

THE RESPONSE TO
STRETCH OF MUSCLE SPINDLE AFFERENTS OF BABOON'S
TIBIALIS ANTICUS AND THE EFFECT OF
FUSIMOTOR STIMULATION

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(Received 21 January 1968)

SUMMARY

1. Systematic studies of the response of baboon's tibialis anticus muscle spindles to stretch were undertaken. Most of the spindle afferents studied had conduction velocities between 72 and 78 m/sec with a range from 39 to 93 m/sec. There was no clear bimodality in the histogram of the conduction velocity. Measurements were made of the axon diameters of the nerve to tibialis anticus. The largest number of the larger axons had diameters from 11 to 13 μ . The largest axon diameter measured 17 μ and there were very few of these.

2. The dynamic index for any given afferent tended to be greater for the more rapidly conducting afferents and lower for the more slowly conducting afferents. However, a statistically significant regression line of this relationship could only be drawn for a stretch velocity of 64 mm/sec.

3. The spindle afferent response to stretch was studied from different muscle lengths. It was found that the velocity sensitive portion of the response to phasic stretch decreased when the stretch extended up to or beyond the maximum physiological length of the muscle.

4. Dynamic and static fusimotor fibres were isolated. The response of the spindle afferent to stretch, while the dynamic fusimotor fibre was being stimulated, was the same as that reported for the cat by P. B. C. Matthews (1962). During static fusimotor stimulation the response of the spindle afferent to stretch was usually like that reported for the cat. In a single case, however, static fusimotor stimulation resulted in a lowering of the peak frequency of the response of the spindle afferent to the phasic portion of stretch.

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INTRODUCTION

There are numerous studies of the response of mammalian muscle spindles to stretch and the conduction velocities of their afferents (P. B. C. Matthews, 1964). A systematic study of primate muscle spindle response to muscle stretch at different velocities could not be found in the literature. In the course of other experiments (Koeze, 1968) observations were made on the conduction velocities of spindle afferents and the response of muscle spindles to different velocities of stretch. These observations are reported here.

METHODS

The conduction velocities of the spindle afferents were collected from thirty-two immature baboons (*Papio* sp.) of an average weight of 5.5 kg wt. (range 4.7–6.8 kg. wt.). The ventral roots (L4 to S2 on the right side) of seven animals were cut and the response of the deafferented muscle spindle to stretch of *tibialis anticus* was studied.

The induction and maintenance of anaesthesia, operative procedures, isolation and identification of spindle afferents, recording of action potentials, measurement of conduction time, frequency measurements, muscle tension measurements, and the method of stretching the muscle have been described elsewhere (Koeze, 1968; Koeze, Phillips & Sheridan, 1968).

In some experiments the ventral root filaments were stimulated in order to observe the effect of fusimotor stimulation on the spindle discharge. A muscle spindle afferent was isolated and then the cut ventral roots were divided into 10–15 large filaments (Crowe & Matthews, 1964). With the spindle afferent on the recording electrode, each of the large ventral root filaments was stimulated in turn with 100/sec, 0.1 msec duration pulses. Those filaments which increased the discharge of the spindle afferent were again split until only this effect was obtained, and no tension change recorded when the filament was stimulated. No detailed study of the fusimotor fibres was made other than to observe that they could be divided into static and dynamic effects on the spindle afferent as demonstrated for the cat by P. B. C. Matthews (1962).

Histological studies. As the fastest conduction velocities for spindle afferents obtained in this study were less than those found in the cat (Hunt, 1954; P. B. C. Matthews, 1963), histological studies of the *tibialis anticus* muscle nerve were undertaken. The muscle nerve in the baboon divides into several branches before entering the muscle, and no attempt was made to remove the nerve completely. Each portion studied was traced back into the muscle and dissected from surrounding muscle fibres and cutaneous nerves for about 5–10 mm. The nerves were removed shortly after death from five immature baboons of approximately the same age and weight as those used in this study. The nerves were fixed in 0.5% osmic acid for 48 hr, then dehydrated, mounted in wax, and cut. Photographs were taken of the mounted sections and the diameters were measured from these photographs.

Nomenclature. The terms for the three portions of stretch, the phasic response, the static frequency, the dynamic index, the resting discharge, and the peak frequency used in this study are defined in the preceding paper (Koeze, 1968).

RESULTS

Conduction velocities and axon diameters. The histogram of the conduction velocities of 100 spindle afferents is illustrated in Fig. 1. The largest number of afferents had conduction velocities between 72 and 78 m/sec. The fastest conduction velocity recorded was 93 m/sec, the slowest

39 m/sec. The bimodality of conduction velocities, often noted in studies of cat spindle afferents (Merton, 1953; Hunt, 1954), was not convincing in this study.

During this study the conduction time of fifteen Golgi tendon organ afferents was recorded to obtain an indication of the conduction velocity of this type of afferent. Not all the Golgi tendon organ afferents found

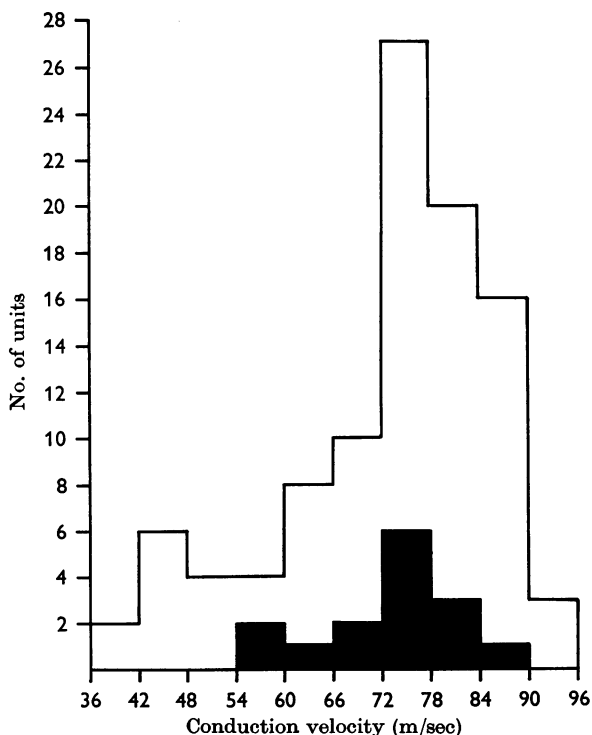


Fig. 1. The conduction velocity of 100 muscle spindle afferents (outline) and fifteen Golgi tendon organ afferents (solid bars) from tibialis anticus. The largest number of both types of afferents occurred in the 72-78 m/sec group.

were studied. The histogram for the Golgi tendon organ afferents is shown in Fig. 1 (solid bars). The conduction velocities ranged from 54 to 86 m/sec, being most numerous in the range 72-78 m/sec.

The axon diameters of the nerve to tibialis anticus were measured in five baboons of age and weight similar to those used in this study. The histograms of the axon diameters obtained from two of these animals are shown in Fig. 2. These show two peaks, one at 2-4 μ , and another at 11-13 μ . If it is assumed that the primary afferents will be in the larger group, then using Hursh's (1939) factor of 6 would give an expected conduction velocity of 66-78 m/sec for these fibres, which is close to that

found. As the largest axon diameter measured was $17\ \mu$, the fastest conduction velocity to be expected would be $102\ \text{m/sec}$. The fastest conduction velocity found in this study was $93\ \text{m/sec}$. The lower con-

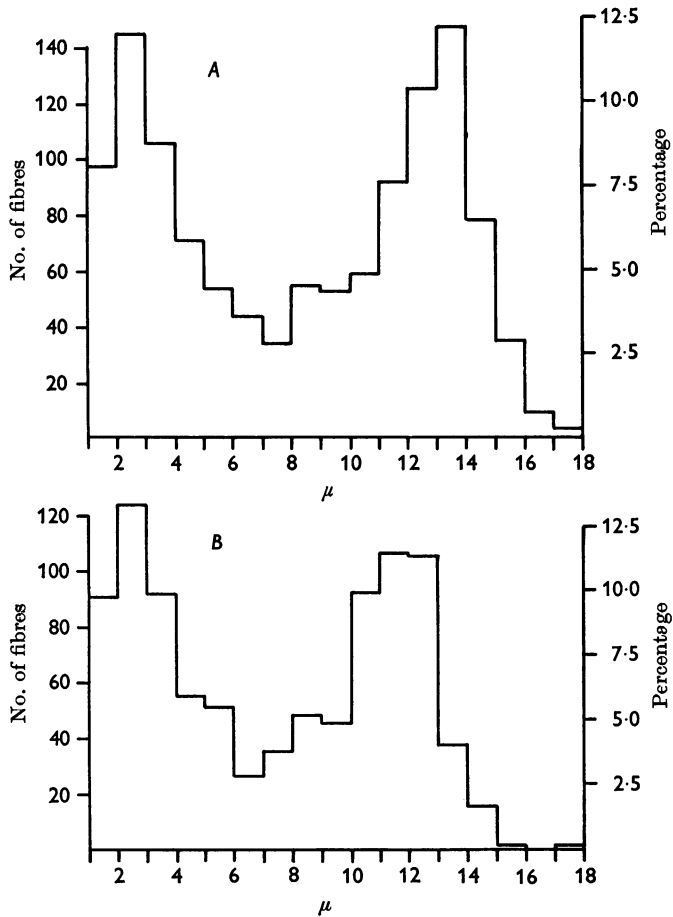


Fig. 2. Axon diameters of a portion of the nerve to tibialis anticus in two baboons. *A*, 5.7 kg wt., female and *B*, 5.5 kg wt., male. The number of fibres is shown on the left, the percentage of the total number of fibres is shown on the right. The largest fibre measured in this series was $17\ \mu$. Histograms of the axon diameters of fibres in the tibialis anticus muscle nerve of three other baboons were similar to those presented here.

duction velocities found in this study are reflected in the smaller axon diameters in the muscle nerve.

Dynamic index and conduction velocity of de-efferented spindle afferents. In the cat P. B. C. Matthews (1963) found a relation between the conduction velocity of the spindle afferent and its dynamic index. In general,

as the conduction velocity increased the dynamic index also increased. In this study the relationship was examined at three different stretch velocities, 16, 44 and 64 mm/sec. The results of the 16 and 64 mm/sec stretch, for a number of spindle afferents of de-efferented muscle spindles,

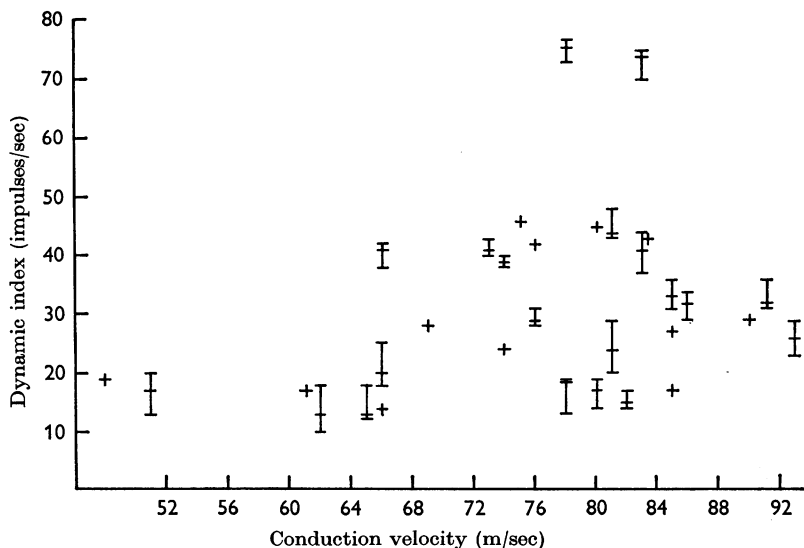


Fig. 3. The conduction velocity in m/sec of thirty-two muscle spindle afferents plotted against the dynamic index in impulses/sec for 16 mm/sec stretch applied to tibialis anticus. A regression line calculated from the average of the dynamic index of several stretches was not statistically significant. The vertical bars represent the range of the dynamic index found, the horizontal bar represents the mean. The + indicates that the dynamic index was identical for all the responses studied.

are shown in Figs. 3 and 4. The dynamic index was measured for a minimum of three, but usually for six to eight stretches. The range of the dynamic index is shown by the length of the vertical line while the horizontal bar shows the mean. Regression lines for each of the three different velocities of stretch were calculated from these means.

In each case the regression line showed a positive slope, that is the dynamic index increased with the conduction velocity. However, the slope for the 16 mm/sec stretch (0.450 (impulses/sec)/(m/sec), $r = 0.31$, $t = 1.735$, $0.10 > P > 0.05$, s.e. ± 0.25) and for the 44 mm/sec stretch (0.501 (impulses/sec)/(m/sec), $r = 0.238$, $t = 1.29$, $0.30 > P > 0.20$, s.e. ± 0.397) were not statistically significant. The slope for the 64 mm/sec stretch, 1.845 (impulses/sec)/(m/sec), was significant ($r = 0.645$, $t = 2.39$, $0.05 > P > 0.02$, s.e. ± 0.75).

For most afferents the dynamic index became greater with an increase in the velocity of stretch. However, in a single case, the dynamic index

for a 44 mm/sec stretch was greater than the dynamic index for the 64 mm/sec stretch. For the thirty-two de-efferented spindle afferents studied during 16 mm/sec stretch the greatest peak frequency found was 150 impulses/sec for a spindle afferent with a conduction velocity of 83 m/sec, while the lowest was 47 impulses/sec for an afferent with a conduction velocity of 66 m/sec. The static frequency was little affected by the stretch velocity. With some units, however, there was a slight fall in the static frequency at the fastest velocity of stretch.

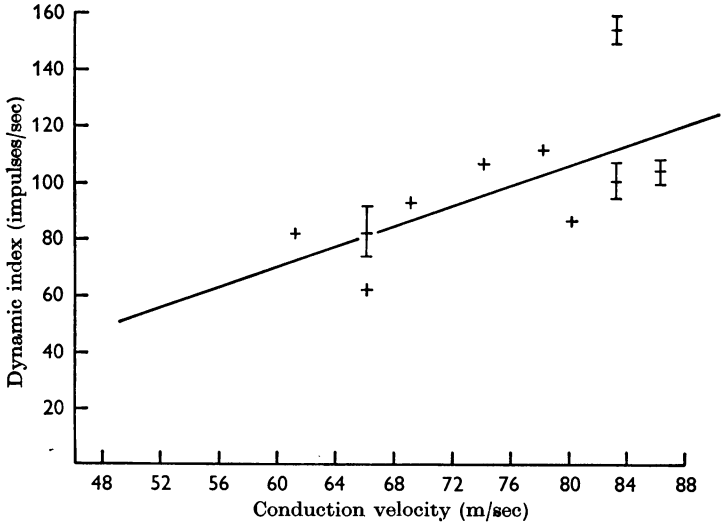


Fig. 4. The condition velocity in m/sec of ten muscle spindle afferents plotted against the dynamic index for a 64 mm/sec stretch applied to tibialis anticus. The regression line was calculated as in Fig. 3. The symbols are as in Fig. 3.

The slowest conduction velocity of the thirty-two de-efferented muscle spindles was 48 m/sec. This afferent had a dynamic index of 20 impulses/sec. The dynamic response of this afferent was similar to that of afferents with a much higher conduction velocity. At the end of phasic stretch there was an abrupt fall in discharge frequency, and there was no discharge during release of stretch. Some afferents, with their efferent innervation intact, responded to stretch with a low dynamic index, and continued to discharge during the release of stretch. These afferents had conduction velocities below 48 m/sec and were probably secondary spindle afferents, but this is not certain as their efferent nerve supply was intact.

Atypical spindle afferent response. The response for most of the spindle afferents closely resembled those in Fig. 6 for stretches from the 'initial length'. One spindle afferent, however, showed responses to stretch that were rather different. The frequency of discharge of this afferent (con-

duction velocity 78 m/sec) showed a slow adaptation during tonic stretch, and when stretched from the minimum physiological length plus 5 mm the phasic response and static frequency were increased. The afferent response to muscle stretch of this 'atypical' afferent closely resembled the atypical afferent shown by P. B. C. Matthews (1963, his fig. 4, record C). One spindle afferent was also seen which responded maximally in the middle rather than at the end of the phasic portion of stretch. This resembled the afferent response reported by P. B. C. Matthews (1963, his fig. 7).

Response of spindle afferents in extensor digitorum longus to tibialis anticus stretch. In the preparation used for this study it was possible for extensor digitorum longus muscle spindles to escape denervation, and it was important to differentiate between spindle afferents from this muscle and those from tibialis anticus. Because of the numerous fascial attachments between extensor digitorum longus and tibialis anticus, stretching tibialis anticus may stretch portions of extensor digitorum longus, and spindle afferents in that muscle will be affected. The response of extensor digitorum longus spindle afferents to a tibialis anticus stretch is shown in Fig. 5. In this experiment two mechanical hydraulic stretchers were used, one connected to the tibialis anticus tendon and the other to the extensor digitorum longus tendon. A spindle afferent responding to extensor digitorum longus stretch is shown in Fig. 5A. When tibialis anticus was stretched the myograph attached to extensor digitorum longus tendon showed an early relaxation followed by a slight increase in tension. This relaxation in tension was reflected in the extensor digitorum longus spindle afferent discharge as a pause in the resting frequency before the acceleration of the discharge (Fig. 6B). However, the afferent discharge during tonic stretch was greater than the resting discharge, while the extensor digitorum longus muscle tension during tonic stretch was still below that of the resting tension before tibialis anticus stretch. At the end of the tibialis anticus stretch the muscle tension of extensor digitorum longus returned to the resting level. The explanation for these results is obscure and probably involves complex mechanical coupling arrangements between the two muscles. The pause in the extensor digitorum longus afferent discharge during early tibialis anticus stretch was consistent in the four extensor digitorum longus afferents tested in this way. When a spindle afferent was found that responded in this manner it was discarded from the study.

Spindle afferent response at the limits of physiological stretch. The results presented above were for muscle spindles stretched from the shortest physiological length of the muscle. There was a poor correlation between the magnitude of the dynamic index and the conduction velocity of the afferent fibre. A possible explanation was that some muscle spindles were more sensitive to length changes near the physiological maximum length. A number of observations were made on the effect of stretch of the muscle below, at, and beyond the maximum physiological length. Figure 6 illustrates the changes in the response of three de-efferented spindle afferents (A, B and C) that occurred when 5 mm was added to the minimum physiological length and the muscle was stretched from that point. In Fig. 6A the response at the initial length is shown on the left. Five millimetres was added to the minimum physiological length, and the

muscle was extended from that distance with the same length of stretch used in the record marked 'initial length'. The effect of the added length on this spindle afferent during the phasic portion of the record was to decrease the slope of the frequency-extension relationship. In Fig. 6*B* the phasic response approaches a maximum earlier, and appears to remain almost constant during the terminal portion of the phasic stretch. In Fig. 6*C* the response of this spindle afferent to stretch is nearly constant during most of the phasic portion of the stretch. Five millimetres added to the

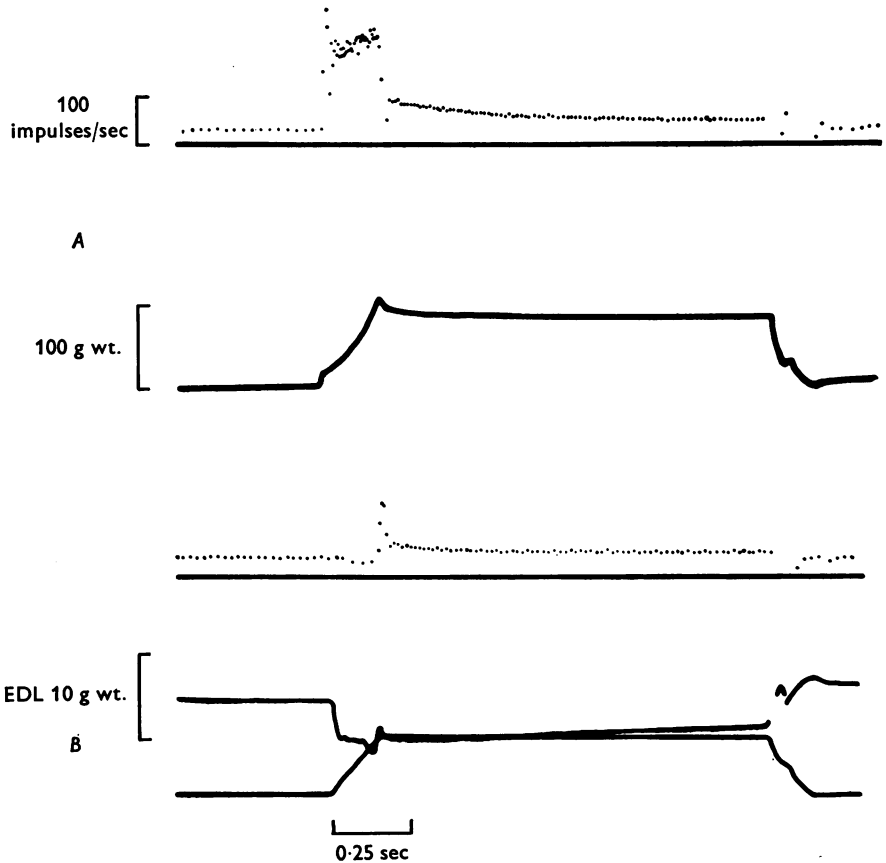


Fig. 5. Response of a muscle spindle in extensor digitorum longus to stretch of extensor digitorum longus (EDL) and stretch of tibialis anticus (TA). Conduction velocity of the afferent 83 m/sec. *A*. 44 mm/sec stretch of extensor digitorum longus. *B*. 44 mm/sec stretch of tibialis anticus. Ramp of stretch applied to tibialis anticus directly beneath myograph record of extensor digitorum longus. Note decrease in the frequency of discharge associated with relaxation of extensor digitorum longus when tibialis anticus is stretched and the lower dynamic response of the unit. Frequency meter, myograph, and stretch ramp retouched for reproduction.

physiological minimum length caused the frequency of the discharge to approach a maximum and then to fall. Of the twenty-one afferents studied in this way, eleven showed a decrease in the slope of the frequency-extension relationship, while seven showed no change and three showed an increase.

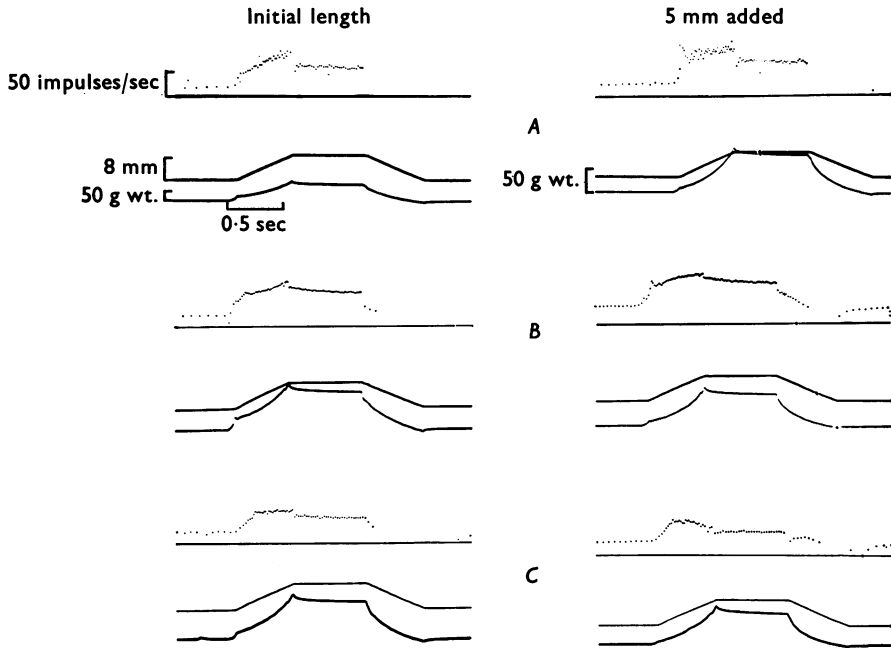


Fig. 6. The response of three de-afferented spindle afferents. *A*, conduction velocity 86 m/sec; *B*, conduction velocity 51 m/sec; and *C*, conduction velocity 65 m/sec. On the left is the response to stretch, 16 mm/sec, from the initial length. Five millimetres was then added to the initial length and the muscle stretched at the same rate and distance as before. Afferents *A* and *C* were stretched 3 mm beyond the maximum physiological length, afferent *B*, to its maximum physiological length. Note the change in the frequency-extension relationship and its deterioration in *C* on the right. Myograph calibration for *A* on the right applies to the myographs of *B* and *C*. The stretch ramp, just above the myograph record, is shifted slightly to the right of the myograph record. This was an artifact that occurred in photographing the traces on the oscilloscope screen.

The effect on the dynamic index of adding 5 mm to the minimum physiological length is summarized in Fig. 7. Two points are plotted, the dynamic index at the end of a 16 mm/sec stretch, which extended from the minimum physiological length to a 9 mm extension, and the dynamic index for a 16 mm/sec stretch which extended from the minimum physiological length plus 5 mm to a 14 mm extension of the muscle. The distance from the minimum physiological length is scaled along the

abscissa. The solid bar just above the abscissa indicates the distance from the minimum to the maximum physiological length. In Fig. 7A the stretch beginning at 5 mm beyond the minimum physiological length ended at the maximum physiological length. In Fig. 7B it extended 1 mm beyond the maximum physiological length, and in Fig. 7C it extended 3 mm

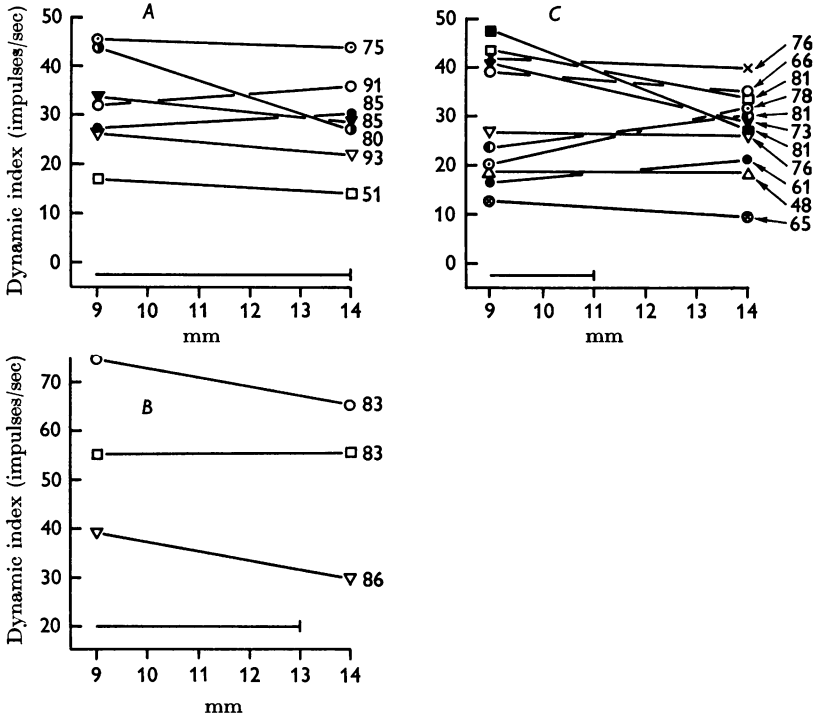


Fig. 7. Summary of the effects of adding 5 mm to the initial length on the dynamic index of de-efferented muscle spindle response to 16 mm/sec stretch. The dynamic index (impulses/sec) is scaled on the ordinate, the length in millimetres at the end of stretch on the abscissa. The horizontal bar just above the abscissa indicates the maximum physiological length of the muscle. Graph A, stretch ends at the physiological length; B, stretch ends 1 mm beyond the maximum physiological length and C, stretch ends 3 mm beyond the maximum physiological length. The conduction velocity is shown just to the right of the last point plotted.

beyond. Of the spindle afferents studied in this way the response of eleven afferents showed a decreased dynamic index, five remained unchanged and in five the dynamic index was increased. The conduction velocity for each unit is given just to the right of the last point plotted. There appears to be no clear relationship between the increase or decrease of the dynamic index with the extent of stretch, the conduction velocity, or the extent of stretch beyond the maximum physiological length. However, the eleven afferents which showed a decrease in the dynamic index also

showed a decrease in the slope of the frequency-extension relationship. Possible implications of these findings are discussed below.

Effects of fusimotor stimulation. A limited number of observations were made on the effects of fusimotor stimulation. Ten fusimotor fibres were isolated, but only in three was it possible to stimulate the fusimotor fibre without any detectable activation of alpha fibres. Both static and

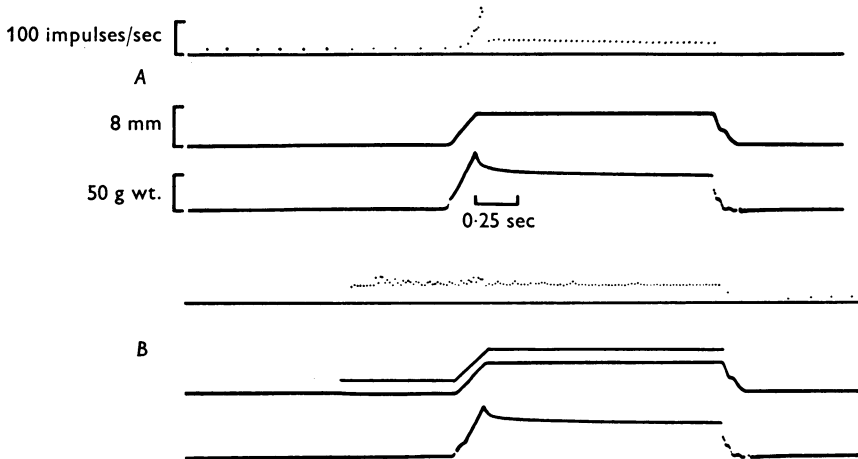


Fig. 8. Static fusimotor fibre. Spindle afferent conduction velocity 69 m/sec. Fusimotor fibre conduction velocity 25 m/sec. *A.* Spindle afferent response to 44 mm/sec stretch. *B.* Spindle afferent response to 44 mm/sec stretch during 100 sec tetanic stimulation of the fusimotor fibre. For this spindle afferent both the peak frequency and the dynamic index were decreased. Usually both the peak frequency and static response were increased, but the latter more so, with a resultant decrease in the dynamic index.

dynamic types of fusimotor fibres described by P. B. C. Matthews (1962) were found. The effects of stimulation of the one dynamic fusimotor fibre and one of the static fusimotor fibres on the spindle afferent response to stretch was the same as those described for the cat by other authors (P. B. C. Matthews, 1962; Crowe & Matthews, 1964; Appelberg, Bessou & Laporte, 1966).

When stimulated, the other static fusimotor fibre (Fig. 8) decreased the peak frequency of the dynamic response, while the static response was increased. As a result the 16 mm/sec stretch had no dynamic index. The dynamic index was decreased by static fusimotor stimulation at all velocities of stretch.

DISCUSSION

The experiments on the effects of cortical stimulation on spindle afferent response were almost entirely concerned with primary spindle afferents (Koeze, 1968). Many spindle afferents which were difficult to isolate were

discarded. Possibly, because the secondary afferents are smaller, they are more difficult to isolate. This bias would account for the lack of secondary spindle afferents in this study, and would be responsible for the lack of bimodality in the conduction velocity histograms. Spindle afferents were found with low conduction velocities and responses which appeared to classify them as secondary afferents. However, since the ventral roots were intact, it was difficult to be certain.

The conduction velocities of the primary spindle afferents were slower than those found in the cat. The value of 72 m/sec is usually used as the lower limit of conduction velocities of primary afferents in the cat (Hunt, 1954). In this study the largest number of primary afferents had conduction velocities between 72 and 78 m/sec. These conduction velocities correlated very well with the measurements of the larger axons of the muscle nerve. The variation in the axon diameters from animal to animal was probably caused in part by taking the nerves at different distances from the muscle and variations in branching may have occurred (Eccles & Sherrington, 1930).

Another difference between primary spindle afferents in baboon and cat is the relationship between conduction velocity and dynamic index. Only for the most rapid stretches (64 mm/sec) could a statistically significant slope for a calculated regression line be found. Comparison with the plot of this relationship for the cat (P. B. C. Matthews, 1963) suggests a much steeper slope for the cat. There is no obvious explanation for this difference unless it is assumed that there is a species difference or a difference between muscles (P. B. C. Matthews, 1963, used cat soleus).

The estimation of the shortest physiological length of tibialis anticus was difficult. That this was only an approximation is suggested by the range of the length change from the minimum to the maximum physiological length of 8–19 mm (Koeze, 1968). Since the length of stretch used in this study was usually 7–9 mm, some spindle afferents were stretched to near their physiological maximum limit while others were stretched to less than half that distance. In order to study the effect this might have on the dynamic index, observations were made on the spindle afferent response when the muscle was stretched to just below, at, and beyond the maximum physiological length. Of twenty-one afferents studied in this way, eleven showed a decrease in the dynamic index. These same eleven afferents showed a decrease in the slope of the frequency–extension relationship. The peak frequency was the same for the stretch from the ‘initial length’ and the stretch from the ‘initial length’ plus 5 mm. In record *C*, Fig. 6, the slope of the frequency–extension relationship was nearly flat for the stretch from the initial length. When 5 mm was added to the initial length the slope decreased and peak frequency was less

than the frequency at mid-phasic stretch. However, the peak frequency for these 16 mm/sec stretches was nowhere near the absolute maximum value at which the spindle afferent was capable of firing. During more rapid stretches, 44 mm/sec and 64 mm/sec, the peak frequency was much higher.

The phasic response has two components, that due to the velocity sensitive component, and that due to the length extension component. The decrease in the slope of the frequency-extension relationship could be due to a decrease in either. If the length extension component is decreased while the velocity sensitive component remains constant, the dynamic index will increase or remain the same when the slope of the frequency-extension relationship decreases. This occurs because the length extension component is reflected in the static frequency. This was not the case. In these experiments the dynamic index was decreased when the slope of the frequency-extension relationship fell. These results indicate that the velocity sensitive component decreases when the extension of the muscle approaches or exceeds the maximum physiological length for the muscle spindle. There is, of course, the possibility that both the length extension component and the velocity sensitive component are affected together. The results could be explained by a relative greater effect on the velocity sensitive portion than on the length extension component.

This decay in the velocity sensitive component of the phasic response can be seen in the observations of B. H. C. Matthews (1933), his fig. 7. The cat soleus was stretched at a fixed rate to four different tensions and the dynamic index (as roughly calculated from his graph) fell from about 150 impulses/sec for a stretch to 20 g wt. tension to about 50 impulses/sec for a stretch to 200 g wt. tension. He suggested that as the extension of muscle spindle progresses, the viscous stresses on the end organ became a smaller fraction of the total stress on the spindle. Jansen & Matthews (1962, their fig. 4) also showed an afferent with a tendency for the dynamic index to decrease when the stretch approached the maximum physiological length.

The implications for this study are that the dynamic index may, to some extent, be dependent on the length from which the muscle spindle is stretched. Different muscle spindles, from different experiments, stretched from different physiological lengths relative to the operational range of the individual muscle spindle, may be in part responsible for the scatter of the dynamic index-conduction velocity relationship (Fig. 3).

For a number of spindle afferents the slope of the frequency-extension relationship and the dynamic index was increased when 5 mm was added to the physiological length. That the opposite occurred in other spindle afferents in the same muscle suggests that the physiological extension

limits, in absolute terms, may not be alike for each spindle. This might have occurred as a result of removing the tibialis anticus from its medial attachments and placing it laterally so that the pull was 'in line' with the leg. As a result the spindles in the medial portion of the muscle may have been 'over stretched', while those in the lateral part were 'under stretched', but this is only speculation.

As far as could be determined, the fusimotor fibres of primates have not been investigated for dynamic and static effects on muscle spindle afferents. The only difference in this study from the original observations of P.B.C. Matthews (1962) was in the single case where the peak frequency of the spindle afferent response was reduced by static fusimotor stimulation. Though this reduction of the peak frequency consisted of the loss of only three impulses at the end of phasic stretch, this reduction was consistent and seen with the more rapid 44 and 64 mm/sec stretches. This might be explained by unloading of the nuclear bag region by nuclear chain intrafusal fibres. Both in man (Cooper & Daniel, 1956) and in the baboon (personal observation on extensor digitorum communis) there are more nuclear chain fibres per spindle (up to ten in man and nine in the baboon) than the cat. For this afferent, stimulation of the static fusimotor fibre increased the resting frequency so much that the response to a 16 mm/sec stretch could hardly be seen. The static frequency was in fact the same as the frequency just before the stretch. This was also true for stretches at 44 and 64 mm/sec. More observations on static fusimotor fibres are needed to confirm these findings.

This work was supported in part by American Cancer Society Post-doctoral Research Scholarship PRS 16. The author expresses his appreciation to Professor C. G. Phillips for help, guidance, and use of laboratory facilities; Mr R. Vanhegan for preparing the photographs of the nerves; Mr C. H. Carr and Mr A. Durrance for technical assistance.

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