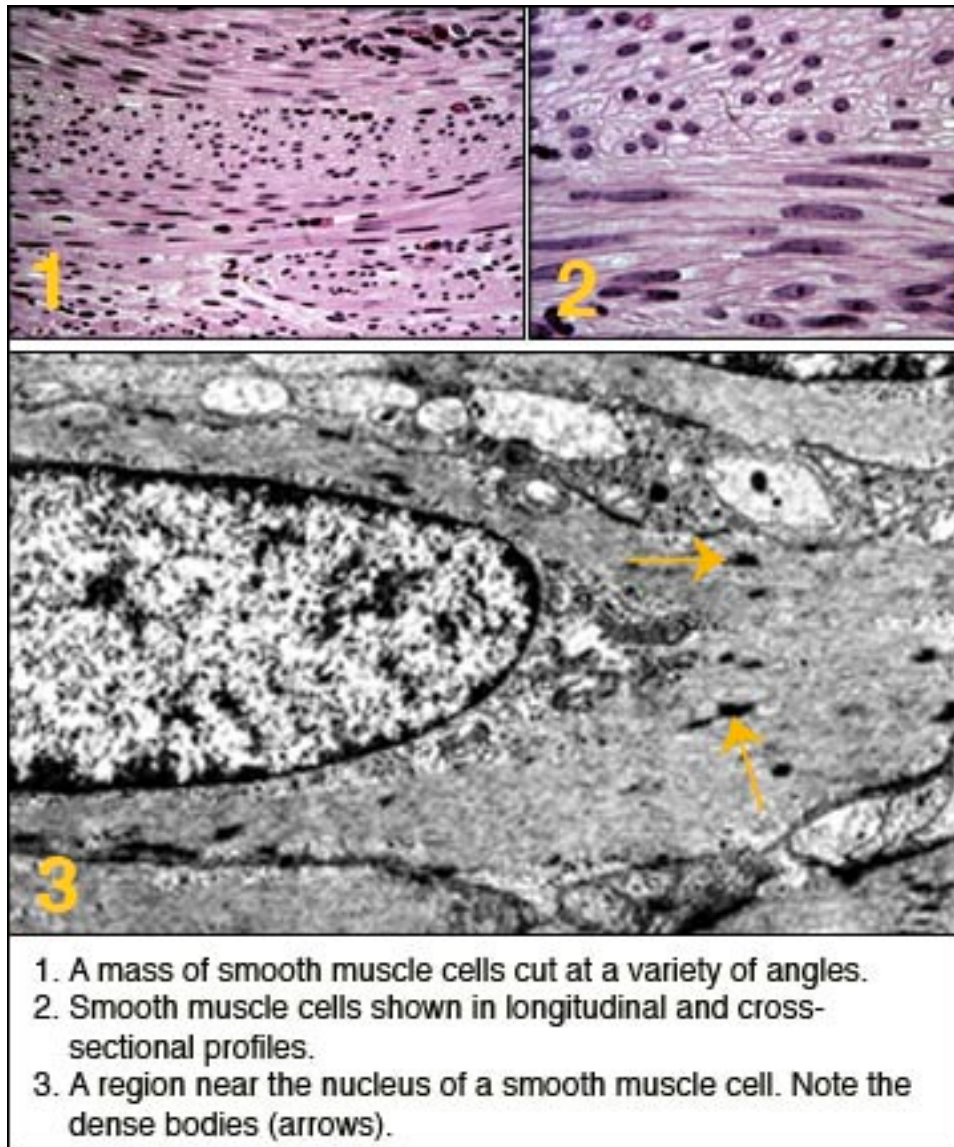


Smooth Muscle



Smooth muscle cells are widely distributed throughout the body and play an essential role in the functions of organs. They form the contractile portion of the walls of blood vessels and of hollow viscera such as the digestive, respiratory, and reproductive tracts. Smooth muscle cells also are present in the skin, where they form small muscles attached to hair follicles, and are in the iris and ciliary body of the eye, in the erectile tissue of the penis and clitoris, and in the stroma of the ovary and prostate.

The Smooth Muscle Fiber (Cell)

Each smooth muscle fiber is an elongated cell with an expanded central region and tapering ends. The cells vary in length in different organs, from 20 μm in small blood vessels to 500 to 600 μm in the pregnant uterus. A single central nucleus occupies the wide portion of the cell about midway along its length, elongated in the long axis of the cell. In a contracted cell, the

nucleus has a wrinkled or pleated outline. The cells lack cross-striations and in the usual histologic preparations appear homogeneous. However, longitudinal striations can be seen after maceration of the cells in acid; these striations may represent the myofibrils. In electron micrographs, the sarcoplasm in the region of the nucleus shows long, slender mitochondria, a few tubules of granular endoplasmic reticulum, clusters of free ribosomes, and a small Golgi complex at one pole of the nucleus. Unlike cardiac and skeletal muscle cells, only a rudimentary sarcoplasmic reticulum is present and a system of T-tubules is absent. The bulk of the cytoplasm contains closely packed, fine filaments arranged in bundles that run in the long axis of the cell. Mitochondria and glycogen granules are interspersed between the myofilaments. Scattered throughout the sarcoplasm are a number of oval dense bodies into which the myofilaments (actin) appear to insert. The cytoplasmic dense bodies contain α -actinin, an actin-binding protein. Desmin, the most abundant intermediate filament, and vimentin also insert into these anchoring points. The sarcolemma is covered externally by a thick external lamina consisting of proteoglycans associated with numerous fine collagenous and reticular fibers that blend with the surrounding connective tissue. In some regions the external lamina is lacking, and the cell membranes of adjacent smooth muscle cells are closely apposed in gap junctions (nexuses) through which excitation impulses spread from one cell to another. Areas of increased density, similar to the dense bodies, occur at intervals along the inner aspect of the sarcolemma, becoming more numerous along the ends of the cells. These dense regions appear to be sites of attachment of myofilaments and intermediate filaments to the cell membrane and have been called attachment plaques. The subplasmalemmal attachment plaques have been shown to contain the actin-binding proteins, vinculin and talin. Between these areas the sarcolemma may show numerous caveolae that form as a result of invaginations of the cell membrane. The caveolae are thought to be the functional equivalent to the T-tubule system of striated muscle. Caveolae of smooth muscle cells contain calcium ion and are intimately related to terminal sacs of endoplasmic reticulum that lie beneath the plasmalemma which also contain calcium ion.

Myofilaments

Thick and thin filaments have been demonstrated in smooth muscle cells by electron microscopy, and actin and myosin have been identified biochemically. The actin filaments of smooth muscle cells are associated with tropomyosin but lack troponin. However, myosin filaments have been difficult to identify in standard electron microscopic preparations, and it has been suggested that in smooth muscle, myosin is labile, aggregating into filaments only on initiation of contraction. Filamentous myosin has been shown in unfixed, rapidly frozen smooth muscle cells where regular arrays of thick myosin filaments have been seen surrounded by rosettes of actin. The myosin identified in smooth muscle is different from that of skeletal muscle in that it will bind to actin only if its light chain is phosphorylated. As in striated muscle, release of calcium ion from the sarcoplasmic reticulum in smooth muscle initiates contraction. In smooth muscle calcium ion is complexed to calmodulin (a calcium-binding protein), and this complex activates myosin light-chain kinase, an enzyme necessary for the phosphorylation of myosin, and permits it to bind to actin. Contraction then occurs. Myosin and actin myofilaments of smooth muscle interact as in striated muscle, and a sliding filament mechanism appears to account for contraction of smooth muscle cells also. Contraction of smooth muscle cells is associated with formation of blebs of the plasmalemma; the blebs are lost as the cells relax. The evaginations increase in size and number as the cell continues to shorten, and when the cell has reached 55% of its initial length, it is completely covered by blebs. In electron

micrographs, the blebs are free of myofilaments, but filaments are prominent in the nonevaginated areas between attachment plaques. In the contracted cell, the thick and thin filaments and the cytoplasmic dense bodies are oriented obliquely to the long axis, criss-crossing the cell, whereas in the relaxed cell these components generally are parallel to the cell axis. The contractile elements unite the attachment plaques with the dense bodies. During contraction, the contractile elements become obliquely oriented. As the cell shortens, its width must increase to accommodate the displaced volume, but this is opposed by the contraction pulling inward at the site of the attachment plaques. Those areas not directly subjected to the inward force bulge outward as blebs. The filaments between the dense bodies represent a contractile unit, several being strung together and anchored at either end in an attachment plaque. In addition to the actin myofilaments, the dense bodies and subplasmalemmal attachment plaques serve as attachment sites for the intermediate filaments (desmin, vimentin), which provide strong cytoskeletal support for the smooth muscle cell. Smooth muscle is richly innervated by the autonomic nervous system, which generally acts to increase or decrease the level of spontaneous contraction. Two physiologically different types of smooth muscle are recognized. Tonic smooth muscle, which is characterized by the lack of action potentials and slow contraction. Tonic smooth muscle tends to generate its own level of rhythmic contraction, which can be initiated by stretch or hormones. The autonomic nervous system acts to increase or decrease levels of contraction rather than actually initiating contraction. Only a few smooth muscle cells of the muscle sheet are innervated and the impulse spreads through gap junctions (single unit innervation).

Examples of this type of smooth muscle are the limiting wall (muscularis externa) of the gastrointestinal tract, urinary bladder and uterus. The other type of smooth muscle called phasic smooth muscle is characterized by distinct action potentials and rapid contraction controlled precisely by the autonomic nervous system. In phasic smooth muscle almost every smooth muscle cell is innervated (multiunit innervation). This type of smooth muscle is found in the wall of the vas deferens, iris of eye, erector pili, and some arteries.

Organization

Smooth muscle cells may be present as isolated units or small bundles in ordinary connective tissue, as in intestinal villi, the tunica dartos of the scrotum, and the capsule and trabeculae of the spleen. They also form prominent sheets in the walls of the intestines and arteries. In any one sheet of muscle, the fibers tend to be oriented in the same direction but are offset so that the thick portions of the cells lie adjacent to the tapering ends of neighboring cells. Thus, in transverse sections, the outlines of the cells vary in diameter according to where along their lengths the cells were cut. Nuclei are few and present only in the largest profiles, which represent sections through the expanded, central areas of the cells. A thin connective tissue consisting of fine collagenous, reticular and elastic fibers extends between the smooth muscle cells and becomes continuous with a denser connective tissue that binds the muscle cells into bundles or sheets. The latter connective tissue contains more abundant fibroblasts, collagenous and elastic fibers, and a network of blood vessels and nerves. The traction produced by contracting smooth muscle cells is transmitted to the reticuloelastic sheath about the cells and then to the denser connective tissue, permitting a uniform contraction throughout the muscle sheet. The reticular and elastic fibers of the reticuloelastic sheath are products of the smooth muscle cells.

