RELATION OF FUNCTION TO DIAMETER IN AFFERENT FIBERS OF MUSCLE NERVES*

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Nerves to muscle contain, in addition to motor fibers, large numbers of myelinated afferent fibers of various diameters (2, 17). Recently the distribution of afferent fibers according to diameter has been studied in de-efferented nerves to a number of hind limb muscles of cat (11, 15). The diameter spectra so obtained show that, as a general pattern, the afferent fiber diameters have three maxima of distribution. Segregation of fibers according to diameter permits classification into the following categories: group I (12 to 20 μ), group II (4 to 12 μ), and group III (1 to 4 μ). The present study attempts to assign receptors of known structure, and function, to fibers of the various diameter groups.

Limb muscles contain two major receptor structures, muscle spindles and tendon organs. The muscle spindle is a complex sense organ, fusiform in shape, which lies parallel to the contractile muscle fibers. Within the encapsulated spindle structure are a number of slender (intrafusal) muscle fibers which receive the terminations of small motor fibers. In the central portion of the spindle the intrafusal muscle elements are entwined by terminal ramifications of afferent fibers (1, 16, 17). Each spindle contains the ending of one large diameter afferent axon, the primary or annulospiral ending. In addition, many spindles receive one or two smaller myelinated afferent fibers which terminate, adjacent to the primary ending, in secondary or flower-spray endings. Stretch deformation of the afferent terminals of the spindles leads to depolarization and initiation of impulses (8). External stretch of muscle evokes discharge in spindle afferent fibers, the frequency of which is a function of rate as well as magnitude of stretch (12). Contraction of the parallel extrafusal muscle fibers decreases the amount of stretch deformation on spindle afferent terminals and causes a cessation or slowing of discharge. Recently another factor has been found to modify discharge in spindle afferent fibers. The group of small diameter (3 to 8 μ) efferent fibers to hind limb muscles of cat has been shown to provide the motor innervation to intrafusal muscle fibers (9, 10). Small motor fibers can be isolated in ventral roots and on stimulation initiate a

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discharge, or increase the frequency of an established discharge, in afferent fibers from spindles; an effect which must result from contraction of the intrafusal muscle fibers. Nerve fibers may be identified as afferent from muscle spindles by discharge pattern during contraction and by their response to excitation of small motor fibers.

The tendon organ is a simpler receptor in which the stretch-sensitive ending of a large diameter afferent nerve fiber lies effectively between the contractile muscle elements and the tendon. Frequency of its discharge provides a fairly direct measure of tension in the tendon whether this be developed by the muscle in contraction or by application of external stretch (12). Increase in discharge rate during contraction is the principal identifying feature of the tendon organ afferent fibers.

Afferent fibers may terminate within the muscle in structures other than spindles and tendon organs. The morphology and discharge characteristics of afferent endings other than those responding to stretch are little known. In addition to myelinated fibers, here under study, there exist unmyelinated afferent fibers from muscle, in smaller proportion than in skin nerves (14). While many afferent fibers from muscle are concerned with stretch reception, others must convey impulses concerned with muscle pain and perhaps other, as yet unknown, types of afferent message.

Afferent fibers from tendon organs and muscle spindles were found to occupy the group I diameter band (12 to 20 μ) although a few smaller spindle afferent fibers were also detected (6). Recently, Merton (13) has also described several spindle afferent fibers from tibialis anterior which were of group II diameter. However, no systematic study has yet been made which would permit assignment of function to the various fiber groups. The present study will show that a reasonably complete accounting of function-diameter relation in groups I and II now is possible. The function of group III fibers remains unknown.

Method

Afferent fibers to soleus and to medial gastrocnemius of the cat have been examined. Individual fibers to these muscles were isolated in filaments of dorsal root, their identity being established by the recording of an impulse following stimulation of the appropriate muscle nerve. Conduction times from muscle nerve to dorsal root were recorded and, at the conclusion of the experiment, the conduction distance was measured. Conduction velocities were calculated from measurements of conduction time and distance. The direct relation between fiber diameter and conduction velocity enabled the latter to be converted to calculated diameter using a factor of 6 (7). Several details of procedure deserve mention.

Laminectomy and limb dissection were performed on adult cats which were either decapitate or anesthetized with dial-urethane. Exposed tissues were covered with

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paraffin oil equilibrated with 5 per cent CO_2 and 95 per cent O_2 and kept at 37–39°C. Fibers in spinal roots were isolated by gentle longitudinal teasing of filaments, usually performed on a glass plate The filaments were raised onto platinum electrodes in oil for recording. Upon completion of the examination of isolated fibers a stimulus was usually applied to the reassembled dorsal root and an antidromic volley recorded from the then cut muscle nerve. The nerve in continuity from dorsal root to muscle nerve was excised and the conduction distance measured with the nerve stretched taut. From stimulus-response intervals 0.1 msec. has been deducted to allow for delay in initiation of impulses at the stimulating cathode.

Damage incurred by longitudinal splitting of dorsal root filaments may cause block or slowing of impulse conduction at some point after, or even before, the filament leaves the rest of the spinal root. To minimize error in latency measurement from this cause the first recording electrode was placed near the point of exit of the filament from volume, latency being measured from shock artefact to onset of spike negativity. Conduction in the final portion of the nerve pathway was often abnormal due to flow of demarcation currents from cut ends as well as from points of injury. Fortunately the region of abnormality represents but a small fraction of the total conduction path and hence was cause for little error in latency measurement.

The aim was to detect fibers of all diameters which were afferent from the muscle under study. Since spike potential amplitude varies with fiber diameter, impulses in larger fibers are recorded most readily. In order to detect the smaller fibers it was necessary to record from thin strands of dorsal root to minimize the external shunt. In each experiment a systematic search was made for afferent fibers in a number of adjacent dorsal root filaments. The rootlets were teased into thin strands and the strands were examined one after another so as to detect, as far as possible, every afferent fiber from the muscle under study. This method of serial examination of root filaments was employed in order to avoid selection of fibers preferentially according to diameter. A different method was used by Hunt and Kuffler (6) to detect muscle afferent fibers. They examined dorsal root filaments for impulses evoked by stretch or contraction of the muscle. The root filaments were subdivided until the response of a single fiber remained. Such a procedure clearly favored isolation of larger fibers since those giving the largest potentials were detected most readily. The method used in the present study was designed to permit isolation of all fibers which yield impulses of detectable size following a stimulus to the muscle nerve. The relation of spike potential amplitude and fiber diameter may be expected to limit the sample to fibers above a certain size but within some diameter range the sample should be representative.

RESULTS

The Sample of Isolated Fibers

By systematic examination of dorsal root filaments, 322 afferent fibers from soleus and 306 from gastrocnemius have been studied. The selection of

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isolated fibers is certain to be influenced by fiber size because of the relation of diameter to spike potential amplitude. In order to determine the diameter range over which a representative sample has been obtained, a diameter spectrum has been made relating numbers of isolated fibers to their estimated diameters (calculated according to the velocity/diameter ratio of Hursh). Fig. 1 shows the reconstructed spectrum of afferent fibers from soleus (solid

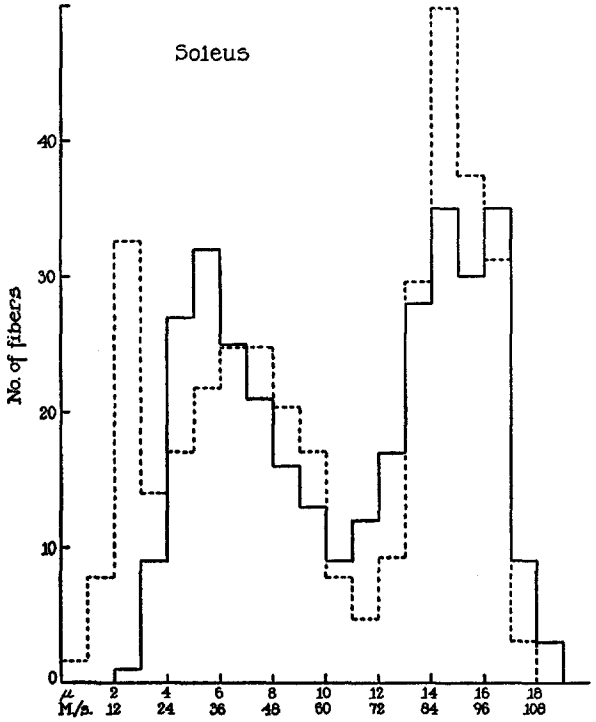

FIG. 1. Comparison of the diameter distribution of isolated fibers and the histological afferent fiber distribution. Soleus nerve. Solid line, numbers of isolated fibers according to conduction velocity and calculated diameter. Dashed line, diameter spectrum by histological measurement (from cat II, Lloyd and Chang (11)). Both distributions are scaled so that the numbers in the range 4 to 20 μ are the same.

line) together with the histological diameter distribution of afferent fibers in a nerve to soleus (dotted line, taken from Lloyd and Chang (11)). The distributions of the fiber diameters in the two spectra are similar for the range above 4 μ, a fact that suggests that fibers in this diameter range can be detected by the isolated fiber technique in proportion to their incidence in the muscle nerve. Further, the similarity of the isolated fiber and histological spectra indicates that the measurement of conduction velocities and the factor used for conversion of velocity to diameter are valid.

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Fig. 2 compares, in the manner described above, the reconstructed isolated fiber diameter distribution and the histological diameter spectrum (from cat II, Lloyd and Chang (11)) of afferent fibers to medial gastrocnemius. As for soleus, comparison of the two spectra indicates a representative sampling of group I and II fibers. Fibers in group III have seldom been detected, the principal difficulty being size of recordable potential.

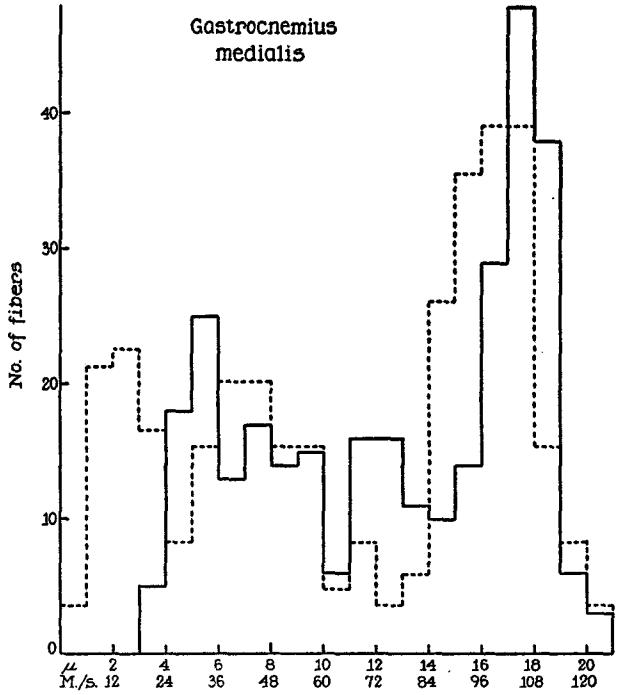

FIG. 2. Comparison of the diameter distribution of isolated fibers and the histological afferent fiber distribution. Nerve to medial gastrocnemius. Solid line, numbers of isolated fibers according to conduction velocity and calculated diameter. Dashed line, diameter spectrum by histological measurement (from cat II, Lloyd and Chang (11)). Both spectra are scaled as in Fig. 1

One factor should be considered in comparing the histological and isolated fiber diameter distributions. The former is derived from one animal, the latter from many. Thus, the isolated fibers from soleus were studied in thirteen animals, those from medial gastrocnemius in ten. The extent of variation from animal to animal in the diameter spectra of muscle nerves has not been studied systematically. However, skin nerves from several animals have been compared. Thus the saphenous nerve is known to vary considerably from cat to cat, not in the relative position of the various fiber groups but in absolute position on the diameter scale (3). The extent to which similar variation occurs in muscle nerves is not known but comparison of maximal conduction

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velocities of afferent volleys in the nerves studied (Table I) indicates that variation in maximal diameter is approximately 10 per cent. If the absolute position of the spectrum on the diameter scale differed considerably among animals, a representative sample of fibers would produce a reconstructed spectrum with contours less distinct than a spectrum derived from one nerve.

Fiber Diameter and Receptor Function

It has been shown that the method of isolation of single afferent fibers used in the present study permits a representative sampling of group I and II

TABLE I

Maximum Conduction Velocities of Afferent Volleys in Nerves Employed for Isolated Fiber Analysis

	Conduction distance	Maximal velocity
	cm.	*m./sec.*
Soleus	16.0	94
Average maximal velocity 101.8 m./sec.	18.0	97
	16.3	102
	16.5	97
	16.0	114
	17.0	97.5
	14.5	111
Gastrocnemius medialis	14.2	112
Average maximal velocity 118.4 m./sec.	14.0	127
	14.8	124
	14.6	111
	14.2	123
	16.7	128
	16.0	113
	16.5	119
	15.3	122

fibers and that the calculation of fiber diameter is without serious error. In addition to measurement of conduction velocity, each fiber isolated was characterized as to its discharge pattern with the purpose of identifying the type of receptor in which it terminated.

Of the fibers isolated with calculated diameter greater than 4 μ, only two from soleus and one from medial gastrocnemius could not be identified as to receptor function. Since these three fibers form a negligible proportion of the group I and II fibers examined and since damage to an occasional fiber distal to the stimulating electrodes on the intact muscle nerve could not be excluded, they have not been entered in the data presented below. All the remaining fibers of group I and II diameter were found to terminate in stretch receptors.

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Group I was found to be composed of fibers of two types: (*a*) afferent fibers displaying discharge patterns characteristic of muscle spindle receptors and (*b*) afferent fibers showing the discharge pattern of tendon organ receptors. Group II as arbitrarily defined in the histological spectrum was composed almost entirely of muscle spindle afferent fibers. The distribution of spindle (A) and tendon organ (B) fibers, plotted according to velocities and calculated diameters, is shown for soleus in Fig. 3 and for medial gastrocnemius in Fig. 4.

If the division between groups I and II is placed arbitrarily at 12 μ all tendon organ (B) fibers fall into group I except four fibers to soleus and two

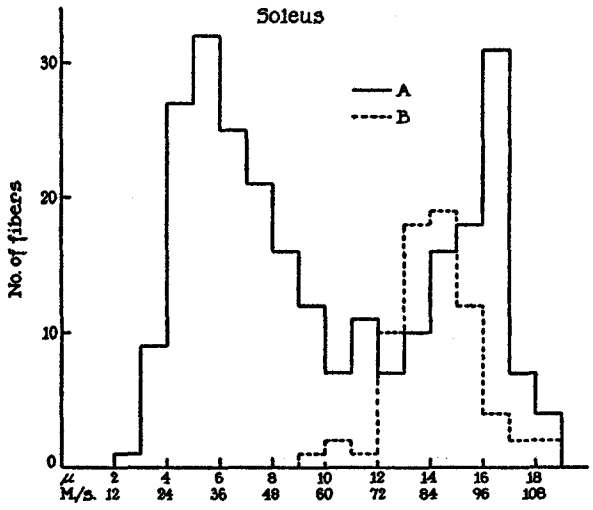

FIG. 3. Diameter distribution of afferent fibers from muscle spindles (A) and tendon organs (B). Soleus nerve. Note the unimodal distribution of tendon organ fibers and the bimodal distribution of afferent fibers from muscle spindles.

to medial gastrocnemius. The distribution of tendon organ fibers is certainly unimodal and all fibers of this type have been included in the category group IB with the reservation that the trailing edge of their distribution may extend slightly into the upper diameter range of group II.

Muscle spindle afferent fibers have a bimodal diameter distribution. The large spindle afferent fibers (12 to 20 μ), hereafter called group IA, together with tendon organ fibers (IB), account for the total of group I fibers. Group II appears as a virtually homogeneous population of spindle afferent fibers. The two distinct groups of spindle afferent fibers can be seen in the diameter distribution of fibers from soleus (Fig. 3) and from medial gastrocnemius (Fig. 4). Certain differences exist between the afferent supply to the two muscles; these may be of general interest since soleus and medial gastrocnemius are

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red and pale muscles respectively. For instance, isolated fiber analysis shows that fibers from medial gastrocnemius have larger maximal diameter than those from soleus, a fact in accord with histological measurement (11). A comparison of the reconstructed spectra of the two muscle nerves also shows that for soleus the distribution maximum of group IA fibers falls at a slightly higher diameter than the peak of group IB fibers, while for medial gastrocnemius the maxima of groups IA and IB coincide.

It was shown above that afferent fibers of groups I and II were isolated in proportion to their numbers in the muscle nerve. Since each fiber was detected by recording the impulse therein which followed a stimulus to the

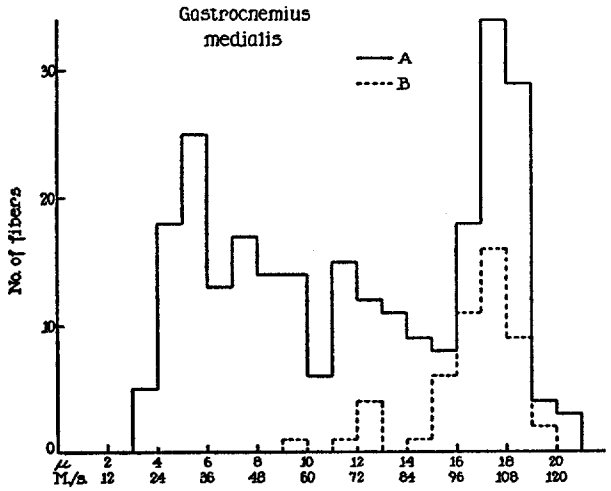

FIG. 4. Diameter distribution of afferent fibers from muscle spindles (A) and tendon organs (B). Nerve to medial gastrocnemius. Note the unimodal distribution of B fibers and the bimodal distribution of A fibers.

muscle nerve, no factor other than diameter should enter into the selection of fibers. In other words, fibers of the same diameter but with different discharge patterns should be detected with equal ease. Therefore, the incidence of the various fiber types (A and B) in groups I and II may be considered representative. From the total number of group I and II fibers in a muscle nerve and from the proportion of different fiber types determined by isolated fiber analysis, one may estimate the number of fibers in the various categories (IA, IB, and II) to a muscle. This has been done for soleus and medial gastrocnemius (Table II). Several comparisons may be made: The numbers of fibers in group I and in group II appear in very nearly the same ratio in both isolated fiber and histological counts. The nerve to medial gastrocnemius differs from that to soleus in having a larger number of fibers, the majority

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of which appear in group IA. Thus both nerves have a similar number of fibers in group IB and in group II.

Characteristics of the Receptor Discharge in Fibers of the Various Groups

Two types of afferent fiber from muscle spindles may now be recognized, those contained in group IA and those in group II of the diameter distribution. Fibers of group IA probably terminate in primary endings while group II fibers probably terminate in secondary endings within the spindles (see Discussion). A comparison of the receptor discharge in fibers of these two types was undertaken to determine any differences which might exist in receptor characteristics. The discharge patterns have been compared in the following circumstances: externally applied stretch, active contraction, and small motor fiber stimulation.

TABLE II

Incidence of Various Afferent Fiber Groups from Gastrocnemius medialis and Soleus

	I	IA	IB	II
Gastrocnemius medialis				
Histological (Lloyd and Chang)	156	—	—	98
Calculated fiber types in representative nerve*	150	108	42	104
Soleus				
Histological (Lloyd and Chang)	106	—	—	95
Calculated fiber types in representative nerve*	103	58	45	98

* Calculated so that the total of group I and II fibers equals that determined in the histological study of the representative muscle nerve.

Responses to External Stretch.—Threshold to steady stretch was determined in a number of group IA and II spindle afferent fibers by measurement of the minimal amount of stretch required to evoke maintained discharge. Individual threshold values have been entered on a plot relating stretch threshold to conduction velocity (Fig. 5). The average threshold of twenty group IA fibers (conduction velocity above 72 m./sec.) was 3.3 gm., while the average threshold for thirty-six group II fibers (conduction velocity 24 to 72 m./sec.) was 19.0 gm. However, it is clear that the two fiber groups cannot be separated completely on this basis for some of the group II receptors may have lower thresholds than certain of the IA fiber receptors. In comparison with tendon organs the receptors of muscle spindles, both of the group IA and group II afferent fiber type, exhibit a low stretch threshold. The receptors of B fibers usually require tensions of 100 to 200 gm., or more, for sustained firing.

Responses during Contraction.—During the period of contractile shortening of extrafusal muscle fibers, the stretch-evoked discharge in spindle afferent

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fibers is slowed in frequency or completely silenced. Considerable variation exists in the modification of discharge during contraction among different fibers of group IA. To detect such small differences as may exist in this respect between fibers of groups IA and II would require more extensive an analysis than has been considered feasible. In short, it seems doubtful whether there is any difference of functional significance in the behavior during contraction between receptors of the two groups of spindle afferent fibers.

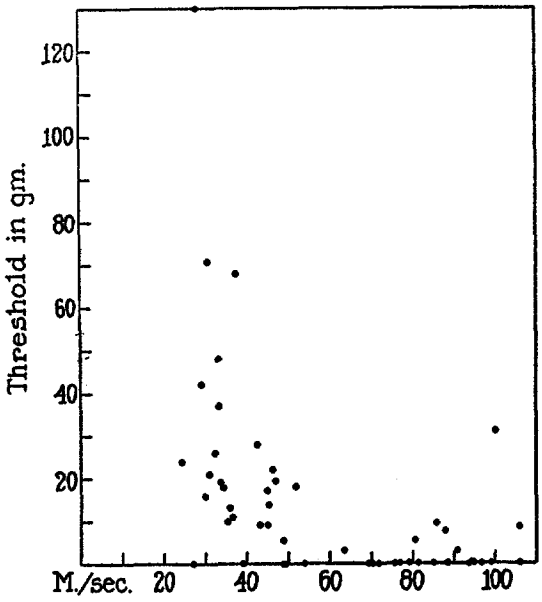

FIG. 5. Threshold to steady stretch of spindle afferent fibers from soleus. Individual fibers are entered on the plot relating the minimal amount of tension in grams which causes the receptor of the fiber to discharge continuously and the conduction velocity of the fiber. Note that the fibers conducting at group I velocities (above 72 m./sec.) have the lower average threshold to steady stretch.

When a muscle is caused to contract under rigidly isometric conditions certain afferent fibers from spindles may exhibit an increase in discharge rate during the period of tension development and yet if some shortening is permitted they show a typical silent period. Matthews (12) considered fibers which showed this discharge characteristic (his A2 units) to come from primary endings within the spindles, the increased discharge resulting from contraction of intrafusal muscle elements. Hunt and Kuffler (6) suggested that the A2 type of discharge was probably not the result of intrafusal fiber contraction, but was caused by some unusual distribution of tension within the muscle which increased the amount of stretch deformation on some spindle endings during

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rigidly isometric contraction. A number of spindle afferent fibers of groups IA and II have been examined for the above pattern. Certain fibers of both groups have shown the A2 type of discharge. If group IA and II fibers terminate in primary and secondary endings respectively (see below), this increased

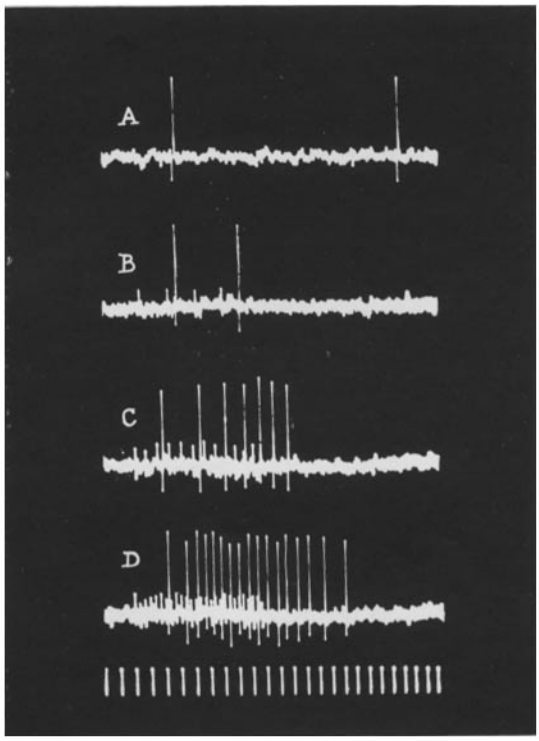

FIG. 6. Response of a group II afferent fiber to stimulation of an isolated small nerve fiber to its spindle. This afferent fiber from soleus had measured conduction velocity of 51 m./sec. (calculated diameter 8.5 μ) and showed a discharge pattern during contraction typical of a spindle receptor. A, base line discharge at low initial tension. B, C, and D; stimulation of small motor fiber. B, 4 stimuli at 55/sec. C, 12 stimuli at 130/sec. D, 27 stimuli at 300/sec. Time 100 cycles/sec.

discharge during isometric contraction cannot be attributed only to the primary endings.

Following a stimulus to an intact muscle nerve, certain afferent fibers from muscle exhibit a brief, high frequency burst of impulses which occurs very early in contraction (6). This "early discharge" has been seen less frequently in group II fibers than in fibers of group IA and has also tended to consist of fewer impulses at lower frequencies when it has occurred in group II fibers.

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The origin of early discharge is unknown but if it is produced by early tension changes during contraction, as has been suggested (6), the differences noted may reflect the higher average threshold to stretch of receptors of group II fibers.

Responses to Stimulation of Small Motor Fibers.—Stimulation of small motor fibers, isolated in ventral roots, increases discharge in afferent fibers from spindles. This effect has been compared with respect to spindle afferent fibers of groups IA and II. Qualitatively the response is, in all respects, similar in fibers of both diameter groups. Fig. 6 displays the response of a group II afferent fiber (calculated diameter 8.5 μ) to stimulation of an isolated small motor fiber to its spindle. The base line discharge in record A shows the response to the small amount of external tension maintained during this and succeeding records. Records B, C, and D show responses to tetanic stimulation of the small motor fiber. Duration of tetanus remained constant, but stimulation frequency was increased between records B and C and records C and D. Characteristically successive stimuli to the small motor fiber are increasingly effective in modifying the spindle afferent discharge; *i.e.*, there is a facilitation during the initial period of a tetanus. Also higher frequencies of stimulation are more effective in increasing the afferent discharge. This manner of behavior is similar to that seen in group IA fibers (see references 5 and 9).

Considerable variation exists in the responses of an individual spindle afferent fiber to stimulation of different small motor fibers to the same spindle, and further, a given small motor fiber may influence to a different extent intrafusal muscle elements within several spindles (5). For these reasons a quantitative comparison of responses of group IA and II fibers to small motor excitation does not seem feasible.

No new information has been obtained concerning the pattern of discharge in afferent fibers from tendon organs. The characteristic "in series" behavior, typified by an increased frequency of discharge during contraction, and the high threshold to external stretch of these receptors, have been repeatedly observed.

DISCUSSION

The present study indicates that groups I (12 to 20 μ) and II (4 to 12 μ) of the afferent fiber diameter spectrum of muscle nerves to soleus and medial gastrocnemius of cat are composed of fibers from stretch receptors, both muscle spindles and tendon organs. There appears to be no significant representation of any other receptor type in fibers of the above diameter groups. Fibers transmitting impulses from tendon organs are largely confined to the diameter range above 12 μ; they have a simple unimodal diameter distribution. Fibers from muscle spindles occupy the remainder of group I and sub-

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stantially all of group II: their spectrum shows a bimodal distribution. Thus, afferent fibers from muscle spindles may be divided into two groups according to diameter, namely IA (12 to 20 μ) and II (4 to 12 μ). Whereas the distribution of the two spindle fiber groups probably overlaps, the wide separation of their distribution maxima suggests a difference in their mode of termination within the muscle. Anatomically speaking, muscle spindles contain two types of afferent ending that possibly may be correlated with the two fiber groups. The primary (annulospiral) ending arises from a larger nerve fiber than does the secondary (flower spray) termination. Barker (1) has measured the diameters of afferent fibers near their termination within the spindles and found the fibers of the primary endings to be 8 to 12 μ in diameter in contrast to the fibers of the secondary endings which were 6 to 9 μ. Fiber diameters measured in or near the spindle are considerably smaller than the average diameters of the same fibers between muscle nerve and dorsal root. Exactly where the change in fiber size occurs is not known. It seems reasonable to associate the primary endings, derived from the larger axons, with the larger diameter (group IA) fibers in the muscle nerve; and the secondary endings, the terminations of smaller axons, with the smaller diameter (group II) fibers. More data on the diameters of axons which terminate in the two types of ending are needed before the above correlation can be regarded as definite.

An estimate has been made of the number of muscle spindles, in the two muscles studied, based on the assumption that each IA fiber represents one primary ending and that there is one primary ending per spindle. On this basis soleus would contain about 58 spindles and, if each group II fiber represents one secondary ending, there would be some 98 secondary endings in these spindles (see Table II). This estimate of the number of spindles is in substantial agreement with the count of 56 spindles found in soleus on histological search by Hagbarth and Wohlfart (4). The number of IA fibers in a nerve to medial gastrocnemius is estimated at 108 and the number of group II fibers at 104. These figures suggest that medial gastrocnemius contains about 108 muscle spindles with an equal number of secondary endings. Hagbarth and Wohlfart found only 45 spindles in this muscle. Since the division between groups I and II is arbitrary, estimation of the number of spindles based on the number of IA fibers is uncertain. While the number of spindles estimated in medial gastrocnemius may be high, it seems very unlikely that this muscle contains fewer spindles than does soleus.

Functional test of fibers in the group I and II bands reveals a unimodal diameter distribution of fibers which are afferent from tendon organs, suggesting only one type of afferent fiber from these receptors in the 4 to 20 μ range. On the assumption that each tendon organ has one large afferent fiber (of group IB), these receptors would number about 42 in medial gastrocnemius and 45 in soleus (Table II).

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The only significant difference in behavior exhibited by muscle spindle receptors of group IA and II fibers is in threshold to steady stretch. Whereas some overlap in this characteristic exists between the two groups, fibers of group IA have a lower average threshold to maintained stretch than do fibers of group II. Receptors of both fiber groups adapt slowly and display qualitatively similar responses to phasic stretch, during muscle contraction, and to activation of intrafusal muscle elements by small motor fiber stimulation. It would seem that discharge in both types of fiber should be influenced in a similar manner by phasic activity of the muscle and by reflex discharge in the small motor fibers. In a quiescent muscle difference in threshold to steady stretch, although small, might be a significant factor in determining the amount of background discharge in the two groups of spindle afferent fibers. Thus, with slight external stretch and with a certain amount of "tonic" efferent discharge in small motor fibers to the spindle, it is possible that the background discharge would be largely confined to group IA fibers. Whether the spindle functions, with the muscle at rest or in postural contraction, within the critical range which would affect differentially the two types of endings is not known.

SUMMARY

1. A method of isolation of individual afferent fibers from muscle has yielded a representative sample of the fibers which comprise groups I (12 to 20 μ) and II (4 to 12 μ) of the afferent fiber diameter distribution of muscle nerves in cat.

2. Afferent fibers from muscle stretch receptors account for groups I and II of the afferent diameter spectrum of muscle nerves to soleus and medial gastrocnemius. Fibers from tendon organs are largely confined to the diameter range above 12 μ. This fiber group, which has a simple one-peak diameter distribution, is termed group IB. Fibers from muscle spindles show a bimodal diameter distribution and account for the remainder of fibers in the 12 to 20 μ group (termed IA) and substantially all of group II (4 to 12 μ).

3. No significant difference has been found in the receptor characteristics of the large (group IA) and intermediate sized (group II) spindle afferent fibers other than a slightly higher threshold of the latter to steady external stretch.

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