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Structural features of mammalian muscle spindles

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Introduction

MUSCLE SPINDLES are proprioceptors found within skeletal muscle. They serve to perceive the tension of the muscle in order to regulate the tone, posture, and accuracy of fine movements of the muscle. They consist of intrafusal muscle fibres, which are smaller than extrafusal or ordinary muscle fibres, enclosed by a sheath of connective tissue known as the capsule, and are supplied by afferent (sensory) and efferent (motor) nerve fibres.

Historical aspects

Muscle spindles have attracted the attention of many investigators for more than one hundred years. Kuhne (1863) was the first investigator who labelled this structure as "Muskelspindeln" because of its fusiform shape. Sherrington (1894) referred to muscle fibres within spindles as intrafusal fibres, possessing equatorial and polar regions, towards the centre and periphery of these fibres respectively. The periaxial space of Sherrington was the term used to describe the space separating the axial bundle of intrafusal fibres from the capsule of the spindle.

Ruffini's elegant descriptions (1893-1897) of the innervation of muscle spindles still stand out as valid observations till today. He described three types of nerve endings – namely primary or annulo-spiral endings at the mid-equatorial region; secondary or flower-spray endings away from the equatorial region; and plate endings towards the extreme ends of the fibres. He considered all these three nerve-endings to be sensory in function. It was later shown that the first two were sensory endings, but plate endings were motor in function. To the latter has been added trail endings – another ending with a motor function. Boyd (1956), and Cooper and Daniel (1956), separated the intrafusal fibres into two types, based on their morphological features, and labelled them as nuclear-bag and nuclear-chain fibres. More recent investigators have focussed their attention on the ultra-structural features of the muscle spindle, and this paper summarises the present-day understanding of these features.

Terminology

The terms used to orientate the intrafusal fibres are the equatorial region in the centre, and the polar region towards the periphery. The equatorial region is sub-divided into the mid-equatorial region at the centre of the equatorial zone, and the myo-tubular region which is the distal equatorial zone. The polar region is sub-divided into the juxta-equatorial or the proximal polar zone, and the polar or distal polar zone.

Capsule

a. **Outer or External Capsule**

This is the connective tissue covering of the spindle. It stands away from the intrafusal fibres, and the space thus formed is the periaxial space of Sherrington which is rich in hyaluronic acid. The capsule is pierced by blood vessels and nerves. The capsule has been described to be composed of collagen fibres, and concentric sheets of cells which are regarded as specialised fibroblasts by Merrileas (1957, 1960). Landen (1966) believes that these cells are thin, flattened, pavement epithelial cells. The nerves entering the spindle pierce the capsule almost at a right angle, and the perineurium of these nerves blends with the capsule. The capsular cells show a prominence of micropinocytic vesicles of varying size, thus implicating the capsule in the major role of transport and providing nutrition to the spindle fibres.

b. **Inner or Internal Capsule**

Each intrafusal fibre is enclosed by a delicate tube known as the internal capsule or the internal axial sheath. This sheath has sparce fibrous material, but an abundance of cells of various types. The internal capsular cells are, however, smaller than those of the external capsule. The main cell type is the fibroblast. The internal capsule forms a link between the outer capsule and the intrafusal muscle fibres.

Intrafusal fibres

The number of intrafusal muscle fibres varies from one to fourteen. The nuclear-chain fibres outnumber the nuclear-bag fibres. However, the author has reported muscle spindles in the lumbrical muscles of the Malaysian long-tailed monkey (proceedings of the Fourth All-Indonesian Congress of Anatomy in Jakarta – Dec. 1976) possessing well over twenty-four intrafusal muscle fibres. The features of the nuclear-bag and nuclear-chain fibres are outlined below.

Nuclear-bag fibres

These fibres were labelled as nuclear-bag fibres because they contain several closely-packed nuclei in the equatorial region. The fibre shows a swelling where this "bag" of nuclei is found. They are larger in diameter, and longer than nuclear-chain fibres, and at the poles of the spindle, they pass out of the capsule to lie among extrafusal muscle fibres, being attached to the endomysium or perimysium of the muscle. Some, or all, of the nuclear-bag fibres may be re-encapsulated, after passing out the capsule, so that two or more spindles in tandem occur.

At higher magnifications, the contractile elements, at the polar region, resemble those of extrafusal fibres, possessing A bands, I bands, and Z bands. As the myotubular region is approached, no discrete myofibrils are seen, and instead a single bundle or a sheet-like arrangement of myofilaments is observed. The I bands become difficult to distinguish, and the Z band thins out. At the equatorial region, only A bands and Z bands are seen. There are no M bands, and the H bands are indistinct. At the mid-equatorial region, the striations are replaced by dense bodies. Thus, these fibres show a transition of contractile units to only A, Z, and I bands, and then to A bands and dense bodies only.

Nuclear-bag fibres also possess specialised junctional complexes which are comparable to the nexus found in smooth muscle, or the intercalated disc found in cardiac muscle. These trilaminar membranous structures are found at the junction of polar and equatorial regions.

The sarcoplasm of nuclear-bag fibres contains glycogen granules, which occur as larger sized alpha granules arranged in rossettes, and Beta granules occurring singly. The sarcoplasmic reticulum and transverse tubular system is not conspicuous.

Nuclear-chain fibres

These fibres were so-named because they contained a single longitudinal row of nuclei in the centre of the fibre. They are smaller in diameter when compared to nuclear-bag fibres, shorter in length, and tend to be entirely intracapsular, being attached at the poles of the spindle to the capsule or the sheath of nuclear-bag fibres. They also out-number the nuclear-bag fibres.

At higher magnifications, the myofilaments are seen to be closely-packed and well-defined. A, I, Z, H, and M bands are clearly defined at both polar and equatorial regions. They tend to have larger and more numerous mitochondria when compared to nuclear-bag fibres. Intercellular bridges are seen where adjacent nuclear-chain fibres touch each other. Micro-ladders, which are believed to arise from nuclear activity, and indicate the beginning of fibre growth in width, and length, are found only in nuclear-chain fibres.

The sarcoplasmic reticulum and transverse tubular system are well-formed, and a variety of couplings like dyade, triads, tetrade, etc. are seen. The sarcoplasmic reticulum also displays dilated cisternae in the centre of sarcomeres. Glycogen particles are also seen abundantly in the viscinity of the sarcoplasmic reticulum dilatations, where mitochondria are also observed intimately related to these terminal cisternae or dilatations.

Conclusion

It can be seen that nuclear-bag and nuclear-chain fibres in muscle spindles have profound differences in structure – both at the light and electron microscopic level. This structural dichotomy of intrafusal muscle fibres must necessarily be a reflection of the different physiological roles, each type of fibre has to play in the functioning of the muscle spindle as sensitive stretch receptors.

SUMMARY OF STRUCTURAL FEATURES

Feature	Nuclear-Bag Fibre	Nuclear-Chain Fibre
Number	Fewer	More
Diameter (at mid-point)	Greater diameter-average 20 – 30 microns	Smaller diameter-average 10 – 15 microns
Length	Greater length-average 4 – 8 mm. – extend beyond capsule	Shorter length-average 2 – 4 mm. – entirely intracapsular
Nuclei	Arranged in a cluster or "bag" in equatorial region	Single longitudinal row in centre of fibre
Contractile elements	Transition of contractile units to only A, I, and Z bands, and then to A bands and dense bodies Sheet like arrangement of myofilaments	Well-defined A, I, Z, and H bands. Discrete arrangement of myofilaments
H bands	Ill-defined	Well-defined
M bands	Absent or ill-defined	Present
Sarcoplasmic reticulum and transverse tubular system	Poorly-developed	Well-formed, variety of couplings like dyads, and triads
Triads	If present, at junction of A and I bands	Within A bands
Mitochondria and oxidative enzyme levels	Lower content of mitochondria and oxidative enzymes	Larger and more numerous mitochondria High oxidative enzyme content e.g. Succinic dehydrogenase and mitochondrial ATP-ase
Type of contraction	Contract slowly	Contract rapidly
Function	Dynamic response (position and velocity sense of a rapidly adapting nature)	Static response
Junctional compleses	Present	Absent
Intercellular bridges	Absent	Present
Microladders	Absent	Present
Myoglobin	Myoglobin-rich	Myoglobin-poor

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