THE MUSCLE SPINDLE — AN ANATOMICAL AND PHYSIOLOGICAL APPRAISAL

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SYNOPSIS

Muscle spindles are proprioceptors found within skeletal muscle. This paper summarises some of the historical landmarks which led to a better understanding of their structure and function. The salient features of their morphology, innervation and physiological role are also outlined.

INTRODUCTION

Muscle spindles are stretch-receptors found within striated (skeletal) muscle. Their function is to perceive the tension of the muscle in order to regulate its tone, posture, and accuracy of fine movements. They are made up of intrafusal muscle fibres, which are smaller than ordinary or extrafusal muscle fibres, bounded by a capsule, and supplied by a rich network of sensory (or afferent) and motor (or efferent) nerve fibres.

HISTORICAL SURVEY

The muscle spindle has attracted the attention of many investigators for more than one hundred years. Early observations were made by Hassal (1851) who described thin fibres within skeletal muscle. Kuhne (1863) labelled this structure as "muskelspindeln" in view of its fusiform shape. Felix (1888) found muscle spindles to be present in the foetus also. By selective rhizotomy, Onanoff (1890) demonstrated the presence of both motor and sensory nerve supplies to muscle spindles. Sherrington (1894) referred to fibres within the spindle as intrafusal fibres, to distinguish them from ordinary or extrafusal muscle fibres; possessing equatorial and polar regions. He also described the periaxial space of Sherrington, which refers to the space separating the connective tissue capsule and the mass of intrafusal fibres.

The classical work on muscle spindles was, however, done by Ruffini (1897). He described very elegantly the nerve endings seen in these structures, and labelled them as primary or annulo-spiral endings, in the mid-equatorial region of the spindle fibres; secondary or flower-spray endings in the myo-tubular region; and plate endings towards the poles of the fibres. He considered all these three endings to be sensory in function. However, it was left to later workers to show that only primary and secondary endings were sensory end-organs, and that plate endings were motor in function.

In the early decades of the twentieth century, no significant descriptions of muscle spindles was done. Most of the earlier work was done using the cat as a primary experimental model. tThe work of Cooper and Daniel (1963) is a notable exception. They described muscle spindles in the lumbrical muscles and deep muscles of the neck in humans. It was Cooper and Daniel (1956) and Boyd (1956), who separated the intrafusal fibres into nuclear-bag and nuclear-chain fibres based on some gross morphological differences.

Physiological experiments by Leksell (1945), Kuffler, Hunt, Quillian (1951) showed that muscle spindles derived their motor supply from a group of small motor fibres labelled as gamma or fusimotor fibres. Barker, Stacey, and Adal (1970) further subdivided the motor endings into plate and trail endings. The picture then emerged of muscle spindles being highly-sensitive stretch receptors; and the structural dichotomy into nuclear-bag and nuclear-chain fibres reflected a physiological difference in function. The nuclear-bag fibres were believed to be responsible for perceiving position and velocity sense of a rapidly adapting nature (dynamic response), and nuclear-chain fibres were static and slowly adapting in nature.

STRUCTURAL FEATURES

The outer or external capsule surrounds the intrafusal muscle fibres. It is made of collagen fibres, and concentric sheets of cells which are regarded as specialized fibroblasts (Merrillees 1959, 1960). The inner or internal capsule is more delicate, and surrounds each intrafusal muscle fibre. The cells are smaller but the main cell type is still the fibroblast. The capsular cells show micropinocytic vesicles of varying sizes thus implicating the capsule in the important role of transport. The external capsule stands away from the intrafusal fibres, and the space (periaxial space of Sherrington) contains fluid rich in hyaluronic acid.

The number of intrafusal fibres varies from 1-18. There are more nuclear-chain fibres in a spindle when compare to nuclear-bag fibres. The nuclear-chain fibres are characterized by a single longitudinal row of nuclei in the centre of the fibre, whereas nuclear-bag fibres have a "bag" or cluster of nuclei in the equatorial region. Nuclear-chain fibres tend to be smaller (average diameter 10-15 microns), shorter (average length 2-4 mm), and are entirely intracapsular; whereas nuclear-bag fibres are larger (average diameter 20-30 microns), longer (average length 4-8 mm), and their ends extend beyond the capsule to be attached to connective tissue septa of the muscle.

Ultrastructurally, the two types of fibres show gross differences. The contractile elements ofnuclear-bag fibres show a sheet-like arrangement of myofilaments, and there is a transition of contractile units from the poles to the equator, until only A, I, and Z bands are seen, and finally only A bands and some dense bodies can be made out. Nuclear-chain fibres, on the other hand, show well-defined A, I, Z, and H bands, and have a discrete arrangement of myofilaments. The so-called M bands are a characteristic feature of nuclear-chain fibres only, and these fibres also tend to have a well-formed sacroplasmic reticulum and transverse tubular system with a variety of couplings like triads; and larger and more numerous mitochondria and thus a higher content of oxidative enzymes.

The intrafusal fibres are arranged in parallel with the rest of the extrafusal muscle fibres. The ends of the capsule of the spindle are attached to the tendons or the sides of extrafusal fibres.

NERVE SUPPLY

A. SENSORY ENDINGS

1. *Primary or annulo-spiral endings*
   These are found in the equatorial region of the intrafusal muscle fibres, wrapped around the fibres in a complex manner, where the nuclear concentration in the fibres is highest, and the density of myofilaments is lowest. The afferent nerves supplying these endings are large group Ia afferent fibres with an average diameter of 12-20 microns, and conduction velocities of around 100-120 metres/second. They occur mainly on nuclear-bag fibres, but a branch of the group Ia afferent fibre may wrap a few times around a nuclear-chain fibre. These receptors respond to stretch.
2. *Secondary or flower-spray endings*
   They are found in the juxta-equatorial regions, predominantly on nuclear-chain fibres. A variable spray may be seen on nuclear-bag fibres. They are the endings of Group II afferent fibres (average diameter 6-12 microns), and occur on that region of the intrafusal fibre where the striations are better-developed. These receptors also respond to stretch.

B. MOTOR ENDINGS

1. *Plate endings*—These have been subdivided into:—
   (a) *Classical plate endings (P2 endings)*—They are found on both nuclear-bag and nuclear-chain fibres, and occur in the polar regions of these

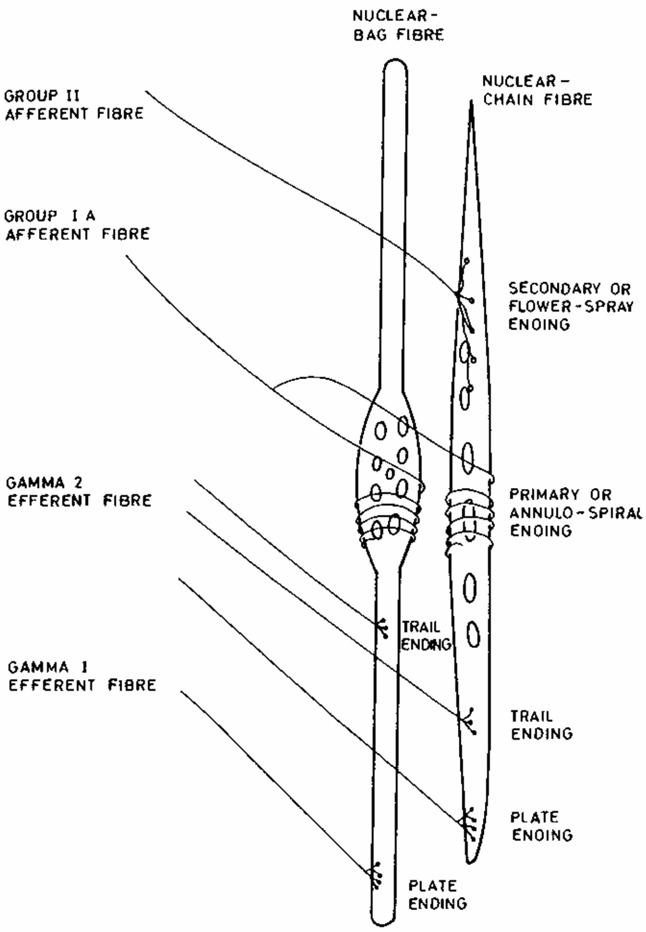

Fig. 1 Diagram of nerve supply to a muscle spindle.

fibres. They tend to be similar to ordinary motor end-plates on extrafusal muscle fibres. They are supplied by Gamma I efferent fibres of Leksell or fusimotor nerve fibres, with an average diameter of 3-7 microns.

(b) *PI Plate endings*—These have been described on the extreme poles of nuclear-bag fibres only. They are supplied by Beta fibres, which are collaterals of alpha nerves supplying extrafusal muscle fibres. They represent a persistence of a phylogenetically primitive state, found in lower animals, where extrafusal and intrafusal fibres share a common nerve supply. They are functionally unimportant in humans.

2. *Trail endings*

They exist on both nuclear-bag and nuclear-chain fibres, and are the endings of Gamma 2 efferent fibres. They are found nearer to the equatorial region when compared with plate endings.

FUNCTIONAL ASPECTSS

The sensory nerve endings relay information to the spinal cord when they are stimulated by contraction of the intrafusal fibres. This contraction could arise actively, by motor stimulation via the gamma efferent fibres, or passively by stretching of the surrounding extrafusal fibres. Information to the cord is carried via the Group Ia or Group II afferent fibres from primary and secondary endings respectively. By a mono-synaptic reflex arc, these afferent neurones synapse upon alpha motor neurones, bringing about a contraction of extrafusal muscle fibres of the same or a functionally related muscle, thus regulating the tone, posture, and accuracy of fine movements of the muscle. The afferent fibres also end, via interneurons, on alpha motor neurons supplying antagonistic muscles, inhibiting their contraction. As the muscle contracts, there is a period in which all discharge from the splindle ceases. An example of spindle function is the stretch reflex. Tapping a tendon stretches the muscle. The sensory receptor is the muscle spindle. The impulse is carried to the central nervous system by fast sensory fibres which pass directly to the large alpha motorneuron by a monosynaptic pathway, and reflex contraction of the muscle results. This is the basis for the tests of tendon reflexes which are done routinely in clinical practice.

BEHAVIOUR OF SENSORY ENDINGS

B.H.C. Mathews (1933),. found no difference in the behaviour of primary and secondary endings. Cooper (1961) showed that the velocity-sensitivity of primary endings was greater than those of secondary endings, although the sensitivity to maintained-increase in length was the same. It can be concluded that primary endings respond to a combined stimulus of steady-stretch and the velocity at which the length is changing. The secondary endings are relatively insensitive to changes in velocity but respond to changes in length or steady-stretch of the muscle. This difference in behaviour could arise from the fact that primary endings and secondary endings lie in areas of the intrafusal fibre which are structurally different, and that these areas have different visco-elastic properties. Thus the spindle and its reflex connections operate to maintain muscle length. If the muscle is stretched, spindle firing increases and reflex shortening occurs; whereas if the muscle is shortened, the spindle discharge decreases and the muscle relaxes.

BEHAVIOUR OF MOTOR ENDINGSS

The gamma efferent fibres cause a contraction of the intrafusal fibres, without any increase in tension of the muscle as a whole (Kuffler and Hunt 1951). They serve to prime the sensory nerve endings to fire when a critical level of distortion is obtained. The primary and secondary endings relay via the Group Ia and Group II fibres which have their cells of origin in the dorsal root ganglia. Therefore, the sensitivity of the spindles to stretch is directly proportional to the rate of gamma efferent discharge.

STATIC AND DYNAMIC FUSIMOTOR FIBRES

The existence of two types of motor fibres to muscle spindles has been a subject of controversy. Jansen and Matthews (1962), believe that their existence would allow the two facets of response of spindle sensory endings-namely responses to changes in velocity and length to be explained. Stimulation of certain gamma efferents has been shown to increase the sensitivity of the spindle to dynamic changes and stimulation of other fibres to static events. Dynamic fibres could cause velocity response of sensory endings to be increased, and static fibres could cause the length response of sensory endings to be increased. Dynamic fibres were believed to end on nuclear-bag fibres thus eliciting position and velocity sense of a rapidly adapting nature (dynamic response), and static fibres were believed to end on nuclear-chain fibres (static response). However, some authors doubt the existence of separate dynamic and static fibres.

CONTROL OF GAMMA EFFERENT ACTIVITY

The gamma efferent neurons are spontaneously active, but their discharge is modified from activities in the higher centres. Certain groups of neurons in the brain stem have a motor function and come under the regulatory influence of such higher centres as the cerebral cortex, basal ganglia, and the cerebellum. The entire compoex is referred to as the extrapyramidal system in order to differentiate it from the direct or pyramidal system. Many fibres connect these brain-stem nuclei with the gamma neurons supplying intrafusal muscle fibres. Stimulation of the gamma neurons by these descending motor fibres causes contraction of the intrafusal fibres, thus adjusting the sensitivity of the spindle.

Other factors also modify gamma efferent activity. Anxiety causes an increased discharge, thus accounting for brisk tendon reflexes seen in anxious patients. Cutaneous stimulation e.g. a pinprick, increases gamma efferent discharge to flexor muscles thus bringing about a protective flexor withdrawal reflex. In reinforcement of tendon reflexes, as by asking a subject to pull his hands apart with his flexed fingers (Jendrassik's manouvere), it is believed that there is increased gamma efferent activity initiated by afferent impulse from the hand. There is also an increased gamma motor activity involved with activity of the alpha motoneurones that initiate movement. The physiological significance of the simultaneous contraction of the extrafusal and intrafusal fibres that could result is uncertain, but appears related to co-ordinating movement.

CONCLUSION

Neuromuscular spindles are amongst the most complex of the sensory receptors, both structurally and functionally. They provide sensory information for spinal reflex adjustments of muscle tone. Each spindle is supplied with two types of sensory nerve endings, and are unique amongst sensory endings, in also having an efferent or motor innervation. Their simplest role is one of being a stretch receptor. The sensory endings are stimulated by increased gamma efferent activity and a nerve impulse passes to the alpha motor neurones supplying the main mass of the muscle. The latter then contracts, through a monosynaptic reflex arc, with minimum synaptic delay. Stimulation of the spindle ceases when the muscle contracts, because the spindle fibres are arranged in parallel with the other muscle fibres. The stretch reflex is put into constant use in the maintenance of muscle tone and also forms the basis of the tests for tendon reflexes.

ACKNOWLEDGEMENTS

Grateful thanks to Mrs. S.P. Lee for her typing assistance.

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