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## Muscle Spindles

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### Abstract

Based on a Dissertation presented to the Society on 6th November, 1964

The action of our muscles is controlled with a remarkable delicacy, and components of the nervous system at every level contribute to this. On the afferent side, the stretch receptors of muscle spindles are the most peripheral elements and have been known to histologists and physiologists for more than a century, Hassall must receive the credit for the discovery of muscle spindles in 1851, but the first systematic description was Weissmann's in 1861. Each spindle consists of a parallel bundle of striated muscle fibres—intrafusal fibres. The bundle is 7 to 12 mm. long, and is surrounded by what Sherrington later called the lymph space, because he was able to inject it with dye via the lymph vessels: this space is enclosed by a thin fibrous capsule. The intrafusal fibres vary in their length and diameter, and are attached to one another at their ends; the ends of the longest fibres are attached to extrafusal endomysium. The spindle is supplied with nerves of various diameters terminating in different types of ending on the intrafusal fibres.

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# Muscle Spindles

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## I. HISTORY AND HISTOLOGY

The action of our muscles is controlled with a remarkable delicacy, and components of the nervous system at every level contribute to this. On the afferent side, the stretch receptors of muscle spindles are the most peripheral elements and have been known to histologists and physiologists for more than a century. Hassall must receive the credit for the discovery of muscle spindles in 1851, but the first systematic description was Weissmann's in 1861. Each spindle consists of a parallel bundle of striated muscle fibres—intrafusal fibres. The bundle is 7 to 12 mm. long, and is surrounded by what Sherrington later called the lymph space, because he was able to inject it with dye via the lymph vessels: this space is enclosed by a thin fibrous capsule. The intrafusal fibres vary in their length and diameter, and are attached to one another at their ends; the ends of the longest fibres are attached to extrafusal endomysium. The spindle is supplied with nerves of various diameters terminating in different types of ending on the intrafusal fibres.

Kölliker's theory that these were embryonic centres for the growth of new muscle fibres, and another hypothesis, that they were pathological structures, were not abandoned until around 1890. In 1888 Kerschner had suggested that the muscle spindle was a sensory organ under motor control, and two years later Onanoff performed the crucial experiment of cutting the ventral roots and later examining the innervation of the spindle. In 1894 Sherrington repeated this, concluding that the muscle

spindle had equally rich sensory and motor innervations.<sup>1</sup>

At the same time, Ruffini was making a detailed study of the nerve fibres in muscle spindles, and finally identified three types of ending reaching the spindle—the primary, secondary and plate endings.<sup>2</sup> The primary ending divided into ribands which spiralled around the centre of the intrafusal fibres—the annulospiral terminals. The secondary afferents “quickly break up into a large number of varicose axis cylinders . . . of diverse form, round, forked, triangular, leaflike, etc., and often resemble in arrangement a spray of flowers”: they lie on the intrafusal fibre on either side of the annulospiral endings. Ruffini's third ending, the plate ending, had previously been noted by Kerschner, who suggested that it was motor. These nerve fibres are the smallest reaching the spindle, running a very tortuous and independent course: unlike the other nerves, they never divide before terminating. He compared the plate endings with extrafusal motor end-plates, and concluded that their structures were so different that both could not be motor. He felt that he did not have enough evidence about primary and secondary endings either to accept or to reject Sherrington's view that the sensory modality they subserved was probably mechanical. Sherrington had never specified which endings were affected by total root section, recording only that the innervation of the spindle was halved. It was not until 1928 that Hines and Tower repeated the

experiment and concluded that the plate endings had a motor function since they disappeared after ventral root section.<sup>3</sup>

A recent and important advance has been the recognition that there are probably two types of intrafusal muscle fibre, with different patterns of sensory innervation, and independent motor innervations. Sherrington first noticed a variation in size of intrafusal fibres sixty years ago, and the idea that this represented more than a normal distribution of values was strengthened by Cooper and Daniel's description in 1956 of qualitative differences between two types of fibre.<sup>4</sup> The larger fibres have a spherical dilatation in the equatorial region, filled with a conglomeration of nuclei: consequently these have been called *nuclear bag fibres*. The shorter, narrower type of fibre has its nuclei arranged in a single chain which extends in both directions beyond the equatorial region, hence its name, the *nuclear chain fibre*. Here the nuclei are less tightly packed and there is no central dilatation of the fibre: the myofibrils are rather fewer in number and suspended in more sarcoplasm than in the bag fibre. Boyd, in a detailed and beautifully illustrated paper in 1962, supports the theory that there are two types of intrafusal fibre.<sup>5</sup> He cut serial transverse sections of mammalian spindles and followed individual muscle fibres from section to section, measuring the diameters: plotted as histograms, the results showed two distinct groups. The morphological differences between the two fibres were also confirmed.

Boyd also mounted whole spindles in profile, impregnating the nerve endings with gold chloride. After dorsal root section, two types of fibre were distinguished in the efferent nerves remaining: the larger,  $\gamma^1$  efferents supplied bag fibres, while  $\gamma^2$  efferents supplied chain fibres and had a more diffuse end-plate structure. In spindles dissected after ventral root section, the distribution of primary and secondary afferent endings to bag and chain fibres was analysed: in each spindle the primary afferent had a branch with the annulospiral type of ending on every fibre, bag or chain, in the spindle, while the secondary afferent supplied only chain fibres, with endings of the flower-spray type. This difference is important in allowing the different responses of a muscle spindle to steady and changing tension, and the current anatomical picture of the muscle spindle and its innervation appears to explain the physiological findings very well (Fig. 1).

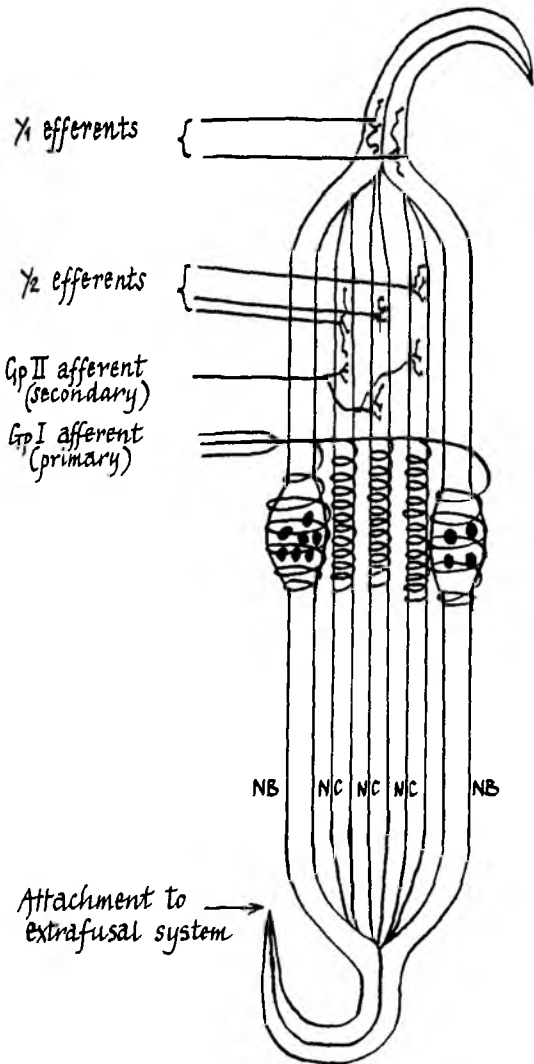


Fig. 1. Diagram of mammalian muscle spindle (after Boyd) showing nuclear bag fibres (NB) with  $\gamma^1$  motor innervation, and nuclear chain fibres (NC) supplied by  $\gamma^2$  motor fibres. The primary afferent has annulospiral branches to all intrafusal fibres, while the secondary afferent has flowerspray branches, to the chain fibres only.

## II. PHYSIOLOGY

### Dynamic and static sensitivity

Adrian and Zotterman made the earliest physiological study of a muscle spindle in 1926, recording from the nerve to the sternocutaneous muscle in a frog<sup>6</sup>; the results revealed relatively little of the behaviour of muscle spindles, but showed how the nervous system handles sensory information at the peripheral level. A series of discrete potentials was recorded, all of similar amplitude and duration; only their frequency altered in response to stretch.

In 1933 B. H. C. Matthews first compared the responses to stretch of different afferent fibres in a muscle nerve, and identified three types of fibre.<sup>7</sup> Some of those in the Group I range of diameter responded to sustained external tension with a transitory increase in rate of firing (adaptation); fibres in the Group II range showed a sustained acceleration of firing while the muscle was stretched, and no adaptation. In both types of fibre the resting rate of discharge was decreased during active extrafusal contraction. A stretch receptor with these properties must be connected in parallel with the extrafusal fibres, corresponding therefore to the situation of the muscle spindle (Fig. 2b).

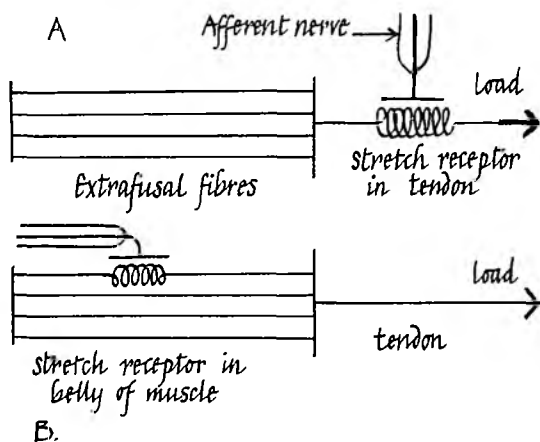


Fig. 2 Diagrams to show the positions of (a) a stretch receptor in series with extrafusal fibres and (b), in parallel.

Matthews also found some fibres of Group I diameter whose rate of firing increased during both passive elongation and active contraction

of the muscle (Gp. Ib); this receptor is clearly connected in series with the extrafusal fibres, corresponding in position with the Golgi tendon organ (Fig. 2a).

These results were confirmed and extended by Cooper in 1959<sup>8</sup>: Group Ia fibres had both a dynamic response—to the rate of stretching, and a static response—to the degree of tension at any one time, while Group II fibres showed only a static response. Group Ia fibres correspond in diameter with the primary afferent of muscle spindles, with its annulospiral endings on bag and chain fibres, and Group II fibres with the secondary afferent with flowerspray terminals on chain fibres only.

### Mechanical properties of intrafusal fibres

How is a mechanical change—in tension—converted into changes in impulse frequency, and what is the basis of adaptation? In micro-electrode studies of the afferent nerve in frog muscle spindles, where impulse conduction had been prevented by anaesthesia, Katz (1950) was able to record graded depolarizations proportional to the rate and extent of stretching.<sup>9</sup> He suggested that small, maintained changes in potential (receptor potential) in the branches of the afferent fibre were transmitted—as a redistribution of charge—to the site of initiation of action potentials. Here, the total amount of depolarizing current from different branches would determine how quickly the membrane potential could be raised from resting to threshold values, and hence its rate of firing.

Adaptation may be either a mechanical property of intrafusal muscle fibres, or an electrical property of the afferent nerve ending. The differences in the arrangement of nuclei and myofibrils in bag and chain fibres, and their different innervations, suggest that adaptation might be mechanical, and there are other reasons. First, flash cine photography has shown mechanical adaptation in another mechanoreceptor, the Pacinian corpuscle.<sup>10</sup> Second, the receptor potential has been recorded in branches of the primary afferent, and shows adaptation<sup>9</sup>; this cannot therefore be a property of the site where action potentials arise subsequently.

From Cooper's (1959) and other work it emerged that the primary afferent, with annulo-

spiral endings on bag and chain fibres, has dynamic and static components in its response to stretch, while the secondary afferent, with endings on the chain fibres only, has a purely static response to stretch. This implies that dynamic sensitivity is a property peculiar to the bag fibres, and a mechanical basis for this adaptation has been suggested. The histological findings are the only clue to the nature of this difference between bag and chain fibres, since the viscous and elastic properties of a single spindle have never been investigated. However, P. B. C. Matthews has developed a useful hypothesis (presented here in modified form).<sup>11</sup>

In the chain fibre (Fig. 3a), the response in its nerve terminals is proportional to the tension applied to its ends: assuming that the nerve terminal responds to changes in its length, then its behaviour could be explained readily if the rest of the chain fibre obeyed Hooke's Law. This states that change in length is proportional to the tension applied; the constant of proportionality (elasticity) would vary with the state of active contraction of the fibre. If the contractile elements in series with the sensory ending were of low elasticity, then all elonga-

tion in response to stretch would occur in the segment of fibre beneath the ending, which would therefore be at its maximum level of static sensitivity. If however the outer segments of the fibre were in a highly elastic state, much of the extension, in response to the same stretch, would occur there. Consequently tension on the sensory region would be less, and the static sensitivity therefore lower.

The simplest assumption to explain the properties of the primary afferent is that its static response derives entirely from its endings on the chain fibres, and its dynamic response from the bag fibre endings. The bag fibre ending could show a response proportional to the velocity of stretching, if the region it covered again obeyed Hooke's Law but was mounted now in series with a viscous and an elastic element (Fig. 3b). The significant property of a viscous element is that it can transmit all or part of the tension applied to it, depending on how quickly the stretch is applied. Thus when the bag fibre comes under tension, the full effect initially reaches the central region, leading to a maximal initial depolarization in this branch of the primary afferent. With more

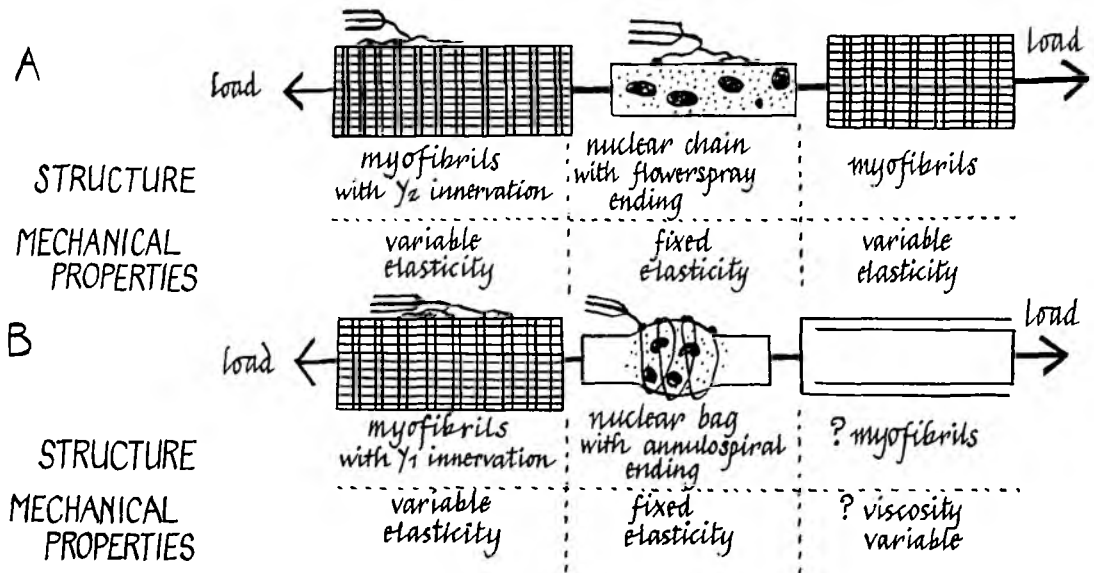


Fig. 3. Diagrams to illustrate possible mechanical properties of (a) nuclear chain and (b) nuclear bag fibres. The viscous element peculiar to the latter may represent a property either of myofibrils in these fibres or of the sarcoplasm of the nuclear bag region.

rapid stretching a greater proportion of tension will be transmitted to the central region, hence its response to the rate of change of tension. The ending adapts because the tension falls off rapidly as the viscous element collapses. The level of dynamic sensitivity of the ending might be controlled by the element of variable elasticity in series with viscous and receptor elements: in this way the amount of extension of the receptor with a given tension would be altered.

Boyd had evidence for separate  $\gamma$  innervations of the nuclear bag and nuclear chain fibres, and it would be reasonable to expect that stimulation of one particular  $\gamma$  fibre might alter either the dynamic or the static sensitivity of a primary afferent fibre to stretch. P. B. C. Matthews performed this experiment, recording from primary afferents in the dorsal root, and stimulating single  $\gamma$  fibres.<sup>12</sup> All thirteen efferents isolated raised the rate of discharge of the primary afferent, at constant length of the muscle: the primary ending has branches to the chain fibres, and according to the above theory the response would occur because the elements of variable elasticity, the myofibrils, shorten when their elasticity is reduced, so stretching the receptor segment. Six of the thirteen efferents increased the dynamic response of a primary afferent to stretch, while the other seven lowered it. This latter group would perhaps act by shortening the chain fibres: since these are connected in parallel with bag fibres, the effect would be to reduce the proportion of tension on the bag fibre endings, and hence their dynamic sensitivity.

### The function of muscle spindles

Merton (1953)<sup>13</sup> suggested application of the principle of control by negative feedback to the monosynaptic reflex (Fig. 4). Any one rate of firing of  $\alpha$  motoneurons will clearly be adequate to maintain the length of a muscle against a particular tension. If the tension is increased, the muscle extends: this increase in length would be reflected in extension of the muscle spindles and accelerated firing in their afferent fibres, some of which have excitatory synapses on  $\alpha$  motoneurons. Consequently, motoneurons at a level of excitation just below their threshold would now fire, the length of the muscle returning to its present value. If the muscle is to be shortened under constant tension, increased fusimotor activity or  $\gamma$  bias can achieve this. Because the endings with static

sensitivity lie in series with contractile elements in the intrafusal fibre, the rate of afferent firing will increase, causing additional  $\alpha$  motoneurons to fire, so that the muscle shortens. Shortening gradually ceases as the extra reflex stimulus to the extrafusal system is reduced by the shortening.

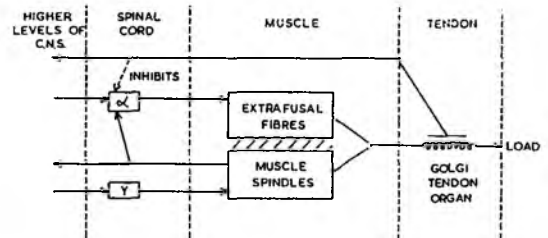


Fig. 4. Control of muscle tone by negative feedback (Merton). For explanation see text.

Owing to the time required for reaction to a changing external load, circumstances may arise where the response never keeps pace with the load. This can be avoided in a stretch receptor with dynamic as well as static sensitivity, since the size of the new load can now be recognized immediately, in terms of the rate of stretch. The initial response will be correspondingly greater, and therefore adequate to absorb the extra load. It is possible that  $\gamma^2$  fibres, through control of static sensitivity, might regulate  $\gamma$  bias and thus the length of a muscle at a given tension, while the  $\gamma^1$  fibres would control the speed with which a muscle reacts to rapid changes in the applied tension.

Over-correction is another possibility: if a muscle maintaining its length under a constant tension now receives an additional load, the monosynaptic arc overcompensates. Overshoot in the opposite direction would follow, and such a mechanism might form the basis of some types of tremor. However, in an overloaded or ischaemic muscle, tremor may perhaps be a purely mechanical property of the extrafusal fibres.

### Conclusion

The type of function suggested for muscle spindles, acting as part of a servoloop to maintain the muscle at preset lengths under varying loads, is well suited to the maintenance of posture: the extensors of the leg are well

supplied with spindles—23 per gm. of muscle in the case of soleus in the cat.<sup>14</sup> However, spindles are also found in smaller muscles subserving finer movements, although the incidence is rather irregular: the extraocular muscles of man, apes, goats and sheep contain spindles, while in other species there are none. Clearly, muscle spindles have a part to play in the control of fine as well as coarse movements, although the inevitable (conduction and synaptic) delays in a servoloop might be a disadvantage in the control of rapid movements.

Some information on the interaction between muscle spindles and higher centres of the nervous system has recently been obtained. Appelberg<sup>15</sup> stimulated the red nucleus of rabbits and found that the dynamic response to stretch in the primary afferent fibre was increased, and its static sensitivity decreased: this could occur if the nuclear bag fibres contracted, or if the chain fibres were inhibited. In either case this would increase the proportion of extension applied to the sensory region of the bag fibre. Appelberg favoured the second explanation since he had also shown that stimulation of the red nucleus reduces the activity in  $\gamma$  fibres (taken as a group). The red nucleus receives efferents from the deep cerebellar nuclei, and this system might therefore form the basis of a cerebellar contribution to the control of tone in anti-gravity muscles. Muscle spindles apparently do not subserve conscious position sense, since this can be

abolished by injection of anaesthetic into a joint.<sup>16</sup>

Once the mechanical properties of muscle spindles are understood, further investigation must inevitably concentrate on their control by structures such as the cerebellum and basal ganglia.

I should like to thank Mr. M. Dixon for drawing three of the diagrams.

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