# Chapter 7
# Contractile Tissues

Contractile activities in animals is carried out by the **Muscle** Tissues

## 7.1. Skeletal Muscle

### 7.1.1. Basic Concepts

The functional cellular component of muscle tissue is the muscle cell or myofiber. In all three classes of muscle tissue the myofiber synthesizes and maintains a group of proteins responsible for the contractile nature of this tissue. Skeletal muscle is described as "striated" due to the intracellular arrangement of the contractile protein filaments which will form alternating bands when viewed under light microscopy in a longitudinal section. The term "skeletal" comes from the muscle typically being attached to the skeleton. There are some exceptions such as the upper esophagus. As a result, skeletal muscle is primarily involved in the initiation of body movement and locomotion. Skeletal myofibers are long, cylindrical cells arranged parallel to one another along the long axis of the muscle organ. The longest of these cells will stretch the length of the muscle organ, from origin to insertion, but shorter cells are more common.

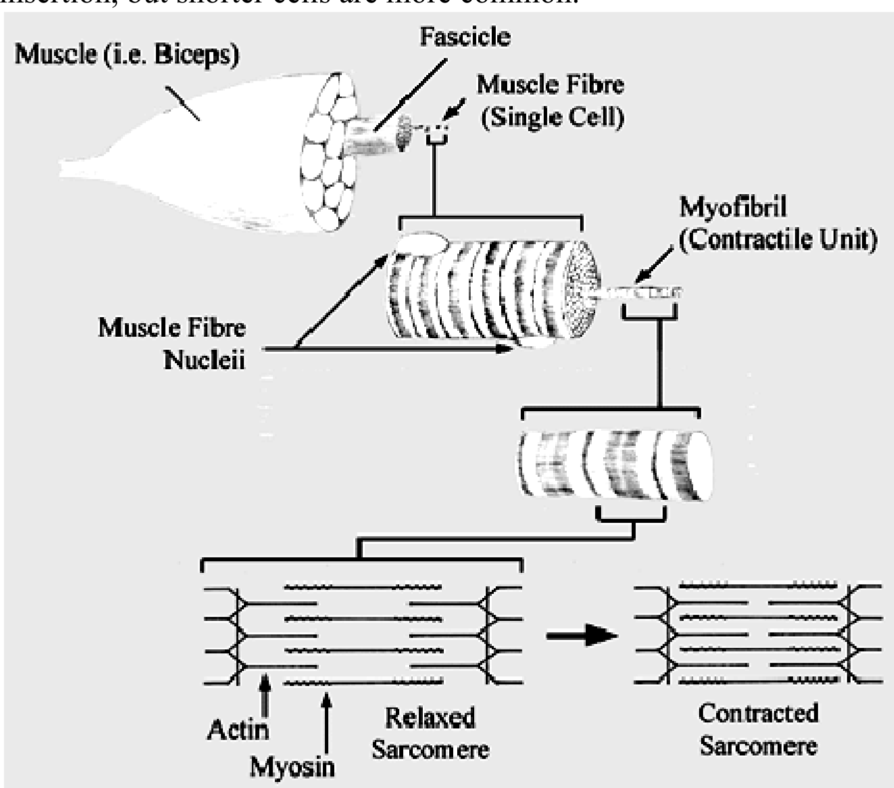


*Fig.7.1. Organization of Skeletal Muscle*

### 7.1.2. Levels of Connective Tissue Organization

Three levels of connective tissue organization confer structural integrity to the contracting muscle:

**1) Epimysium** - a fibrous connective tissue sheath surrounding the external surface of the entire muscle organ. Epimysium consists of collagen and fibroblasts. It is a dense regular connective tissue. Epimysium serves to bind the muscle organ together.
Epimysium is continuous with the tendons attaching the muscle to the origin/insertion. An extension of the tendon's collagenous fibers will enter into the body of the muscle organ to increase the anchoring surface area. Epimysium is sometimes referred to as "deep fascia".
**2) Perimysium** - a fibrous connective tissue sheath surrounding bundles of myofibers termed Fascicles. Perimysium also consists of collagen and fibroblasts. It is a dense regular connective tissue contiguous with the epimysium.
**3) Endomysium** - a loose connective tissue sheath, having reticular fibers, surrounding each individual myofiber.
**4) External Lamina :** The external lamina surround each myofiber just deep to the endomysium. The external lamina is similar in composition and appearance to the basal lamina of the epithelial basement membrane.

### 7.1.3. The Origin of Skeletal Myofibers

Skeletal myofibers arise from Myoblasts. Myoblasts are round, noncontractile cells with a single, central nucleus. Myoblasts are derived from mesenchymal cells. Mesenchyme is of mesodermal origin and so muscle is of mesodermal origin. The mesenchyme that gives rise to the myoblasts arises from various parts of the embryo. Trunk musculature arises from myotomal mesoderm. Limb musculature arises from somatic mesoderm. Facial muscles, muscles of mastication, and muscles of the larynx and pharynx arise from the pharyngeal arch (aka; branchial) mesoderm. During development, myoblasts will fuse together forming increasingly larger mulitnucleated Myotubes which will eventually become mature myofibers.
These myotubes synthesize the contractile proteins. Subsequent to the establishment of innervation the myotubes begin to display contractile behavior. This fusion of myoblasts during the development of skeletal myofibers explains their multinucleated nature. They average between 50 to 100 nuclei per myofiber. The nuclei are located immediately deep to the muscle cell membrane, the Sarcolemma. The major contractile proteins of the myofiber are Actin (a microfilament) and Myosin (a microtubule) also termed Thin and Thick Filaments respectively. These contractile proteins are arranged into parallel bundles called Myofibrils running along the long axis of the muscle cell. Each myofibril is associated with a "sleeve" of sarcoplasmic reticulum which will supply it with calcium for contraction. Mitochondria are located between myofibrils with their long axis being parallel to the myofibrils. The actin and myosin filaments form alternating regions in the myofibril. At rest they slightly overlap but they strongly overlap during contraction.

## 7.1.4. Functional Unit of a Skeletal Muscle

The basic functional unit is the Sarcomere. Many sarcomeres can make up one myofibril. The sarcomere is composed of a central array of 1.5 um long myosin filaments interdigitated at both ends by 1.0 um long actin filaments. These actin filaments are anchored into a transverse structure called the Z line/Z disc. So the Z lines form the borders of a sarcomere. At rest a sarcomere is ~2.5 um long. When contracted it becomes 2.0 um long. The banding, or striated, pattern of skeletal muscle is due to the arrangement of actin and myosin within the sarcomere. There are alternating dark bands (A bands) and light bands (I bands). These bands are named for their refractile properties. A bands are anisotropic and I bands are isotropic. The A band runs the length of the myosin. It includes those portions of actin which overlap with myosin. The I band is an actin pure-myosin free zone. One I band actually overlaps between two adjacent sarcomeres with a Z line being central to the I band. The actin and myosin filaments remain parallel within a sarcomere and between sarcomeres due to intermediate filaments. These intermediate filaments are Desmin and Vimentin. During contraction the actin filaments of the sarcomere slide past the myosin filaments towards the center of the A band shortening the myofibril. The shortening of the myofibrils will cause the myofiber to shorten which causes the muscle to contract. Within the A band is the centrally located H zone. The H zone is a central portion of the A band into which actin does not extend when the muscle is at rest. So it is a myosin pure region in the center of the A band. Within the H zone is a myosin cross bridge free, central area called the M line. The A-I Junction is that portion of the sarcomere where the actin and myosin filaments overlap. During contraction extensions of the myosin filaments, called myosin cross bridges, engage the actin filaments and pull them into the A band towards the M line. These cross bridges are composed of heavy meromyosin (HMM).

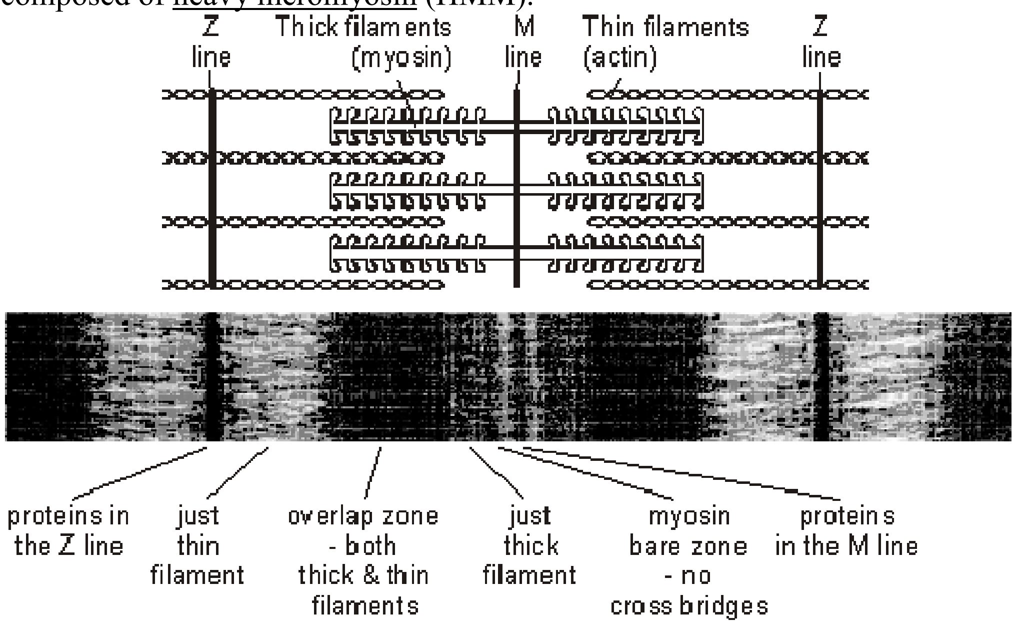


*Fig.7.2. Functional Unit of a skeletal muscle*

## 7.1.5. The Intracellular Control of Muscle Contraction

During contraction ATPase on the myosin filaments is activated, due to elevated calcium ion levels, resulting in the production of ATP to power contraction.

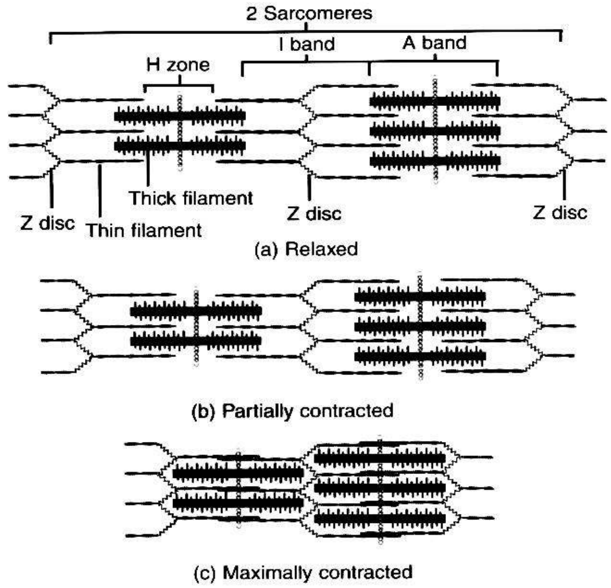

*Fig.7.3. Contraction Process*

This is stimulated by the actin filaments. The actin filaments in turn are controlled by the Troponin-Tropomyosin System/Complex which confers calcium dependency on actin and myosin. The actin filament is a double helix of globular actin monomers arranged around a long filament of tropomyosin. The regulatory protein Troponin is found at periodic intervals along the tropomyosin filament. Troponin will regulate contraction by exerting a conformational constraint on the actin filament. Troponin will sterically mask the binding sites, where the myosin cross bridges will attach, on the actin filament. During contraction calcium will bind to troponin causing a conformational shift which will expose the actin's binding sites to the myosin cross bridges. This allows for the sliding of the filaments past one another.

## 7.1.6. Regulation of Calcium Concentration

Calcium ion concentration is controlled by the sarcoplasmic reticulum (SR). The sarcoplasmic reticulum shuttles calcium between the cytoplasmic/sarcoplasmic compartment and the sarcoplasmic reticulum compartment. Calcium interacts with the myofibrils in the sarcoplasmic compartment. Calcium is stored in the sarcoplasmic reticulum compartment. Calcium is released from the sarcoplasmic reticulum during contraction and retrieved to the sarcoplasmic reticulum to allow for muscle relaxation.

## 7.1.7. The Skeletal Muscle Triad

The triad is made up of three components: A T-Tubule (aka; Transverse Tubule) which is an invagination of the sarcolemma which penetrates deep into the myofiber, and a pair of Terminal Cisternae flanking the t-tubule. The terminal cisternae are dilated, sac like, expansions of the sarcoplasmic reticulum that store calcium during muscle relaxation. The triad is located at each A-I junction. During contraction a wave of depolarization travels along the sarcolemma, down the t-tubules to the sarcomere. This wave of depolarization is caused by the release of neurotransmitters from the motor neuron at the neurosynaptic junction. This wave of depolarization will cause the terminal cisternae to release calcium into the sarcoplasmic reticuli. Calcium will travel through the sarcoplasmic reticuli to the sarcoplasmic compartment where calcium will interact with the myofibrils to facilitate contraction.

## 7.1.8. Motor Innervation of Skeletal Muscle

The junction between a nerve process and a myofiber is termed the Neuromuscular Junction (NMJ). The NMJ is the site of neuromuscular transmission.

The NMJ consists of: Branches of the motor neuron's terminal axon. One branch will synapse with an individual myofiber, a myofiber. Motor End plate - a region of the sarcolemma specialized for nerve transmission. The motor end plate has two levels of organization:

a} Primary Synaptic Cleft/Primary Synaptic Trough - a depression in the sarcolemma occupied by the innervating axonal branch.

b} Secondary Synaptic Cleft - highly infolded areas of the primary synaptic cleft.

Associated with the motor end plate are membrane molecules involved in neurotransmitter transmission. Acetylcholine Receptors - membrane proteins that recognize and bind to the neurotransmitter acetylcholine. Acetylcholinesterase - an enzyme deployed along the inner aspect of the secondary synaptic cleft which destroys the neurotransmitter after contraction has been stimulated. The structural integrity of the NMJ is maintained by the external lamina. The development of skeletal muscle is influenced by neural control. This influence occurs after the establishment of the myotube. This influence results in the establishment of three physiological categories of skeletal myofibers:

**a] Slow Twitch Muscle Fibers:** These fibers have a slower rate of contraction, higher stamina, and display less power. It has oxidative properties which increase stamina (i.e.; it is aerobic).

**b] Fast Twitch Muscle Fibers:** These fibers demonstrate a faster rate of contraction, lower stamina, and more power. It ha a glycolytic enzymatic nature (i.e.; anaerobic).

**c] Intermediate Fast Twitch Fibers:** As the name indicates, these fibers are intermediate in rate of contraction, stamina, and power. It has an anaerobic glycolytic nature as does the fast twitch class.

## 7.1.9. Sensory innervation of Skeletal Muscle

The sensory nerves of skeletal muscles may be myelinated or unmyelinated. Unmyelinated neurons are much less common and found in the perimysium. Sensory nerves can serve a number of functions: Some located in tendons and joints provide proprioceptive information. Some are involved in neural reflex arcs that adjust tension and the length of skeletal muscles. i.e.; neuromuscular spindles and Golgi tendon organs

### a) Neuromuscular Spindles

Neuromuscular spindles are stretch receptors located within skeletal muscles (especially slow twitch extensor muscles used to maintain posture). They monitor static and dynamic aspects of muscle length. They also respond to passive increases in muscle length through a nervous reflex arc called the Stretch reflex. The stretch reflex allows the muscle to resist excessive and injurious over stretching.

Neuromuscular spindles are composed of between 3 to 12 Intrafusal Fibers. Intrafusal fibers are specialized striated muscle fibers encapsulated by perimysium. They are located within the belly of skeletal muscles and are orientated parallel to the surrounding (regular) myofibers. These myofibers surrounding the intrafusal fibers are termed

Extrafusal Fibers. There are two morphotypes of intrafusal fibers within each spindle:
i} Nuclear Bag Fibers - larger in diameter than the other type, they have their nuclei located in an noncontractile equatorial region of the fiber.
ii} Nuclear Chain Fibers - smaller in diameter than the other type, they have their nuclei arranged into a single row among the myofibrils.
Two types of sensory nerves innervate the neuromuscular spindle:
i] Primary Fibers - heavily myelinated and so fast conducting nerves.
ii] Secondary Fibers - unmyelinated and so slow conducting nerves.
The intrafusal fibers receive motor innervation from the Gamma Neurons (aka; fusiomotor nerves). Gamma neurons alter the sensitivity of the neuromuscular spindle tostretch by regulating the contraction of the intrafusal fibers.

### b) Golgi Tendon Organs

Golgi tendon organs are encapsulated sensory nerve endings which monitor increase in muscle tension. They are located within the tendons near the musculotendinous junction.The Golgi tendon organ consists of unmyelinated nerve endings encapsulated by a connective tissue termed the Endoneurium and enmeshed among the collagen bundles of the tendon. Muscle tension is transferred to the tendon. This causes the tendon's collagen fibers to compress the nerve ending.

## 7.2. Cardiac Muscle

Cardiac muscle fibers possess many characteristics which are similar to those of skeletal muscle fibers but with modifications: Cardiac muscle cells are typically uninucleated but can be binucleated. They are smaller cells than are skeletal myofibers and they branch. Myocardial cells are attached to one another at Intercalated Discs. Intercalated discs serve both to bind cells and to allow for communication. The intercalated disc consists of three structurally distinct regions: desmosomes/macula adherens, fascia adherens. The fascia adherens is the site of insertion of actin filaments from themyofibrils into the sarcolemma and gap junctions/macula communicans . Gap junctions allow for cardiac myofibers to be electrically coupled for uniform contraction of the heart chambers. Myofibril organization is similar in cardiac myofibers to that of skeletal myofibers. They show the same striation patterns and their sarcomeres are identical to those of skeletal muscle cells.There are some differences:
a] The sarcoplasmic reticulum is less well developed since cardiac muscle contraction depends to a greater degree on the influx of extracellular calcium.
b] The t-tubules are further apart being located at the Z lines.
c] Instead of a triad, cardiac muscle cells possess a Diad made up of one t-tubule and one terminal cisterna.
e) Unlike the skeletal muscle's neuromuscular junction the nerve-cardiac muscle junction lacks the motor end plate
f) The cardiac muscle cells have many more mitochondria than do skeletal muscle cells.

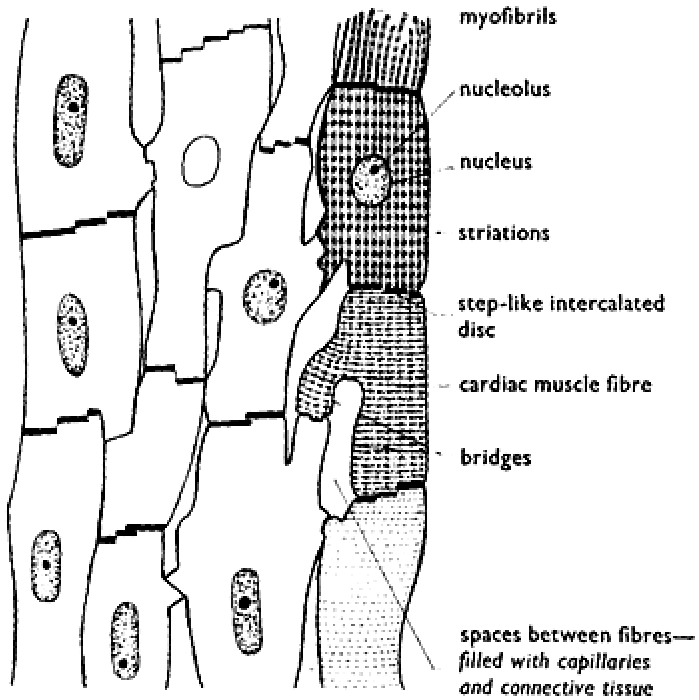


*Fig.7.4. Cardiac Muscle*

## 7.2. 1. Specialized Cardiac Muscle Fibers

The cardiac conduction system consists of highly specialized muscle fibers designed to distribute the impulse for contraction throughout the heart.

**a) <u>Nodal Fibers</u> :** Nodal fibers compose the sinoatrial and atrioventricular nodes. Nodal fibers are specialized cardiac myofibers which exhibit an inherent contractile rhythmicity due to their ability to spontaneously depolarize. They depolarize quicker than do the typical cardiac muscle cells. As a result, they are termed "pacemaker cells".

**b) <u>Purkinje Fibers:</u>** These specialized cardiac myofibers make up the rest of the cardiac conduction system (AV bundle, bundle branches, and Purkinje fibers). They are elongated, thick cardiac myofibers specialized for conduction not for contraction. So Purkinje cells have few myofibrils. Purkinje fibers are not connected to each other by the typical intercalated discs but by desmosomes and gap junctions scattered along the opposing cell membranes. Purkinje fibers are designed to ensure the efficient contraction of the ventricles.

# 7.3. Smooth Muscle

Smooth muscle forms the bulk of the visceral musculature. The only notable exception is the myocardium. Smooth muscle fibers can occur individually or, most often, in sheets.These sheets will be found in:the muscular walls of the digestive organs and the ducts of the associated glands, lining portions of the respiratory tract, lining the urinary and reproductive tracts, the muscular walls of blood vessels and of the larger lymph vessels, and the arector pili muscles.

As is the case with all muscle, most smooth muscle is of mesodermal origin. However, some is of ectodermal origin: dermis, nipple, prepuce, scrotum, glans penis, and the intrinsic muscles of the eye.

### 7.3.1. Appearance

Smooth muscle cells are small, fusiform cells with a single elongate, centrally located nucleus. They average between 20 and 50um in length. But they can range from 20 um in the vascular walls to ~500 um in a gestational uterus. The single nucleus will often have several nucleoli. Smooth muscle sheets are associated with small amounts of collagen and elastin fibers as well as a few scattered fibroblasts. Individual smooth myofibers are supported by reticular fibers. Also closely opposed to the cell surface is an external lamina.

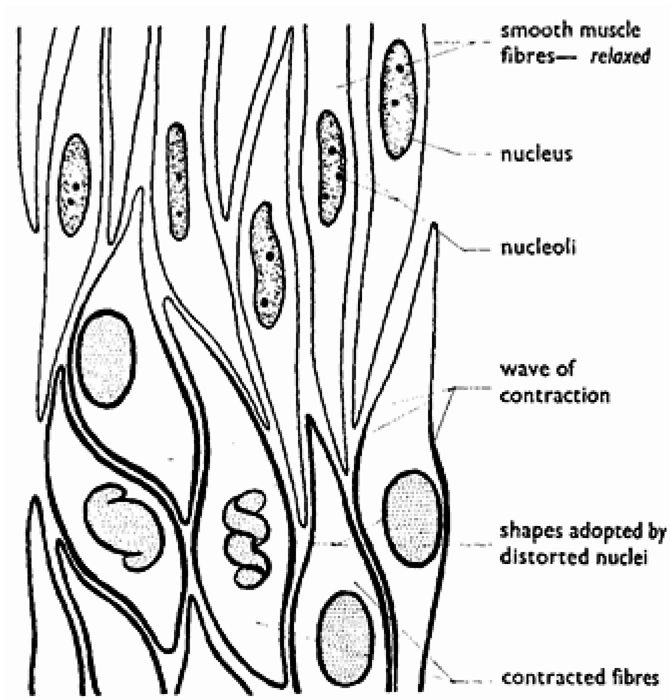


*Fig.7.5. Smooth Muscles*

### 7.3.2. The Cytoskeleton of Smooth Muscle Cells

Actin and myosin are present in smooth myofibers. However, they are not organized into myofibrils, at least when at rest, and so smooth muscle is unstriated in appearance. The smooth myofibers lack sarcomeres when at rest and so are unstriated in appearance. Smooth muscle cells are believed to contract by the sliding filament mechanism, as do the other two classes of muscle tissue, but it is not well understood. It may be that the myosin exist in a disaggregated or morphologically dispersed state when the cell is at rest and will aggregate into distinct thick filaments due to nervous or hormonal stimulation. There is also a network of intermediate filaments present. These intermediate filaments are anchored in dense bodies distributed through both the cell and the sarcolemma. This intermediate filament-dense body arrangement i believed to represent an intracellular cytoskeleton. The interdigitating thick and thin myofilaments, instead, are arranged so as to lay nearly parallel to the long axis of the myofiber. Also running along the length of the myofiber are intermediate filaments.

These intermediate filaments have short, globular segments called dense bodies along their length. The thin filaments anchor into these dense bodies so they serve as Z discs. Also along the length of the intermediate filaments are structures called dense plaques.

Dense plaques also anchor the actin filaments (so they also act as Z discs) but in addition anchor on to the collagen of the surrounding endomysium.

It is believed that this arrangement serves to anchor a functional sarcomere and to allow for contraction by a sliding filament-like mechanism. Smooth muscle cells lack t-tubules. T-tubules may not be necessary due to the small size of the cells and the reliance of smooth muscle on intercellular communication. Smooth muscle is innervated by unmyelinated postganglionic nerve of both the sympathetic and parasympathetic divisions of the ANS. This nerve-muscle junction lacks a motor end plate. Also one axon will service many myofibers due to their high degree of electronic coupling which allows the muscle sheet to contract as a unit. This is single unit innervation.Smooth muscle may also contract due to nonnervous influences such as: hormones, stretch, and spontaneous contractile rhythmicity.