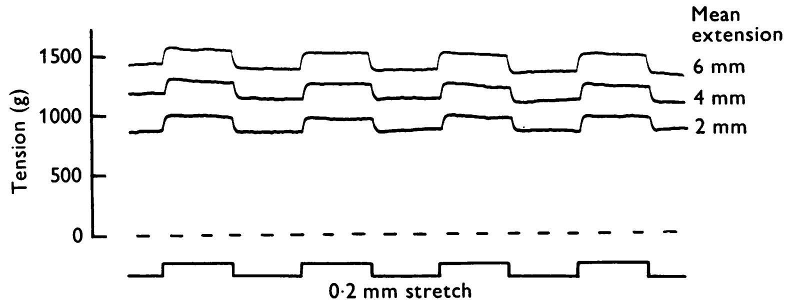

Fig. 8. Myographic records of the reflex responses to alternately stretching and releasing the soleus muscle by 0·2 mm when it was at different mean extensions. Each stretch or release was maintained for 1 sec. Separate records were obtained for the different extensions and subsequently superimposed. The change in passive tension produced by the small amplitude stretching was inappreciable (less than 5 g) and so also were the passive tensions developed by the larger mean extensions (15, 35 and 75 g for extensions of 2, 4 and 6 mm respectively. Same experiment as Fig. 6, but with about 300 g active tension at the initial length).

Figure 8 shows a further point of interest, namely the large size of the reflex elicited by the small amplitude stretching relative to that elicited by large amplitude stretches. The peak tension due to the small stretch applied at a mean extension of 4 mm was nearly as great as the trough tension at the longest length, and the trough tension at 4 mm was nearly the same as the peak tension at the shortest length. Alternate stretches and releases of 0·2 mm changed the tension by approximately 120 g, whereas increasing the mean extension by 2 mm increased the mean tension by 250–300 g. Thus small amplitude stretching was about four times as effective a stimulus, judged by the response to unit displacement, as was the large amplitude stretching. This was not unexpected, as it has recently been found that the Ia fibres behave similarly in comparable preparations (Matthews & Stein, 1969). Indeed, the sensitivity of Ia fibres, expressed in impulses/sec per mm extension, may be up to 45 times greater for small stretches than for large ones. Figure 9 shows the effect on the reflex of varying the amplitude of stretching. As for Ia fibres, there is an initial approximately linear relation between stimulus and response at small amplitude, but the active reflex tension then fails to increase proportionately with the stimulus. The slope of the line fitting the initial points in Fig. 9 is 625 g/mm, whereas immediately beforehand the stiffness of the stretch reflex elicited with large stretches was 174 g/mm. Similar results were obtained in five out of the six experiments on soleus. The approximately linear range extended to 0·2–0·4 mm stretch. The ratio of the reflex sensitivity to small and to large stretches was between 2 and 4. Thus the stretch reflex is shown to be relatively more effective at resisting small perturbations about a given length, than it is at resisting large disturbances. This has obvious functional implications.

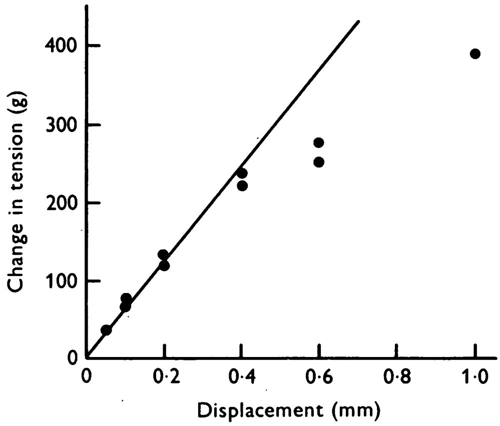

Fig. 9. The relation between the change in active reflex tension and the extent of the displacement, for alternate small stretches and releases superimposed on a mean extension of soleus of 5 mm. The straight line is drawn through the origin and the points for displacements of 0·2 mm and below. (The measurements were averaged over several cycles, and ignored any initial phasic reflex response lasting less than 0·3 sec. Same experiment as Fig. 8.)

The difference in the sensitivity of the stretch reflex to small and to large disturbances is not, however, as great as would be expected from the earlier work on the Ia fibres. This may merely mean that preparations which had good stretch reflexes also had primary endings which behave relatively linearly over a wide range of amplitudes of stretching, conceivably due to appreciable static fusimotor activation. On the other hand, if the stretch reflex depends upon both kinds of spindle afferent, varying the amplitude of stretching would have less effect on the sensitivity of the stretch reflex than on that of the Ia fibres, for the group II fibres give a linear response over a wide range of amplitudes (Matthews & Stein, 1969). The simple addition of a linear signal from the secondary endings and a highly non-linear signal from primary endings would produce the limited degree of non-linearity presently observed in the stretch reflex (Fig. 9).

In one experiment on soleus a linear input-output was found for stretches of up to 1 mm, the largest amplitude tested. This appears similar to the results of Poppele & Terzuolo (1968), who stretched the whole triceps surae sinusoidally at various frequencies by up to 2 mm total extent. In two of the present experiments on the gastrocnemius and soleus muscles the effect of small stretches was investigated. In one, the response remained linear for stretches up to 1 mm; in the other, the findings were similar to those usually obtained on soleus. On direct recording, apparently in different preparations, Poppele & Terzuolo found that the response of Ia fibres ceased to be linear for stretches above 0·05–0·1 mm total extent. They suggested that the factor mainly responsible for the greater linear range of the reflex was a 'distribution in thresholds' of different α motoneurones. However, the occasional wide linear range for the stretch reflex seems equally likely to reflect an occasional similar behaviour of the Ia discharge in the decerebrate cat, possibly resulting from powerful static fusimotor activation (cf. Brown *et al.* 1969). It should be noted, finally, that the present experiments do not demonstrate strict linearity of response to the smaller stretches. The measurements were made directly from myographic records like those displayed, and without the systematic averaging needed to compensate for any spontaneous changes which occurred in the stretch reflex elicited by the pre-existing large extension. Finally, it may be noted that because of their size there seems little doubt that the changes in muscle tension produced by the small displacements were mediated reflexly, rather than by any effect of the displacement on the contractile strength of the muscle. This was confirmed in one experiment in which the muscle was alternately stretched and released by 0·2 mm at 1 sec intervals while the muscle was contracting tetanically in response to stimulation of its nerve at 10–40/sec; any maintained change in tension was then inappreciable ($< 5\%$).

Sampling the efferent discharge

The arguments presented so far have been based on measurements of contractile tension reflexly elicited by various stimuli. An alternative approach is to record the actual efferent discharge, for this largely circumvents any uncertainty introduced by variation of the strength of the muscle with its length. This has been done in three experiments using the gastrocnemius and soleus muscles combined. A sample of the efferent discharge was recorded from a thin branch of the nerve to the lateral head of gastrocnemius, while leaving the rest of the innervation of gastrocnemius and soleus intact. The branch used was the naturally occurring filament which leaves the rest of the nerve on its entry to the muscle. The branch was cut peripherally and dissected free for about 1 cm to allow monophasic recording. With this preparation a number of unitary spikes of fairly uniform size were readily recorded on either stretch or vibration of the muscle. These may be presumed to have been from α motor fibres. Smaller, spontaneously firing, spikes were seen on increasing the amplification, and may be presumed to have been from fusimotor fibres.

The first finding of interest was that, in so far as the discharge of single units could be followed, those which were excited by simple extension of the muscle regularly increased their frequency of firing on vibrating the muscle. This agrees with earlier experiments in which the discharge of single α fibres was recorded from ventral root filaments (Brown *et al.* 1968), and disposes of the possibility that simple stretch and high-frequency vibration excite separate populations of motoneurones.

The second finding was that the combined stimuli of stretch and vibration could excite a greater efferent discharge when the stretch was increased and the vibration remained the same. This is illustrated in Fig. 10, which shows both a direct recording of spikes (below) and an 'integrated' record, on a slower speed, measuring the total efferent discharge in the filament (above). This finding is not readily explained if the stretch reflex is solely due to group Ia input, but is that expected if the stretch reflex is due to both kinds of spindle afferent. The Ia discharge should have been the same at both extensions, namely at the frequency of the vibration, for the amplitude of vibration was adequate to cause a maximal reflex response of the muscle. The group II input, however, would have been greater at the greater extension, so that if it produced autogenetic excitation the efferent discharge would be greater during vibration at the greater length, as observed. On the other hand, if the group II input had produced inhibition the afferent discharge would have been reduced at the greater length. Similar results were obtained in all three experiments.

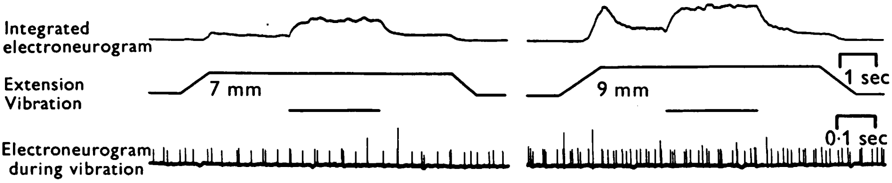

Fig. 10. The efferent discharge sampled by recording from a cut branch of the nerve to the lateral head of the gastrocnemius. The rest of gastrocnemius and soleus remained innervated, and were connected to the stretcher. The 'integrated' records were obtained with a 'leaky capacitor' type of circuit with a time constant of decay of 0·1 sec. The vibration was 150 μ amplitude at 200 Hz for both records. The portion of electroneurogram shown below started 1 sec after the beginning of a response to vibration similar to that shown above, but was recorded slightly earlier on a faster film speed. Records retouched.

The small number of units responding from the filament made this type of recording unsuitable for a systematic quantitative study. The recruitment of a single extra fibre could appreciably increase the size of the integrated response, which thus tended to vary in discrete steps rather than continuously. The effect shown in Fig. 10 could therefore not be shown with every small increase in the extension. It is also uncertain whether the motor fibres in a cut branch provide a random sample of all the excited motoneurones, for they had been deprived of excitation by afferent fibres arising from the same region of the muscle. Appropriate recording of the electromyogram might allow measurement of the total efferent discharge to the muscle which was actually contracting. However, the polyphasic potentials which were recorded in the present experiments with surface leads do not sum in the same way in the presence and absence of vibration (Matthews, 1966), and were not deemed suitable for quantitative study.

DISCUSSION

The experiments have shown that the relative strengths, and the modes of interaction, of the reflex responses of the same muscle to stretch and to vibration largely preclude the usual explanation of the stretch reflex. The various findings would, however, all fall into place if the stretch reflex arises not only from the Ia fibres, but also from some other group of fibres which are also excited by the stretching, but which are not excited by vibration. The only possible such afferents are the group II fibres from the secondary endings of the muscle spindles, for no other known receptor has the right properties to fill the gap. The spindle secondary endings, moreover, seem well suited to help mediate the tonic stretch reflex, for they adapt very slowly and discharge at a frequency directly related to any applied extension. The Golgi tendon organs are excluded by their behaviour, as they respond to the amount of active tension in a muscle and not to its length (Jansen & Rudjord, 1964; Houk & Henneman, 1967), and should be excited equally by a certain contraction irrespective of whether it was evoked by stretching or by vibrating the muscle. On the current belief that they produce autogenetic inhibition, tendon organ activity would have the effect of reducing all the reflex responses and thereby helping to counteract any vibration of contractile strength with muscle length (Matthews, 1959*a*, 1967). Even if they were supposed to produce autogenetic excitation, their action would merely serve to increase the responses to both stretch and vibration from what they otherwise would be (i.e. positive feed-back) and this would still not explain the present results. The receptors supplied by group III and by non-medullated afferents are not excited by stretching a muscle or by its contraction (Bessou & Laporte, 1958, 1961; Iggo, 1961; Paintal, 1960), and so should play no part in modulating the present reflex responses.

The reflex responsiveness to a group II input required to explain the present findings may be roughly estimated from the data of Table 1. Suppose the typical stretch reflex of soleus is taken to have a stiffness of 100 g/mm, the typical responsiveness to vibration to be 4 g/Hz and equivalent to 4 g/impulses/sec of maximal Ia input, and the sensitivity of both primary and secondary afferents to be 5 impulses/sec/mm. Then 20 g/mm of the stretch reflex would be due to the Ia input, leaving 80 g/mm to be explained by the group II input. This would require the reflex responsiveness to the group II input to be 16 g/impulse/sec, or four times the value for the Ia input. Reduction of the assumed spindle sensitivity to 3 impulses/sec/mm would increase the figure for the group II reflex responsiveness to 29 g/impulse/sec, or seven times the Ia value. If the Ia reflex responsiveness were smaller than the figure assumed above, the relative importance of the group II input would be increased, but the absolute value of the required reflex responsiveness would be only slightly increased. These estimates assess the importance of the group II activity solely for the maintained stretch reflex produced by large amplitude stretches. In phasic stretch reflexes, or in tonic reflexes elicited by small amplitudes of displacement, the Ia input would probably be relatively more important than the group II input, because the primary endings are much more sensitive to such stimuli than are the secondary endings. It is also possible that differences in the temporal summation occurring in the reflex centres for the two kinds of input further influence their relative importance in tonic and phasic stretch reflexes. The above estimates seem intrinsically quite reasonable, and it may be provisionally concluded that in the decerebrate cat the spindle group II fibres are responsible for the major part of the tonic stretch reflex.

Receptor specificity of vibration

Partly for ease of presentation, two basic assumptions have been used without question in the development of the argument. The first assumption is that vibration of the amplitude used (usually 150 μ) was sufficiently powerful a stimulus to 'drive' virtually every Ia fibre of the muscle at the frequency of the vibration. The second assumption is that vibration of this amplitude did not significantly excite any other kind of afferent fibre. These assumptions are examined below, with the conclusion that the first is more securely based than the second. However, provided the first assumption is reasonably correct, any doubt in respect of the second does not invalidate the main conclusion that the stretch reflex cannot be due solely to Ia activity, for if it were there should still have been occlusion between the responses to stretch and vibration.

The internal evidence in favour of both assumptions is the finding that increasing the amplitude of vibration from 100 to 200 μ usually had little or no effect on the size of the resulting reflex response (Matthews, 1966). This is what would be expected if the 100 μ vibration was adequate to drive all the Ia fibres, and if the increase to 200 μ did not excite any other afferents with a significant reflex action on the muscle. The first assumption is further supported by the earlier recordings from single Ia afferents (Brown *et al.* 1967). When the soleus was not contracting and when there was no fusimotor activity, all Ia fibres could be driven over a wide range of frequencies by amplitudes of vibration of 25–50 μ provided the muscle was adequately stretched. Fusimotor stimulation lowered this figure to about 10 μ for the majority of endings. Contraction of the muscle elicited by ventral root stimulation, however, raised the amplitude required for driving in spite of some concomitant fusimotor activation; this was probably because the muscle became stiffer, and so less vibratory deformation was transmitted to the spindles (Brown *et al.* 1967). In the present experiments, there was both an unknown amount of fusimotor activation of the spindle primary endings and a variable amount of muscle contraction; the precise effect of the interaction of these opposing factors cannot be predicted. However, virtually all Ia fibres would be expected to have been driven by amplitudes of vibration of 100 μ upwards, for the three Ia fibres systematically studied in the earlier experiments with ventral root stimulation could be driven by amplitudes ranging from 20 to 75 μ, in spite of contractions of soleus ranging up to 1·3 kg, provided there was also appreciable fusimotor activation of the ending. Indeed, the opposite complication seems just as likely to have occurred in the present experiments, namely that when the frequency of vibration was low, some Ia fibres may have discharged more than one spike per cycle of vibration; this would again complicate interpretation. Thus secure driving of Ia fibres of soleus cannot be categorically assured for the present experiments on soleus, but there seems unlikely to have been great error expressed as impulses/sec of Ia input to the spinal cord. The assumption is, however, rather less certain for the combination of ankle extensors used in some experiments, because of their more complicated anatomical arrangement.

The second assumption, that the vibration did not excite any other kind of afferent, is unlikely to have been strictly true. With the present arrangements, vibrations of 100–200 μ amplitude applied to the soleus produced a palpable vibration of the pelvic bones and so presumably excited some receptors in that region, even though the hip region had been widely denervated. The main receptors so excited would probably be Pacinian corpuscles in the skin and elsewhere, other low threshold cutaneous mechanoreceptors, and Ia fibres from muscles of the vertebral column which had not been denervated. Moreover, the vibration would also have affected some receptors on the other side of the body which was not denervated at all. Any slight excitation of Ia fibres from distant muscles seems very unlikely to have had an effect on the soleus motoneurones. The excitation of cutaneous receptors and Pacinian corpuscles may well have had little effect, particularly as many cutaneous reflexes are blocked in the decerebrate preparation (Holmqvist & Lundberg, 1961), but the matter cannot be proved.

More seriously for the interpretation of the present experiments, Brown *et al.* (1967) found that Golgi tendon organs were somewhat excited by vibration of 100 μ amplitude when the muscle was contracting sufficiently strongly to increase their initial frequency of discharge, in the absence of vibration, above about 75/sec. Some excitation of Ib fibres would therefore have been expected to have occurred in the present experiments. It would, however, have been expected to have increased appreciably when the amplitude of vibration was increased from 100 to 200 μ. The reflex, if it changed in size at all, always increased rather than decreased on so increasing the amplitude of vibration. As the Ib fibres probably produce autogenetic inhibition, increasing the amplitude of vibration above 100 μ would have been expected to decrease the reflex response. The fact that this did not occur suggests that any Ib excitation was not sufficient to produce a significant effect on the size of the reflexes studied which were elicited by amplitudes of 150 μ. Alternatively, an inhibitory effect might have been masked by an excitatory effect from some other kind of afferent fibre. Probably a few of the group II spindle afferents were also slightly stimulated on increasing the amplitude of vibration above 100 μ, and any such excitation would increase with increase of the amplitude. If these fibres were producing autogenetic excitation, as here suggested, the absence of inhibition with increasing amplitude would be explained; on the other hand, if they were producing autogenetic inhibition the matter would be still unresolved. Yet another possibility is that the reflex actions of the Ib afferents were largely absent in the present preparations, because of inhibitory effects exerted by supraspinal activity.

In the absence of systematic single fibre recording in experiments of the present type, there can be no final answer to the amount of 'stray' excitation by the vibration of receptors other than the spindle primary endings of the vibrated muscle. A certain amount of inhibitory input elicited by vibration of 100–150 μ would cause the figures given in Table 1 for the reflex responsiveness to a Ia input to be spuriously low, and invalidate the computation of the Ia input needed to produce stretch reflexes of the observed size. However, this would not of itself negate the present conclusion that the Ia activity produced on stretching is inadequate to explain the stretch reflex. This conclusion also rests on the failure to find occlusion between the responses to stretch and vibration; the argument based on this finding seems secure in spite of the existence of some concomitant inhibitory input, provided the vibration was adequate to drive the majority of Ia fibres. Vibration applied at a greater length of the soleus would then still have excited no more Ia discharge than at a shorter length, and so occlusion should still have occurred in spite of some stray inhibition. Thus, it may be concluded that although there is inevitably some uncertainty about the specificity of vibration as a stimulus, the experimental findings cannot be readily explained without postulating an autogenetic excitatory effect for the spindle group II afferents.

Previous evidence on the reflex function of the spindle secondary endings

The current view on the reflex action of the spindle group II fibres is that they produce excitation of flexor motoneurones with inhibition of extensor motoneurones, whatever their muscle of origin (Hunt & Perl, 1960; Ruch & Patton, 1965). Indeed, they are often classified along with other afferents producing a generalized flexor reflex and called part of the FRA system (Flexor Reflex Afferents, Holmqvist & Lundberg, 1961; Lundberg, 1964). The experiments on which this view is based, however, have mostly depended upon electrical stimulation of nerves with single shocks, and have mostly been performed on preparations in which the presently proposed autogenetic excitatory actions might well not have been present.

Lloyd (1946*a*, *b*) initiated the use of monosynaptic testing of motoneurone excitability to compare the reflex effects of a stimulus to a muscle nerve which excited only group I fibres, with those produced by stronger stimuli which excited both groups I and II. He found weak flexor effects for the group II fibres of extensors and this was subsequently confirmed in more systematic experiments (Brock, Eccles & Rall, 1951; Laporte & Lloyd, 1952). Later, Eccles, R. M. & Lundberg (1959*b*) recorded intracellularly from various motoneurones and also usually found a flexor pattern of effects on increasing the stimulus strength so as to excite group II fibres. All these experiments were on spinal preparations, sometimes also lightly anaesthetized with barbiturate. In unanaesthetized decerebrate preparations no changes at all were usually detectable in motoneurone excitability on single shock stimulation of group II fibres, probably because the relevant interneurones were 'blocked' by inhibitory fibres activated by higher centres (Eccles, R. M. & Lundberg, 1959*b*). But as Alvord & Fuortes (1953) emphasized, the activation of reflex pathways by single volleys, rather than repetitively, cannot be expected to disclose the full range of physiological action. In the present experiments, however, repetitive activation of group II fibres along with others in the medial gastrocnemius nerve also inhibited the stretch reflex of soleus.

These flexor effects obtained on stimulating muscle group II fibres are usually attributed to spindle afferents, on the assumption that there is no other sensory receptor in muscle which has afferent nerve fibres of group II diameter. The only evidence for this assumption is provided by the experiments of Hunt (1954), who recorded from about 300 single group II afferents from the soleus and gastrocnemius muscles of the cat and found that all but two or three of them behaved as if they came from a muscle spindle. In contrast, Paintal (1960) later found that in a sample of thirty-two afferents from 'pressure-pain' receptors seven had conduction velocities which placed them in the group II, or even in the group I range (highest value, 91 m/sec; group II range taken as beginning at 24 m/sec). Histological work suggests that in some but not all muscles the great majority of group II muscle afferents do come from spindle secondary endings (Boyd & Davey, 1968), but is not precise enough to exclude the possibility that in every muscle a certain number of group II fibres terminate in other kinds of receptor. Indeed, Barker (1967) believes that up to 30 % of muscle group II afferents of even the soleus of the cat do not supply muscle spindles. Thus the assumption that the group II afferents of any muscle consist *solely* of spindle afferents does not appear to be established on the balance of present evidence, and the group II innervation of many muscles is certainly not so restricted (McIntyre, 1962). If even relatively few group II fibres come from nociceptors, or if a few group III fibres are excited by stimuli supposedly restricted to group II fibres (Kuno & Perl, 1960), then the usual interpretation of the results obtained with electrical stimulation is invalid, for reflexes elicited by nociceptive stimuli are prepotent over others. Sherrington (1906) found that 'Of all reflexes it is the tonic reflexes, e.g. of ordinary posture, that are in my experience the most easily interrupted by other reflexes'.

Laporte & Bessou (1959), however, performed an experiment which was based on adequate rather than electrical stimulation, and which also suggests that in the spinal preparation the spindle group II fibres from extensor muscles do produce autogenetic inhibition. By stimulating a muscle nerve with rather strong shocks they were able to inactivate the group I fibres without blocking the group II fibres, so that any reflex effects of muscle stretch could be presumed to depend upon the spindle group II afferents. Under these conditions, stretching the soleus muscle depressed the monosynaptic reflex elicited by stimulating the nerve to lateral gastrocnemius and soleus above the block. The acutely spinal cat, however, lacks a tonic stretch reflex so these results cannot be extrapolated to the decerebrate cat which possesses one. The interneurones through which spinal reflexes are transmitted are well known to be influenced by fibres descending from higher centres, so that the reflex behaviour of different preparations may be quite different (Sherrington & Sowton, 1915;

Eccles, R. M. & Lundberg, 1959*b*; Kuno & Perl, 1960). Of particular interest in this respect is the finding that electrical stimulation of extensor group II fibres may occasionally give extensor facilitation with inhibition of flexors, rather than the reverse (Eccles, R. M. & Lundberg, 1959*a*; Holmqvist & Lundberg, 1961). In one illustrated example, increasing the strength of a stimulus to the gastrocnemius nerve from 2·2 to 4·3 times the Ia threshold appreciably increased the size of the EPSP (excitatory post-synaptic potential) evoked in a gastrocnemius motoneurone by polysynaptic pathways (Fig. 9, Eccles, R. M. & Lundberg, 1959*a*). To explain certain related findings, Eccles, R. M. & Lundberg (1959*a*) suggested that there might be 'two alternative pathways from group II and III afferents onto flexor motoneurones, one excitatory and one inhibitory' and with 'some sort of reciprocal linkage' between them so that only one of them could work at a time. Alternative reflex pathways which can be activated by a single afferent input have also been invoked to explain the spinal effects of DOPA (Dihydroxyphenylalanine; Andén, Jukes, Lundberg & Vyklicky, 1966). Thus, quite possibly the spindle group II afferents may produce different effects in different preparations and this would also be compatible with certain other findings in the anaesthetized cat (Bianconi, Granit & Reis, 1964; Granit, Kellerth & Szumski, 1966). At any rate, the previous experiments do not appear to conflict seriously with the present suggestion that the secondary endings of the muscle spindle are partly responsible for the tonic stretch reflex of the decerebrate cat. More direct evidence is, however, obviously desirable before the newly suggested role for the spindle group II fibres can be regarded as established. The present type of experiment is also naturally unable to show the nature of the central mechanisms involved in producing the postulated autogenetic excitation. It is simplest to believe that the spindle group II afferents can produce this action unaided by a purely spinal reflex, and that it is mediated by a chain of excitatory synaptic connexions. Various other possibilities of a range of complexity remain open, including the disinhibition rather than the direct excitation of motoneurones. It may be noted, however, that even if the central pathways should prove to be somewhat circuitous, the effect would still seem properly described as an 'autogenetic excitation', since whatever the details of the mechanism this term describes what happens to the motoneurones.

Implications of suggested role of spindle secondary ending

If it is provisionally accepted that the secondary ending of the muscle spindle may produce autogenetic excitation various matters may be looked at anew, and it seems of interest to note and comment upon some of them.

1. Most simply, a similar role may be suspected for the secondary

ending in the development of some of the pathological increases in muscle tone in man.

2. The tendon jerk and the tonic stretch reflex are seen to differ in more than their time course. The tendon jerk must depend almost entirely on the primary endings, for these are strongly excited by a small rapid extension, whereas the secondary endings are not (Matthews, 1964). The tonic stretch reflex depends, it is now suggested, upon both kinds of afferent. Thus a new factor becomes available to explain the fact that in both animals and man there is often little correlation between the briskness of the tendon jerk and the degree of hypertonicity shown by a muscle.

3. The role of the static fusimotor fibres assumes a new prominence. These excite both primary and secondary endings of the spindle (Appelberg, Bessou & Laporte, 1966), while the dynamic fusimotor fibres control the primary endings alone. In the decerebrate cat any 'spontaneous' static fusimotor discharge will help lower the threshold extension required to elicit a stretch reflex by increasing the discharge of both primary and secondary endings, and the action on the secondary endings may well be the more important in this respect.

4. If the spindle is conceived as the part of a servo-system of muscle control into which 'command signals' are injected by fusimotor activity (Merton, 1953), then any such command transmitted by static fusimotor fibres is likely to be mediated by changes in firing of secondary as well as of primary endings. The secondary ending, moreover, will give the more accurate signal of the 'misalignment' of the actual value of muscle length from the commanded value, because unlike the primary ending it is relatively unaffected by dynamic stimuli. A complication in the interpretation of such signals by a human observer, however, is that strong static fusimotor activity may increase the sensitivity of the secondary ending to extension (i.e. increase the slope of its frequency–extension relation; Brown *et al.* 1969), so that a given frequency of firing will not refer to the same misalignment, expressed as a length, at different degrees of fusimotor activity.

5. The interneurones which mediate the reflex effects of spindle group II activity are seen to occupy a crucial position. It seems possible that the occurrence of a tonic stretch reflex in the decerebrate cat is partly due to interneurones mediating autogenetic excitation being 'switched on' by supraspinal activity, while those mediating inhibition are 'switched off'. Such switching of stretch reflex activity might play a part in normal movements, as for example in landing from a jump. It is interesting in this respect that a tonic stretch reflex can be made to appear in the calf muscles of a normal man by the Jendrassik manoeuvre (Mark, 1963), and that this procedure can change the effect of dorsiflexion of the ankle on the Hoffman

reflex from inhibition to excitation (Mark, Coquery & Paillard, 1968).

6. The action of local anaesthetics in reducing hypertonus in man or animals when applied to nerve, spinal roots or injected into muscle may still be attributed to preferential paralysis of fusimotor fibres (Matthews & Rushworth, 1957), for these are mostly smaller than the majority of group II afferents. Blockade of the static fusimotor fibres seem likely to be the most important in this respect, especially as the smaller fusimotor fibres are more commonly found to be static than dynamic ones (Brown, Crowe & Matthews, 1965). Some reduction of hypertonus would also be expected to occur before motor paralysis because of block of the smaller group II fibres. However, if this occurred on a significant scale certain earlier finding would be difficult to explain (Matthews, 1958, 1959*b*), and it remains to be shown whether group II fibres are paralysed significantly before Ia afferent and α motor fibres.

7. The similarity of the frequency–response curves for the two kinds of spindle afferent ending obtained on sinusoidal stretching seems more understandable (Matthews & Stein, 1969) if they can both have similar central actions. When the stimuli were small enough for the endings to behave linearly the responses of the two kinds of ending differed by a constant scaling factor, but they increased very similarly on increasing the frequency of sinusoidal stretching. This would have the effect of extending the range of response of the muscle spindle considered as a single device. The primary ending would enable small deviations from a pre-existing length to be signalled with a high gain, but would soon saturate; the secondary endings would enable larger inputs to be signalled linearly, but without the same high sensitivity. Poppele & Terzuolo (1968) suggested that the increase in response of the primary ending with increasing frequency of stretching merely served to compensate for the inverse lag in the stretch reflex loop produced by the slowness of the contractile response of muscle. If the two kinds of ending are both producing a stretch reflex it would then seem appropriate that the behaviour of both should reflect the properties of muscle.

8. The attribution to spindle group II fibres of an autogenetic action which may apparently be continuously graded from excitation to inhibition, is teleologically more satisfying than the previous view that they produced non-specific flexor effects. Indeed, proponents of the earlier view felt it necessary to suggest that the flexor reflex actions from the secondary endings were normally kept entirely switched off so that they were 'prevented from exerting any action during locomotion' (Eccles, R. M. & Lundberg, 1959*b*). The continuous measure of the length of a muscle which is provided by the spindle secondary endings (Matthews, 1964) seems more

appropriately used to produce a continuous gradation of the functionally meaningful response of the stretch reflex.

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