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AUTOGENETIC REFLEX ACTION ON TO GAMMA MOTONEURONES BY STRETCH OF TRICEPS SURAE IN THE DECEREBRATED CAT

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SUMMARY

1. Tonically firing gamma motoneurones of known conduction velocity (total eighty-seven, range 15–43 m/sec) have been isolated in peripheral muscle nerves to triceps surae. Their responses to stretch of triceps surae have been studied in decerebrated cats. A small amplitude, quick stretch and release was used to provide a selective stimulus for primary endings of muscle spindles.

2. To check the selectivity, recordings were made from 135 afferents from triceps surae under conditions closely similar to the reflex experiments. The threshold of all but a few primary endings of muscle spindles lay below 50 μm whereas threshold was above 50 μm for the majority of secondary endings and tendon organs. A 20 μm stretch excited approximately half the primary endings but only one of thirty-six secondaries and no tendon organs responded to such a small stretch. Nine group III afferents were also studied but none responded to stretch.

3. Stretch of up to 50 μm excited twenty-three and inhibited eleven gamma motoneurones while thirty-three remained unaffected. A further twenty showed mixed responses, being inhibited initially before being excited at longer latency. Thresholds for reflex responses of gamma motoneurones frequently occurred below 20 μm and responses were close to maximal for stretch of 50 μm.

4. Excitation always had a lower threshold to stretch than did inhibition for those gamma motoneurones showing mixed responses and was the more potent of the two effects.

5. Excitation to stretch had central delays, to the incoming group Ia volley, ranging from 5 to 14 msec while similarly calculated delays for excitation of alpha motoneurones ranged from 0·6 to 3·0 msec. Central delays of the gamma inhibitory responses lay in an intermediate range of 1·7–7·0 msec.

6. The long central delays of excitation of gamma motoneurones in response to stretch do not reflect transmission in supraspinal pathways since the reflex persisted following spinal section.

7. Excitation of gamma motoneurones was weak in comparison with that of tonically firing alpha motoneurones recorded in the same preparations and it was always necessary to sum a number of responses in order to reveal an effect.

8. On using longitudinal vibration (170 Hz) of the muscle at less than 50 μm as a stimulus, forty-one gamma motoneurones were excited, forty-five unaffected and only

one inhibited. With a few exceptions those excited by vibration comprised the gamma efferents which showed both excitation and mixed responses to stretch whereas those unaffected by vibration included those which were solely inhibited by stretch as well as those which did not respond.

9. It is concluded that impulses in group Ia afferents can excite their homonymous gamma motoneurones via a spinal reflex in the decerebrated cat. It is likely that the inhibition of gamma motoneurones seen in response to stretch is also a consequence of discharges in group Ia afferents although participation by receptors other than primary endings cannot be ruled out.

10. An assessment is made of the likely role of these reflexes.

INTRODUCTION

Background nerve impulse activity of gamma motoneurones is a feature of several different mammalian laboratory preparations. It is readily influenced by activity in descending spinal nerve tracts from the brain stem and by segmental inputs from skin and group III muscle afferents. In contrast, stretch of skeletal muscle has generally been thought to have little effect upon gamma motoneurone discharge. The literature concerning the connexions from muscle afferents to gamma motoneurones, particularly where autogenetic control from stretch receptors has been investigated, does however contain several conflicting reports. The conflict can probably be attributed to the use of a variety of methods and preparations, and, in many cases, to a lack of selectivity in the stimuli used to excite muscle afferents. The situation was last reviewed by Matthews in 1972.

In 1967, Brown, Engberg & Matthews showed that vibration of a muscle can be used to excite the primary endings of muscle spindles selectively. Brown, Lawrence & Matthews (1968*a*) used this technique to show that some gamma motoneurones of unknown destination were inhibited by vibration of triceps surae in the decerebrated cat. These findings were confirmed by Trott (1975, 1976) but, when her study was restricted to neurones of the same muscle, vibration was found to excite some gamma motoneurones and was never seen to evoke inhibition. A further study by Fromm & Noth (1975, 1976), however, stressed the fact that vibration induced autogenetic inhibition of some gamma motoneurones although excitation was also seen. They thought this inhibition was recurrent inhibition (Ellaway, 1968, 1971; Brown, Lawrence & Matthews, 1968*b*) brought about as a consequence of alpha motoneurones responding to vibration.

The present work was undertaken to examine the time course and route of the reflex excitation of gamma motoneurones by impulses in homonymous group Ia afferents and to compare the properties of the reflex with the concomitant excitation of alpha motoneurones. We first examined the responses to electrical stimulation of the muscle nerve at group I strength. This produced inhibition in approximately two thirds of gamma motoneurones to the same muscle (Ellaway & Trott, 1976*a*) and of those about one half were also excited at longer latency. However, we rejected this approach since electrical stimulation does not discriminate between Ia and Ib axons, and in our preparation, antidromic volleys were elicited also in alpha motoneurones. Instead we have used a single brief stretch and release of the muscle to excite a

reasonably coherent volley in group Ia afferents. In agreement with Lundberg & Winsbury (1960) and Stuart, Mosher, Gerlach & Reinking (1970) we find that such muscle stretch can provide a selective stimulus for primary endings.

Preliminary communications of some of this work have been presented (Ellaway, Pascoe & Trott, 1976; Ellaway & Trott, 1976*b*).

METHODS

Preparation. The experiments were performed on adult cats decerebrated intercollicularly under halothane in oxygen anaesthesia. The left hind limb and part of the tail were denervated as completely as possible with the intention of leaving only the nerve supply to triceps surae intact. In some experiments a lumbar laminectomy was performed to expose spinal roots L7 and S1. The Achilles tendon was detached from its insertion on the left foot and attached to a mechanical stretcher. Before detaching the tendon the limit of its maximum natural extension was marked with a small suture. After decerebration halothane anaesthesia was discontinued and the animals were allowed to breathe freely from the atmosphere for 1–2 hr before experimentation. Cats were then paralysed with an I.V. injection of gallamine triethiodide (Flaxedil, May and Baker) so that no reflex contraction could ensue in response to stretch. Ventilation was achieved with a Starling Ideal pump and further doses of gallamine were injected when necessary to maintain paralysis.

Isolation and identification of motoneurones. One fascicle of the triceps surae nerve was cut, desheathed and split until the impulses of a single tonically firing motoneurone were recorded in isolation. Usually a unit was isolated from the gastrocnemius medialis nerve but occasionally one from gastrocnemius lateralis or soleus was selected. The remainder of the nerve supply was preserved to provide an adequate afferent pathway.

Gamma motoneurones were identified by their axonal conduction velocity calculated over the length of nerve from the ventral root, or sciatic nerve in the thigh (see Trott, 1976) to the recording site. Velocities ranged from 15 to 43 m/sec; these neurones would, in the adult cat, all be fusimotor in function (Matthews, 1972, p. 221). Tonically firing alpha motoneurones were identified by their conduction velocity in the same manner (range 52–109 m/sec). There are no exclusively fusimotor neurones whose axons conduct faster than 50 m/sec (Ellaway, Emonet-Dénand, Joffroy & Laporte, 1972). In addition to their separate conduction velocity ranges, the two types of motoneurones could be distinguished by the relatively low threshold of gamma motoneurones to skin stimulation and of alpha motoneurones to muscle stretch. Furthermore, the tonic discharge of alpha motoneurones almost invariably starts and/or finishes with 'double' spikes having a short interval between them compared with the mean interval; gamma fibres do not have this property.

Isolation and identification of afferent neurones. Muscle afferents of triceps surae with axons throughout the myelinated range (groups I to III) were examined for their response to brief stretch of the parent muscle. Decerebrate cats and cats anaesthetized with sodium pentobarbitone were used for this study and in both types of preparation ventral roots L7 to S2 were cut and recordings made from L7 and S1 dorsal root filaments. To ensure that no axon was overlooked, afferent units were detected by noting their direct response to electrical stimulation of the muscle nerve and conduction velocities of all units were assessed from their response latencies to such stimulation.

In the group I range of conduction velocities, primary spindle endings were identified by their sustained firing on extension of the muscle, their high dynamic sensitivity and a pause in discharge during contraction of their muscle. Golgi tendon organs were identified by the group I conduction velocity of their axons and an increased discharge during twitch contractions of their muscle. In the group II range, secondary spindle afferents were identified by their sustained firing to muscle extension, a pause to contraction and a low dynamic sensitivity to stretch. A number of spindle endings had axons with conduction velocities in the intermediate range between groups I and II axons (65–75 m/sec) and these we have not allocated to either group. Within the group III range, i.e. axons with conduction velocities below 25 m/sec, one unit possibly fulfilled the criteria of a secondary spindle afferent but the others were not responsive to stretch and responded weakly, if at all, to contraction.

Recording of nerve impulse activity. Nerve impulses were recorded by conventional means and

displayed on an oscilloscope. Permanent records of discharge frequency were obtained by feeding shaped impulses into an integrating circuit, the output of which was displayed on a chart recorder.

Analysis of impulses by computer. Shaped impulses were also used to signal events to a special purpose computer (Biomac, Data Laboratories) or to a programmable computer (LINC-8 Digital) for further analysis.

Peri-stimulus time histograms (PSTHs) which give the probability of firing of a cell in relation to a stimulus, were constructed in real time and displayed in the laboratory at the end of the required number of sweeps. As an adjunct to the PSTH, a cumulative sum technique was developed to assist the detection of minimal responses and to interpret complex responses in the PSTH (Ellaway, 1977). To obtain the cumulative sum (Fig. 3), counts in each bin of the PSTH were first expressed as the amount by which they exceeded or fell short of the mean value (measured in a control period). The values thus obtained for successive bins were then added together, so that the value at each time indicates the accumulated total. A progressively increasing cumulative sum (Fig. 3) thus indicates a level of neural activity higher than the mean.

Stretch of the muscle. The muscle was lengthened or shortened by a servo-controlled electromagnetic stretcher (Series 400, Ling Dynamic Systems) having an overall stiffness of approximately 0·2 mm/kg. Brief stretch and release of the muscle of up to 200 μm with a rise time of 3 msec and return in 5 msec was achieved. Displacement amplitude could be resolved to approximately 2·5 μm. To achieve selective but powerful stretch activation of spindle primary endings, the muscle was held within 5–10 mm of its maximum physiological length. The passive tension was then 100–200 g.

Abbreviations used: CUSUM, cumulative sum. PSTH, peri-stimulus time histogram.

RESULTS

The stimulus required for this study of reflex excitability of gamma motoneurones was one which would excite selectively the primary endings of muscle spindles and which would allow accurate latency measurements of reflex effects. Before using brief, low amplitude stretch of a muscle for this purpose, we decided to ensure that such a stimulus was indeed selective in exciting primary endings. We intended to use a powerful combination of averaging techniques (PST histograms and cumulative sums) to reveal reflex actions and we were concerned that these might uncover the misleading synaptic connexions of just a few, particularly low threshold afferents in a population which was predominantly unresponsive to the stimulus.

Analysis of the response of muscle afferents to muscle stretch

Fig. 1 shows the number of afferent units which responded to stretch of different amplitudes. Inclusion of a unit in a particular column indicates that it responded in 50% of the trials to stretch of that amplitude. The muscle concerned was the triceps surae which was held extended to within 5–10 mm of its maximum natural length. Over half of the forty-five primary endings had thresholds (defined in this way) below 20 μm and 87% were recruited by the time the amplitude of stretch had been raised to approximately 50 μm. Some spindle endings with axons conducting in the intermediate range of 65–75 m/sec, also had low thresholds to stretch but these may also have been primary endings. In contrast to the spindle primary endings the majority of secondary endings and tendon organs had high thresholds to stretch or did not respond to the largest stretches examined (usually 200 μm.)

The responses to vibration of these same afferents were studied. Threshold was defined as that amplitude of longitudinal vibration (usually at 170 Hz) applied to the Achilles tendon that clearly produced a maintained increase in the frequency of discharge of a unit throughout the

period of vibration. A relatively high sensitivity of primary endings was again observed with twenty-five out of forty-three receptors having thresholds below 50 μm. In contrast only two secondaries and no tendon organs had thresholds to vibration below excursions of 50 μm.

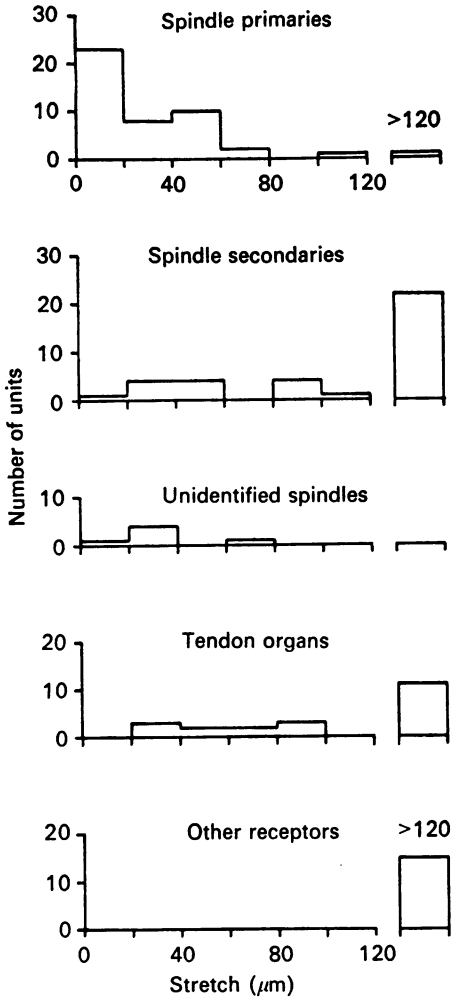

Fig. 1. Threshold to stretch of 123 afferent units supplying triceps surae. The columns whose abscissae are labelled > 120 μm indicate not only the number of units with thresholds greater than 120 μm but also those units which were inexcitable to stretch up to 200–300 μm. The data comprise forty-five primary endings (axon conduction velocities 78–118 m/sec), thirty-six secondary endings (26–64 m/sec), six spindle endings with intermediate axon conduction velocities (66–73 m/sec), twenty-one tendon organs (69–104 m/sec) and fifteen other receptors including nine group III axons (8–22 m/sec).

Fig. 1 includes fifteen units which were not classified as spindles or tendon organs. The majority of these were high threshold group III mechanoreceptors. None of these units responded to brief small amplitude stretch of triceps surae or to longitudinal vibration at least up to 120 μm amplitude.

Reflex connexions to gamma motoneurones

Having established the conditions under which stretch would provide a selective stimulus for primary endings of muscle spindles this stimulus was employed while recording from single tonically firing gamma motoneurones to triceps surae. Responses to stretch could not be detected after a single stimulus and in this respect they differed from the responses of alpha motoneurones recorded in the same preparations. However, the gamma responses could be revealed by constructing PST histograms. When this was done it became clear that twenty-three of the eighty-seven neurones studied were excited by stretching their own muscle through less than 50 μm, eleven were inhibited and thirty-three were unaffected. A further twenty neurones showed mixed responses with inhibition preceding excitation although the excitation invariably had the lower threshold.

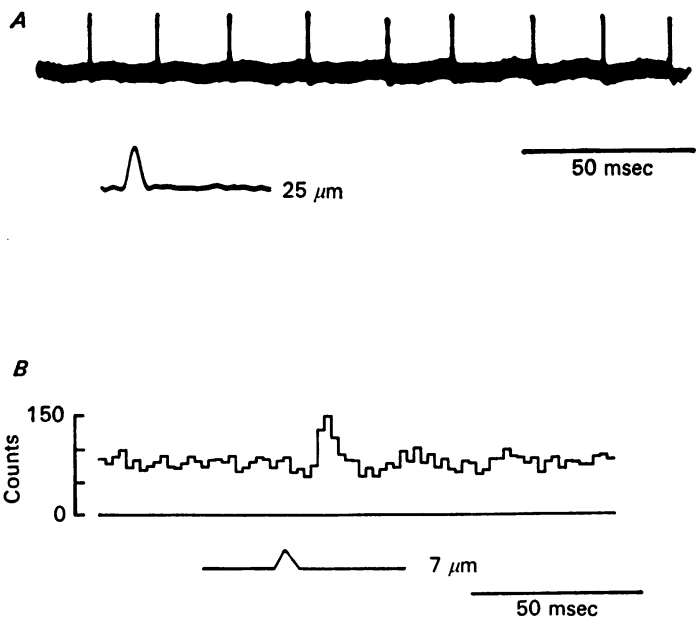

Fig. 2. Response of a gamma motoneurone (gastrocnemius medialis 36 m/sec) to stretch of the whole triceps surae. *A*, the tonic discharge (mean frequency 48 impulses/sec) in the upper trace appears to be unaffected by stretch of 25 μm located 25 msec after the start of the sweep. The inset lower trace is the output of the length transducer. *B*, a PST histogram of 1024 trials of the form shown in trace *A*. Approximately 15 msec after the start of a 7 μm stretch of triceps surae the probability of firing is raised showing that the gamma motoneurone was facilitated by the stimulus.

Gamma motoneurones excited by stretch. Fig. 2 illustrates the response of a gamma motoneurone which was excited by stretch of its own muscle. Excitation occurred in response to stretch of only 7 μm and grew in size as the amplitude of stretch was increased, reaching 90% of its maximum value in the range 50–75 μm. The average increase in firing rate during the period of excitation can be assessed from the cumulative sum in Fig. 3. For a 25 μm stretch the slope of the cumulative sum for the

period of the response is 4·6 counts/bin. This represents the average increase in counts of the PSTH, during the response, over the mean control level of 6·5 counts/bin. Translated to the original discharge frequency of the neurone this is equivalent to an increase in firing rate from 50 to 86 impulses/sec but lasting only 5·5 msec. The data in Fig. 4*A* relates the degree of excitation to stretch amplitude in five different neurones. The average degree of excitation was assessed in each case from the slope of the cumulative sum histogram for the period of the response. Fitting such a line is

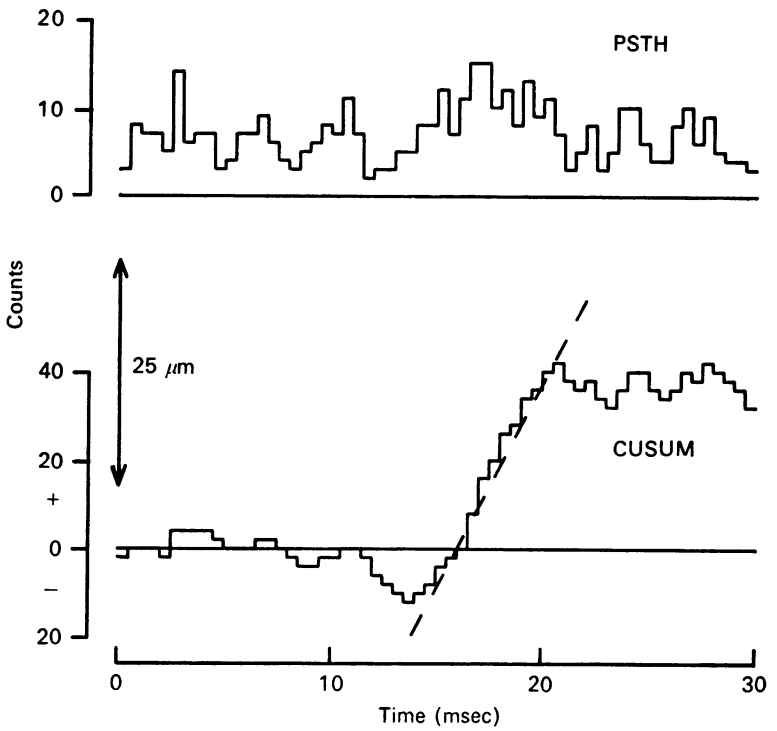

Fig. 3. Quantitative assessment of the response of a gastrocnemius medialis gamma motoneurone to a 25 μm stretch of triceps surae. Upper trace: part of a peri-stimulus time histogram (PSTH) derived from 257 sweeps. Bar width 0·5 msec. Lower trace: the cumulative sum of the PSTH above. The mean of the counts in 550 bins (not shown) which occurred before the stimulus, was used as a reference value to construct the cumulative sum. The slope of the dashed line indicates the average increase in the probability of firing for the duration of the response (see text).

clearly rather arbitrary and this relatively crude assessment probably accounts for the large scatter in points for any one neurone. None the less, it is evident that thresholds for excitation lie below 20 μm and that increasing the amplitude of stretch above 50 μm adds little to the responses. From the accompanying graph in Fig. 4*B* it is noticeable how closely the curve of threshold to stretch for primary spindle endings matches that of gamma motoneurone excitation. No other afferent type has an appreciable number of units with thresholds below 20 μm and there is not more than 25% recruitment of any other afferent on raising the amplitude of stretch to 50 μm.

Excitation of gamma motoneurones consisted typically of increases in the probability of firing of 20–60 %, lasting for 5–10 msec.

Central delay of the response to stretch was estimated by subtracting from the overall latency of response both the conduction time in the gamma axon and the latency of the earliest component of the group Ia afferent volley. The group Ia response was recorded at the dorsal root entry point to the spinal cord and the volley typically lasted 3 msec. The response latency itself was taken as the time to the first visible indication of a change in probability of firing of the neurone as evident from

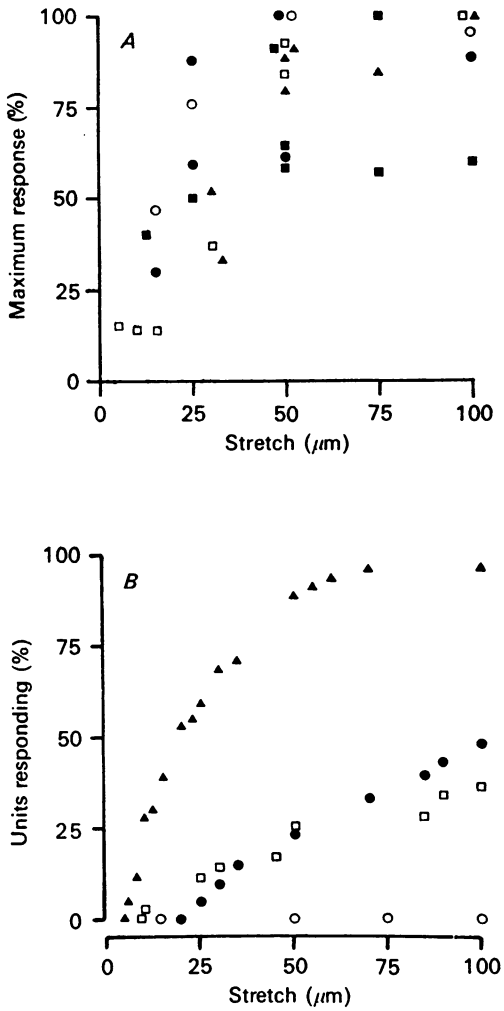

Fig. 4. *A*, the relation between the degree of excitation and the amplitude of stretch of triceps surae for five different gamma motoneurones of that muscle. The ordinate has been normalized to make the largest response of each neurone equal to 100 %. *B*, the percentage of afferent units which discharge on more than 50 % of occasions in response to a given amplitude of stretch. The graph shows primary endings (▲, total forty-five), secondary endings (□, total thirty-six), Golgi tendon organs (●, total twenty-one) and other receptors (○, total fifteen). Note the similarity between the degree of gamma excitation and the sensitivity of the primary endings.

the PSTH or its cumulative sum. The distribution of central delays of gamma excitation (range 5·1–13·7 msec) can be seen later in Fig. 7 and are quoted for stimuli somewhat above threshold since, on increasing the amplitude of stretch, latencies generally decreased by 1–2 msec.

The usual arrangements for these experiments was to leave the innervation of triceps surae intact except for one fascicle of the gastrocnemius medialis nerve

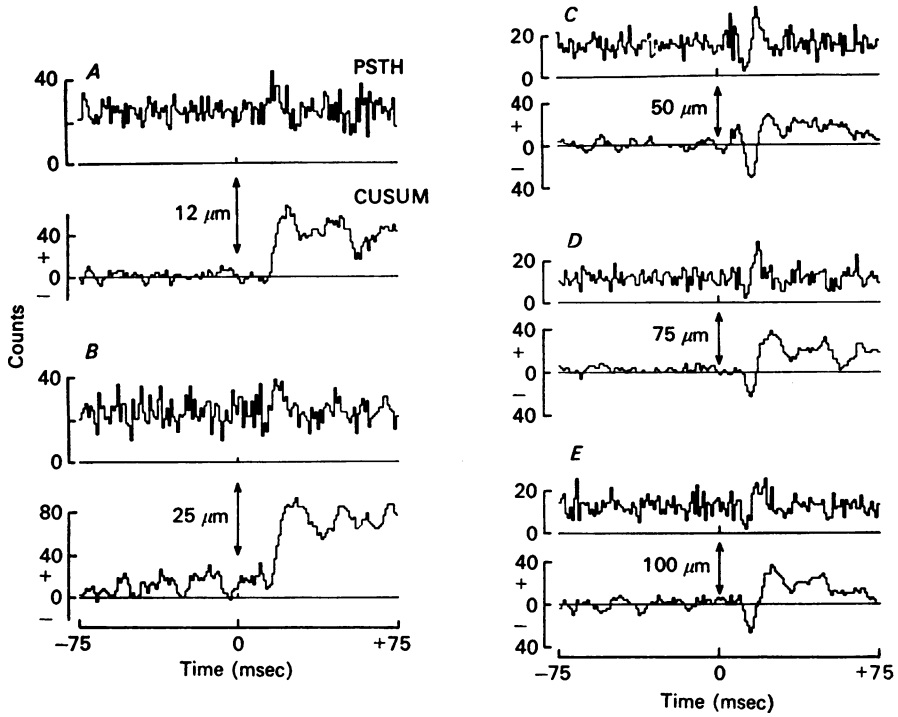

Fig. 5. Examples from a gamma motoneurone which was excited by stretch of its own muscle at amplitudes of 25 μm or less but showed a mixed response, with inhibition preceding excitation, after stretching through 50 μm or more. The bin width in all histograms is 1 msec and the number of trials in *A* and *B* (512) was double that in *C*, *D* and *E* (256). *A*, *B*, pure excitatory responses, latency 15 msec. *C*, *D*, *E*, inhibition is indicated by a lowered probability of firing in the PSTHs and its duration can be assessed by the length of the negative slopes of the cumulative sums. Inhibition precedes the excitatory response by 4–5 msec. In *C*, *D* and *E* the cumulative sums revert to the positive side of zero, following the period of positive slope, indicating that the net effect of the stimulus was excitatory. Note that, following the initial responses the cumulative sums and, to a lesser extent, the PSTHs show continuing oscillations with a period of 21 msec. These are a consequence of the stimulus tending to rephase the rather regular discharge (47 impulses/sec) of the neurone to give some degree of synchronization of spikes. The phenomenon can be seen in other Figures.

which was cut for recording purposes. At the end of the experiment gastrocnemius lateralis and soleus nerves were cut. This sometimes abolished the response but, on occasions, the remaining gastrocnemius medialis nerve supply provided an adequate afferent pathway for the reflex showing the excitation to be truly autogenetic. Finally, cutting the medialis nerve abolished the response. Thus there was no

possibility of the effects we have observed arising in receptors other than those in the triceps surae.

Gamma motoneurones to the triceps surae can be powerfully excited by squeezing the Achilles tendon. In some experiments therefore the tendon was anaesthetized with 5% procaine. After 10 min the response to pinching the tendon had disappeared whereas the response to brief stretch was undiminished.

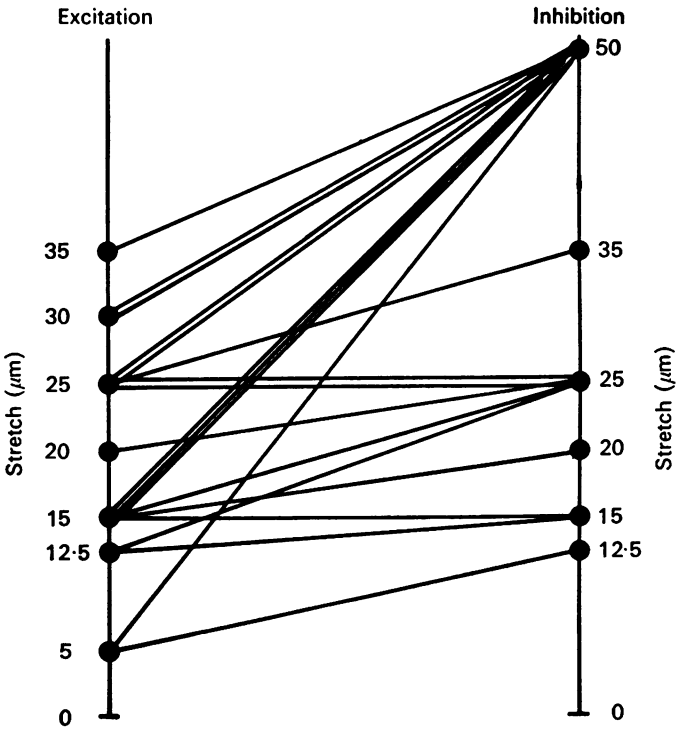

Fig. 6. The lowest amplitudes of stretch for nineteen individual gamma motoneurones at which the two responses, excitation and inhibition, were observed.

Gamma motoneurones inhibited by stretch. Twenty out of the forty-three gamma motoneurones excited by stretch of less than 50 μm amplitude could be inhibited, at shorter latency, on increasing the amplitude of stretch. This is illustrated for a gamma motoneurone in Fig. 5. Threshold for excitation lies below 12 μm whereas the threshold for inhibition is clearly between 25 and 50 μm. The inhibition is apparent for only a few msec and may well be cut short by the period of excitation. For any given neurone the threshold for inhibition was never lower than that for excitation. Fig. 6 shows the relative amplitudes for evoking the two responses in each of nineteen neurones.

It is relevant that the three neurones of Fig. 6 for which excitation and inhibition had similar thresholds were the only neurones studied from one particular cat. This cat exhibited an unusually high level of tonic alpha motoneurone activity to triceps surae at the maintained length of the muscle and stretch reflex responses of alphas could be elicited at amplitudes of less than 15 μm. In contrast, most other decerebrated cats in this study had little or no tonic background discharge in alpha motoneurones to the ipsilateral triceps surae and had higher thresholds for stretch reflexes.

Central delays of inhibition ranged from 1·7 to 7·0 msec (see Fig. 7). This data includes a further eleven gamma motoneurones which were inhibited by stretch at thresholds 12·5–50 μm but which showed no subsequent excitation.

As with excitation, inhibition of the tonic discharge of a gamma motoneurone is not obvious on giving a single brief stretch to the muscle. Furthermore, it is not possible to assess the degree of inhibition from the PST histogram in the case of a

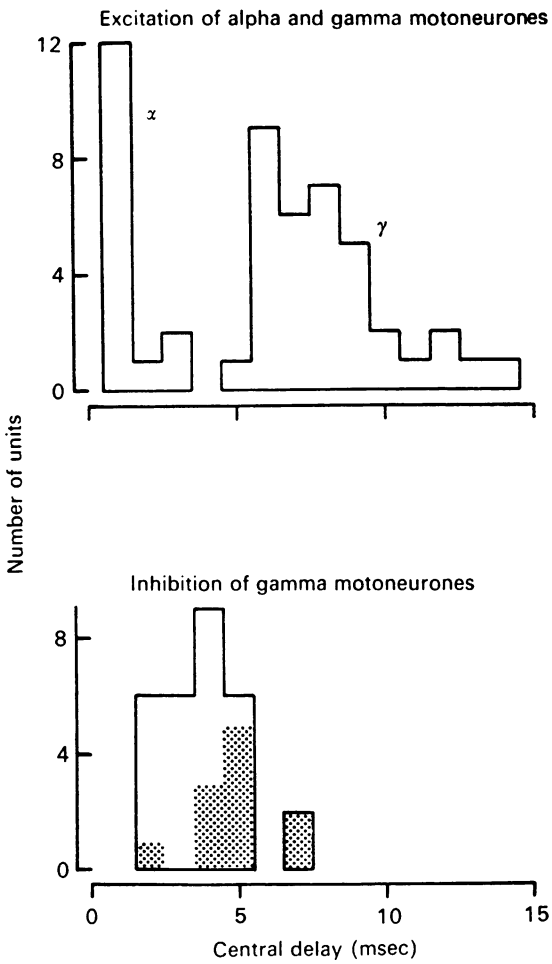

Fig. 7. Central delays of the responses of alpha and gamma motoneurones to stretch of less than 50 μm of their own muscle (triceps surae). Upper graph: excitation of alpha and gamma motoneurones. The two distributions do not overlap. Lower graph: inhibition of gamma motoneurones including delays for those simply inhibited (shaded area) and those where inhibition preceded an excitatory response (open area).

mixed response since the excitation may be obscuring the true time course of inhibition. The onset of inhibition does seem to be sharper than that of excitation and its duration, assessed from pure inhibitory responses, is of the order of 10–15 msec. When a mixed response was evoked the amount of excitation received by the neurone

clearly outweighed the inhibition. This is apparent if the cumulative sums of the responses of Fig. 5 are examined. The technique effectively integrates the response and, as can be seen, the cumulative sum eventually ends up on the positive side of zero, showing that the net effect of the stimulus was excitation.

Gamma motoneurones unaffected by stretch. In each decerebrated cat some gamma motoneurones were not firing; none of these was ever found to fire in response to stretch of their muscle at amplitudes even up to 200 μm. The number of tonically

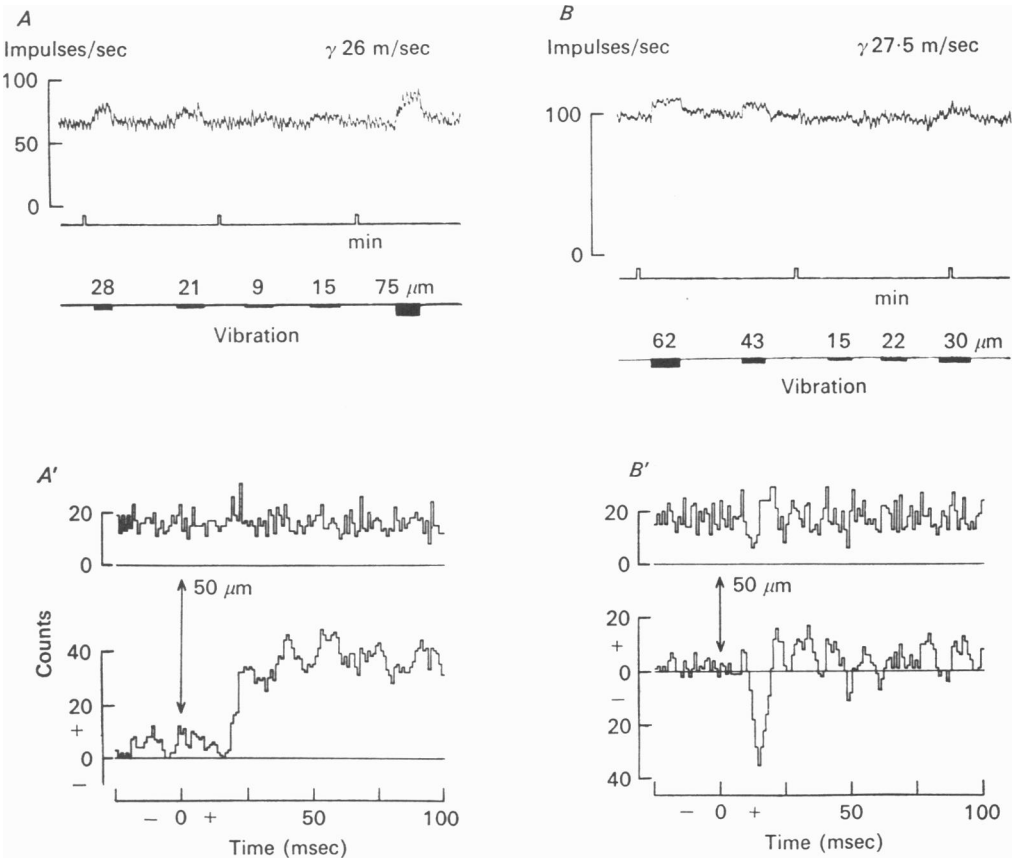

Fig. 8. The common excitatory effect of vibration on gamma motoneurones which show different responses to single stretches of their muscles. *A*, *B*, integrated frequency of discharge and responses to vibration. *A'*, *B'*, PST histograms (above) and their cumulative sums (below) for the same neurones. The neurone in *A*, *A'* shows only a period of excitation in response to stretch of 50 μm. The other neurone (*B*, *B'*) shows a mixed response to a similar stimulus with excitation preceded by inhibition. Histogram bin widths 1 msec, number of sweeps 256.

firing gamma motoneurones which were unresponsive to stretch (thirty-three out of eighty-seven) were not evenly distributed among the thirty cats studied. Occasionally, for example, a decerebrated cat was prepared in which none of a total of six to eight gamma motoneurones isolated showed any response to stretch even though stretch reflex responses of alpha motoneurones could be elicited.

The effect of vibration on gamma motoneurone discharge. In a previous article (Trott, 1976) it was reported that vibration of a muscle, used as a selective stimulus for primary endings, caused autogenetic excitation in nineteen of twenty-seven fusimotor

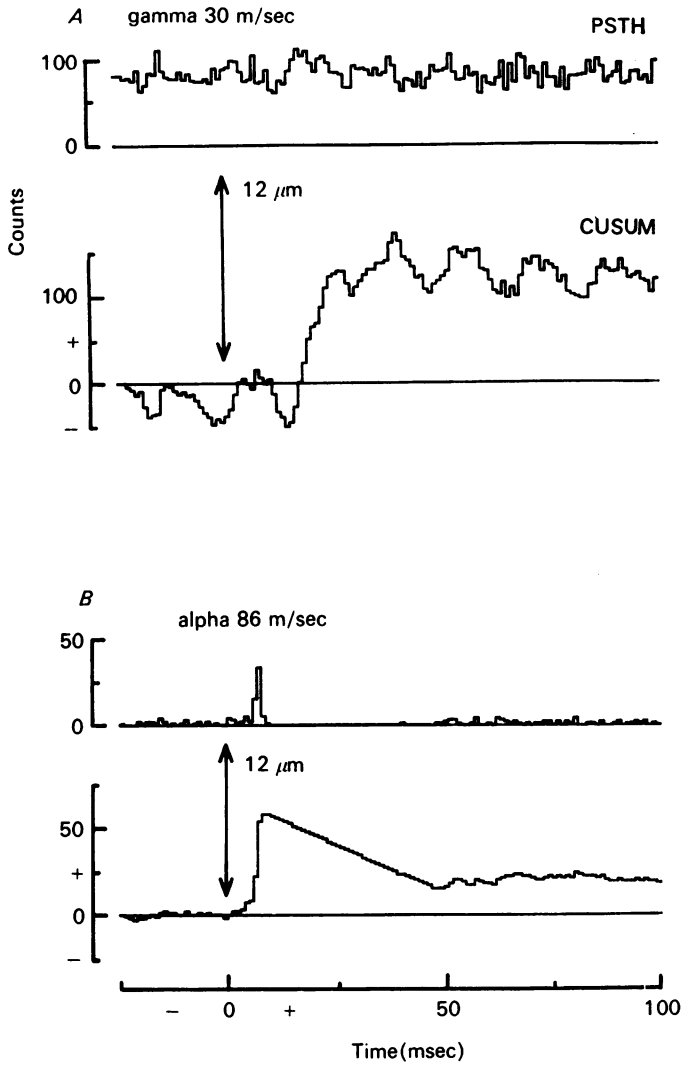

Fig. 9. Responses to a 12 μm stretch of triceps surae of tonically firing alpha and gamma motoneurones in the same decerebrated cat. Note that the response of the gamma motoneurone (*A*) is weaker, more prolonged and occurs with longer latency than that of the alpha motoneurone (*B*). Bin widths of the histograms are 1 msec in duration and the number of trials was 1176 in *A* but only 117 in *B*. The mean discharge frequency of the gamma motoneurone was 23 impulses/sec whereas the alpha motoneurone was firing only intermittently.

neurones whereas inhibition was never seen. We have noted the effect of vibration on the larger sample of gamma motoneurones studied here. Fig. 8 shows the responses to vibration and stretch of two gamma motoneurones. In both cases the neurone is

excited by vibration of triceps surae at 170 Hz with thresholds of around 10–20 μm and increases in the size of the responses are seen as the amplitude of vibration is raised. These two neurones, however, showed different responses to brief stretch. One was excited whereas the other showed a mixed response with inhibition preceding excitation. None of the twenty neurones showing mixed responses to stretch could be inhibited by vibration and the majority (eighteen) were excited. Of the eleven gammas showing pure inhibition to stretches of less than 50 μm only one was clearly inhibited by vibration of 50 μm amplitude and two were slightly inhibited when the amplitude of vibration was raised. Of those gammas unaffected by stretch only a few were excited by vibration, the majority (twenty-nine out of thirty-three) being unresponsive.

A comparison of alpha and gamma excitation by stretch. Sixteen alpha motoneurones with axonal conduction velocities in the range 52–109 m/sec were studied. Tonically firing alpha motoneurones rather than those which showed no background discharge were chosen for a direct comparison of stretch reflex responses with gamma motoneurones, though there were relatively few in our decerebrated preparations which had extensively denervated ipsilateral hind limbs. Responses of a tonically firing alpha and gamma motoneurone from the same cat are shown in Fig. 9. The stretch reflex response of the alpha motoneurone is clearly greater than that of the gamma motoneurone and the alpha motoneurone is being driven at a fairly fixed latency. However, the actual threshold amplitude of stretch for excitation of the two neurones is clearly below 12 μm in both cases. Similarly low thresholds for tonically firing alpha and gamma motoneurones were commonly seen in cats whose alpha motoneurones showed a background discharge. Alpha motoneurones which had no background discharge could be excited by stretch but amplitudes in excess of 100 μm were often needed. By contrast, the silent gamma motoneurones were inexcitable.

The short latency, driven response of alpha motoneurones was quite different from the excitation of gammas caused by stretch. Estimates of the central delay of the alpha stretch reflex in response to the Ia volley are given in Fig. 7 and range from 0·7 to 3·0 msec. The longer central delays for gamma excitation (5·1–13·7 msec) clearly indicate that the reflex was not monosynaptic and this poses the question whether the pathway is polysynaptic at a spinal segmental level or is transmitted through supraspinal structures.

A spinal pathway for gamma excitation to stretch. Reflex excitation of gamma motoneurones was sought in decerebrated cats with acute spinal section in the mid-thoracic region of the cord. The number of experiments was limited by the fact that few extensor gamma motoneurones have a background discharge in the spinal cat. We also needed to know whether a gamma motoneurone observed in the spinal cat would have been excited by stretch before spinal section. Four neurones from three cats were eventually selected which had the typical pattern of excitation to stretch in the decerebrated cat and retained a persistent background discharge following spinal section. In two of these gamma motoneurones reflex excitation was retained after spinal section and with a similar threshold and central delay. The reflex was comparatively much weaker in the third and absent in the fourth neurone.

Lack of participation of tap receptors (paciniform endings). In order to examine the possible part played by paciniform endings, the effects of muscle stretch and release

were compared. A longer (20 msec) length change was used for this purpose so that stretch and release could be seen as separate events. It was invariably found that the excitation of both alpha and gamma motoneurones was linked to stretch of the muscle rather than to release. It is likely that paciniform endings would have responded to movement in either direction.

DISCUSSION

There have been periodic reports in the literature, starting with that of Hunt in 1951, that stretch of a muscle may inhibit the discharge of gamma motoneurones supplying the spindles of that muscle. We do not intend to discuss this work which, apart from an article by Fromm, Haase & Noth (1974) has already been reviewed (Matthews, 1972) but will concentrate on the recent finding that *excitation* of gamma motoneurones can be the dominant response to discharges from primary spindle endings. The first reports that gamma motoneurones can be excited by muscle stretch receptors came independently from two laboratories where vibration had been used with the intention of exciting, selectively, the primary endings of muscle spindles (Trott, 1975; Fromm & Noth, 1975). Reflex excitation of gamma motoneurones by Ia afferents was an unexpected finding since gamma activity, in turn, increases the firing of spindle endings. The consequences of such positive feed-back in the spindle control of skeletal muscle makes it imperative to establish that the receptors involved are indeed the primary endings.

In this study the strongest evidence that it is the primary endings which excite gamma motoneurones when the muscle is stretched comes from a comparison of thresholds and response curves (see Fig. 4). Although the experiments have shown that few afferents other than primaries responded to low amplitude stretch under conditions where gamma excitation was seen, it is noteworthy that no units were found which might have been described as having paciniform endings. The fact that gamma excitation occurs only in response to lengthening of the muscle and not to release is further circumstantial evidence against the participation of paciniform endings.

If the excitatory action of stretch is attributed to discharges in group Ia afferents, what can be deduced concerning the origin of the inhibitory action on gamma motoneurones? Comparing the thresholds of reflex inhibition and afferent excitation we again conclude that the reflex response is a consequence of primary spindle afferent discharge. This being so, then certain properties of the reflex suggest that the recurrent inhibitory pathway is involved. The central delay of the stretch evoked inhibition in our study was, on average, 2 msec longer than that for excitation of alpha motoneurones. This agrees well with the estimates of central delay of recurrent inhibition of gamma motoneurones ($2{\cdot}3 \pm 0{\cdot}2$ msec, Ellaway, 1971). Furthermore, gamma inhibition was particularly evident in cats showing a high level of alpha excitability.

In contrast to single stretches, vibration at amplitudes of less than 50 μm did not, with one exception, evoke inhibition of gamma discharge. It is pertinent to recall here that the degree of excitation exceeds that of inhibition when mixed responses are evoked by stretch (see Fig. 5). Since vibration may be considered as a series of brief

stretches and the total period of the mixed response to stretch is short (10–15 msec) it is not surprising that in these cases excitation dominated the response to vibration. Those gamma motoneurones solely inhibited by stretch remained largely unaffected by vibration. The inhibitory response is thus markedly reduced on effectively repeating the stretch at 170 Hz. As recurrent inhibition may well be involved the explanation could lie in the fact that discharges of Renshaw cells excited by vibration decrease substantially within 20–30 msec of the start of vibration (Pompeiano, Wand & Sontag, 1974).

The present results obtained with vibration, together with those of Trott (1976), appear to be at variance with those of Fromm & Noth (1976) who reported that vibration of triceps surae regularly inhibits discharges of its own gamma motoneurones. From discussions with these authors and from inspection of their records it is clear that a considerably higher degree of alpha motoneurone discharge is present in their decerebrated cats. This will undoubtedly increase activity in the recurrent inhibitory pathway in their preparations. However, they also report that the degree of inhibition increases as the amplitude of vibration is raised from 50 to 100 μm. Although the frequency of firing of primary endings is still increasing over this range the stimulus is not selective. Stretch and vibration of such amplitudes, while not exciting group III afferents, stimulate some secondary spindle endings and tendon organs. Discharges in Ib axons have already been implicated in the autogenetic control of gamma motoneurones (Ellaway & Trott, 1976*a*) when contraction of a muscle was found to be a more potent inhibitor of gamma discharges than was stretch.

The reflex excitation of gamma motoneurones could be elicited in the spinal cat and we now feel that the long central delay of this reflex represents transmission in a polysynaptic spinal pathway (cf. Ellaway *et al.* 1976). The interesting possibility is thus raised that this polysynaptic pathway may be the same one that excites alpha motoneurones in the tonic phase of the stretch reflex (Granit, Phillips, Skoglund & Steg, 1957).

Until the recent finding that vibration can cause autogenetic excitation of gamma motoneurones interest in the projection of muscle afferents on to gamma motoneurones had always been directed at inhibitory responses. The reason, presumably, was that it was conceptually easier to fit such an inhibitory mechanism into the over-all picture of control of skeletal muscle. Recently, however, Houk (1972) has proposed that a positive feed-back loop from spindles on to gamma motoneurones could be advantageous. The properties of the reflex suggest to us that facilitation of gamma motoneurones may be invoked to provide a degree of reinforcement of spindle discharge for a critical period say, for example, during the initiation of movement. Such an action would have to be under strict control itself to prevent the occurrence of instability inherent in such positive feed-back.

The idea of reinforcement of fusimotor drive from activity in primary spindle afferents is not, of course, a new one. Mixed skeleto-fusimotor or beta axons, which divide to innervate both intra and extrafusal muscle fibres, are present in mammals (Bessou, Emonet-Dénand & Laporte, 1963) and are the only form of spindle motor control in amphibia. Unfortunately, we have little knowledge of the discharge properties and control of beta axons. We assume, since it is unlikely that they have

been excluded from the vast number of studies of alpha motoneurones, that they behave similarly, with respect to inputs from primary spindle afferents and other muscle afferents, to the purely skeletomotor axons. To what extent those gamma motoneurones which are excited by stretch parallel the behaviour of a specific type of alpha or beta motoneurone thus remains unresolved. It is, nonetheless, reassuring when proposing positive feed-back on to gamma motoneurones to know that animals cope with the beta axon system which itself appears potentially unstable.

Biological systems use positive feed-back to advantage, for example, in ionic permeability changes across membranes, but with the proviso that the feed-back loop can virtually be regarded as open for certain periods. Runaway situations are thus avoided and the resulting control is of an all or nothing nature. Further investigation of the control of gamma motoneurones is required to establish whether the rather weak autogenetic excitation of gammas represents merely the minimal state, or 'off' position, of a reflex which can be potentiated when required to assist in movement.

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