THE MUSCULAR SYSTEM

The muscular tissue of the body constitutes from one-third to one-half of the body mass of the average vertebrate.

Muscular tissue functions in:

- movement and locomotion, through its direct connection with the skeletal system
- more subtle movements associated with maintaining posture/vertical position
- help to generate heat due to catabolic reactions that are associated with muscular activity (such that animals shiver or increase overall movement when body temperature drops)
- can be modified into other structures, such as electric organs in some fish

The general structure of a muscle fiber include (Fig. 10.2, p. 347) **myofibrils** (chains of repeating subunits) composed of two kinds of filaments:

- **thin filaments** (composed of **myosin**) and **thick filaments** (composed of **actin**, **tropomyosin** and **troponin**) that interact by binding to produce a sliding movement between the filaments, and that creates tension in the muscle fiber leading to muscle contraction.

There are three generally recognized muscle tissue types: **smooth**, **cardiac** and **skeletal**, each tissue type with a distinct location in the body, cellular organization (histology), and general action of the muscle fibers (physiology)

Because of the multiple functions of muscles, criteria for classifying muscles include:

1. Color

- **red** - highly vascularized and rich in myoglobin; resist fatigue
- **white** - low vascularization and lower in myoglobin; quicker to fatigue

2. Location

- **somatic** - move bone or cartilage
- **visceral** - control activities of organs, vessels, or ducts

3. Nervous system control

- **voluntary** - under immediate conscious control
- **involuntary** - are not

4. Embryonic origin
5. General microscopic appearance

- **skeletal** - Fig. 10.2, p. 347
- **cardiac** - Fig. 10.3, p. 348
- **smooth** - Fig. 10.4, p. 348

Smooth muscle

- found lining the walls of blood vessels, visceral organs (such as the digestive tract and uterus) and are also found attached to hairs in the integument.
- two general types:

  - **unitary** smooth muscle has **self-initiated** or **myogenic contraction** to aid in sustaining the rhythmic movement of the organ with which it is associated

- **multiunit** smooth muscle has **neurogenic contraction**, which requires action potentials sent by neurons to regulate its action.

Cardiac muscle

- are found solely in the musculature of the heart wall
- in cardiac muscle the branching of the cells increase its overall connectivity and the cells are firmly united with each other through the **intercalated disks**
- cardiac muscle does not fatigue readily, which is a desirable trait in the muscles that maintain circulation of blood
- action of the cardiac muscle fibers shows mixed control, such that the myogenic rhythm of the heart is maintained by neurogenic control and the entire unit of the cardiac muscle acts as a **syncytium**, or single functional unit

Skeletal muscle

- skeletal muscles are closely associated with the skeleton and are used in locomotion
- each skeletal muscle fiber is also a syncytium due to the close connection between cellular units
- fibers are closely associated with connective tissues and are under voluntary control by the nervous system.

	Smooth	**Cardiac**	**Skeletal**
Histology			
Striated?	Not striated	Striated	Striated
Shape	Spindle-shaped	Cylindrical	Cylindrical
Branched?	Not branched	Branched	Not branched
Nucleus location	Nucleus central	Nucleus central	Nucleus peripheral
Disks?	No disks	Intercalated disks	No disks
Physiology			
Neurological control	Involuntary	Involuntary	Voluntary
Speed of action	Slow	Fast	Fast

General Muscle terminology

As you are familiar with from lab, many unique terms are associated with the muscular system, ranging from describing how a muscle works to the general shape of the muscle itself.

The term "muscle" has at least two meanings:

- **muscle cell or fiber** - the active contractile component: muscle cells and their endomysium
- **muscle organ** - the whole organ: muscle cells plus associated connective tissues, nerves, blood supply

Action

- takes place by contraction, which creates tension in the muscle so that it shortens and thus moves what it is attached to (whether it is a bone, hair or the epithelium of an organ)
- for skeletal muscles, each muscular unit may be described based on a number of factors, such as where the main body of the muscle (**belly**) is located, such as shoulder muscles, pectoral muscles, gluteal muscles, etc.

Muscle is not attached directly to bone by the contractile muscle fibers - various wrappings of connective tissues extend beyond the ends of the muscle fibers to connect with the periosteum of the bone:

- **tendon** - cordlike attachment
- **aponeurosis** - thin flat sheet
- **fascia** - thin flat sheets of connective tissues that wrap and bind parts of the body together
- **raphe** - junction of two muscles at a band of connective tissue to form a line of fusion, such as the linea alba

Basis for muscle contraction:

- a muscle receiving no nervous stimulus is **relaxed** or in a **resting state** - soft shape retained by surrounding collagen fibers
- when nervous stimuli applied beyond muscle's threshold level, contraction results and **tensile force** is generated, constituting the active state
- the attached bone and/or mass that must be moved represents the **load** - whether a muscle actually contracts depends on the relative balance between the tensile force of contraction and the load to be moved (Fig. 10.6, p. 351)

Major contractile characteristics of a muscle include how rapidly it reaches maximum tension and how long it can sustain this tension

Tension and strength are directly related to the number of cross-bridges between muscle filaments

- in the shortest position, filament overlap interferes with cross-bridge formation and tension is low (Fig. 10.6a)
- in the longest position, filaments overlap very little with few cross-bridge formations and tension low (Fig. 10.6b)
- intermediate lengths generate maximum cross-bridging (Fig. 10.6c)

Tonic fibers:

- relatively slow contracting and produce low force
- can sustain contraction for prolonged periods of time
- comprise most of the axial and appendicular skeleton

Twitch (phasic) fibers:

- generally produce fast contractions so they often make up muscles used for rapid movement
- slow twitch vs. fast twitch relative, but slow take ~2X longer to reach maximum forces

Origin: the end of a muscle that attaches to the more fixed part of the skeleton, which is the proximal end in limb muscles

Insertion: the point of attachment of a muscle that moves the most when the muscle shortens, and is the most distal end of limb muscles

For the biceps, the belly lies anterior to the humerus, the origin the coracoid process of the scapula, and the insertion is the radial tuberosity. For the triceps, the origins are the posterior surface of the humerus and the infraglenoid tubercle of the scapula, and the insertion is the olecranon of the ulna.

The action of skeletal muscles can be:

- **antagonistic** - oppose or resist the action of another muscle (such as is the case of the biceps and the triceps)
- **synergistic** - work together to produce a common effect (such as in the action of making a fist, in which the muscles of the forearm and fingers work together)

Other actions of muscles include:

Flexor - decreases the angle at a joint
Extensor - increases the angle at a joint
Abductor - moves a bone away from the midline
Adductor - moves a bone closer to the midline
Levator - produces an upward movement
Depressor - produces a downward movement
Supinator - turns the palm upward or anteriorly
Pronator - turns the palm downward
Sphincter - decreases the size of an opening
Tensor - makes a body part more rigid
Rotator - moves a bone around its longitudinal axis

We can also describe muscles based on **shape**, such as in the arrangement of the muscle fibers:

Strap-shaped muscles - have parallel fibers and broad attachments (teres major)
Fusiform muscles - parallel fibers, but narrow tendons for attachments (biceps)
Pinnate muscles - diagonally arranged fibers that insert on the side of the muscle into a tendon. (subscapularis)

Or **Size**:

Maximus = largest
Minimus = smallest
Longus = longest
Brevis = shortest

Number of origins:

Biceps = two origins
Triceps = three origins
Quadriceps = four origins

Relative shape

Deltoid = triangular
Trapezius = trapezoid
Serratus = saw-toothed
Rhomboideus = rhomboid or diamond-shaped

The main muscle groups correspond with the divisions used for the skeletal system:

Axial muscles - trunk and tail muscles of fishes and tetrapods
Branchiometric muscles - also called visceral muscles, such as those associated with the gills, jaws and hyoid apparatus
Appendicular muscles - fin muscles of fishes and limb muscles of tetrapods

Muscles arise from three embryonic sources:

mesenchyme - dispersed throughout the body giving rise to smooth muscles within the walls of blood vessels and some viscera
splanchnic layer of the lateral plate mesoderm - develops into the smooth muscle layers of the digestive tract and into the walls of the heart
paraxial mesoderm, or somites, and specifically the myotome layer of the somite - the primary source of skeletal muscles during development

- within the head region, the myotome does not become completely segmented, and instead forms seven pairs of somitomeres that will produce the musculature of the head region (Fig. 10.22a, p. 365)
- the remainder of the somites in the body develop into the trunk and appendicular muscles

Homologies

During muscle evolution, some muscles have fused with one another, others have split into distinct new muscles, some have become reduced in prominence, and others have changed their points of attachment and hence their evolution

Muscle homology can be determined in three ways:

- attachment similarity
- functional similarity
- nervous innervation, due to conserved relationships between a muscle and its nerve supply

Establishing similarity can help compare the different groups of muscles (cranial, axial and appendicular) among the different vertebrate classes

Cranial muscles

External ocular muscles - six extrinsic ocular muscles which attach to the surface of the eye and are responsible for moving the eye within the orbit (Fig. 10.23, p. 366):

Dorsal (superior) oblique	Ventral (inferior) oblique
Dorsal (superior) rectus	Ventral (inferior) rectus
Medial rectus	Lateral rectus

These muscles are innervated by the oculomotor nerve

Some tetrapods also have a **retractor bulbi**, which pulls the eyeball further into the orbit to allow for coverage by the nictitating membrane (lacking in humans)

Branchiometric muscles - develop from the myotomes caudal to those that produce the ocular muscles

- closely associated with the visceral skeleton so they are used in both breathing and feeding.
- perform the function of operating the jaw, opening and closing the spiracle (which functions in water intake into the gills when the fish is eating)
- may be subdivided based on what visceral arch they are associated with:

Fishes' gill arch	Muscle	Action
First arch	Adductor mandibulae	closes jaw
	Intermandibularis	compresses throat
Second arch	Constrictor	compresses gills/pharynx
	Levator	lifts gill bars
Third to seventh arch	Constrictors	compresses gills/pharynx
	Levators	lifts gill bars

The **cucullaris** is attached to the last branchial arch but is associated with the pectoral girdle

In tetrapods the branchiometric musculature changed in tandem with changes in the visceral skeleton to make the animals more adapted to a terrestrial environment - resulted in a loss of many branchiometric muscles

Tetrapod gill arch	Muscle	Action
First arch	Masseter	closes jaw
	Temporalis	closes jaw
	Pterygoids	function in jaw movement
	Digastric	opens the jaw

Second arch	Mylohyoid	opens the jaw
Other arches	Platysma	moves skin of face and neck
	Sternomastoid	turn head
	Cleidomastoid	turn head

Epibranchial and hypobranchial muscles - dorsal and ventral muscles associated with the head and trunk region that perform functions associated with jaw and tongue movement

- muscles of fishes associated with feeding and breathing include:

  - Coracoarcuals - opens mouth
  - Coracomandibular - opens mouth
  - Coracohyoid - helps in feeding
  - Coracobranchial - helps in swallowing

- muscles in tetrapods are associated with the hyoid apparatus and the tongue:

  - Tongue muscles - hyoglossus, styloglossus, genioglossus
  - Geniohyoid - draws hyoid cranially
  - Sternohyoid - draws hyoid posteriorly
  - Sternothyroid - draws larynx caudally
  - these muscles are also used in speech and sound production in tetrapods

Homologies between the branchial and hypobranchial muscles of several different vertebrate taxa are shown in Table 10.3.

Trunk/axial muscles

The axial musculature associated with the trunk can function either in locomotion or breathing
Axial musculature begins as myotomes separated by myosepta which are then further divided into two regions:

- **epaxial muscles** - muscles on the dorsal part of the body
- **hypaxial muscles** - muscles on the ventral part of the body that are separated by the lateral septum (Fig. 10.26, p. 368)

Fishes

In fishes, the trunk muscles remain divided into folded muscle segments or myomeres, that are divided into myosepta

- these muscles contract alternately to produce an undulating motion that propels the fish through the water
- internally, these muscles remain divided into **dorsal (epaxial)** and **ventral (hypaxial)** sections by the **lateral septum**

Tetrapods

In tetrapods, the trunk muscles function more in maintenance of posture, head movement, and respiration rather than in locomotion, which has shifted to the appendicular muscles

The epaxial muscles of the tetrapod trunk skeleton include:

Longissimus dorsi - extends vertebral column
Iliocostalis - draws ribs together
Multifidus spinae - extends vertebral column
Spinalis dorsi - extends vertebral column

The hypaxial muscles of the tetrapod trunk skeleton include:

Abdominal muscles:

Rectus abdominis - compresses abdomen
Internal oblique - compresses abdomen
External oblique - constricts abdomen
Internal oblique - constricts abdomen

Respiratory muscles:

Serratus - draw ribs cranially)
Scalenus - flexes the neck)
Diaphragm - separates the thoracic/abdominal cavities, functions in breathing
Intercostals - protract/retract ribs

Appendicular muscles

Appendicular muscle development originates from the somites as ougrowths of the somite myotome into the limb bud - **myotomic buds to the appendages**

As the limb bud grows, the appendicular musculature subdivides into the muscle mass that lies above the appendicular skeleton (dorsal muscles) and the mass that lies below the appendicular skeleton (ventral muscles)

These muscle masses later differentiate into multiple muscle groups depending on the type of organism

Fishes

In general, most of the locomotion of fishes is dependent on the action of the axial musculature, which undergoes alternate contraction and relaxation to produce undulating movements of the body

Fins (appendicular appendages) function more in maintaining stability, braking and maneuvering - thus, the range of movement of fins is much more limited than that of tetrapod limbs

- **ventral muscles** in fishes go to the formation of the **abductor muscle**, which pulls the fins ventrally and cranially
- **dorsal muscles** go to the formation of the **adductor muscle** found on the posterodorsal part of the fin and moves the fin dorsally and caudally

Tetrapods

The tetrapod appendicular musculature is more complex than that of fishes because the limbs function in both support and locomotion

In tetrapods the **function** of the dorsal and ventral muscle groups is **reversed** from that seen in fishes

- the **dorsal** muscles, which in fishes were responsible for adduction will instead **abduct or extend the appendages**
- the **ventral** muscles formerly used for abduction are instead used for **adduction or flexion**

Pectoral region	**Dorsal muscles (extensors)**	**Ventral muscles (flexors)**
Muscles of the back	Latissimus dorsi Cutaneous maximus	
Muscles of the chest		
Muscles of the shoulder	Deltoids Subscapularis Teres major	Pectoralis Supraspinatus Infraspinatus
Muscles of the arm	Triceps	

Pelvic region	Supinator Extensors of the digits **Dorsal muscles (extensors)** Gluteal muscles Quadriceps rectus femoris vastus medius vastus intermedius vastus lateralis Sartorius Iliopsoas Extensors of the digits	Biceps Pronator Flexors of the digits **Ventral muscles (flexors)** Adductor femoris Semimembranosus Semitendinosus Gracilis Biceps femoris Gastrocnemius Caudofemoralis Flexors of the digits

Locomotion

The study of locomotion completes our understanding of the skeletal and muscular systems, because it examines the functional relationship between the two systems as well as between the organism and its environment

We will discuss three important categories of locomotion: swimming, terrestrial locomotion, and flight.

Swimming

We can first distinguish vertebrates that swim by whether they are **primary swimmers** (species for which swimming is the sole pattern of locomotion) or **secondary swimmers** (species which have readapted completely or partially to an aquatic mode of life).

Some general requirements of swimmers are that they must:

1) reduce the resistance that water offers to motions of the moving body
2) propel themselves in a relatively dense medium
3) control vertical position in the water
4) maintain orientation and steer the body

In addition, secondary swimmers must also undergo secondary adaptations to their circulatory, respiratory and sensory systems to tolerate the high pressures and exposure to water that swimming entails

Primary swimmers are generally undulatory swimmers that use the musculature of the fins only, or the fins in combination with the trunk and tail to propel themselves through the water

Characteristics of the primary swimmers are:

- a fusiform body that is held rigid by strong articulation of the vertebral column
- segmented myomeres that allow individual muscle units to exert forces over the entire side of the body
- integument that is attached strongly the underlying musculature by connective tissue to increase the compactness of the body

The musculature, skeletal system and integument form an integrated unit that helps to streamline the animal and reduce drag as it moves through the water

Secondary swimmers are generally oscillatory swimmers that propel themselves through the water with paddle-like movements of the appendages

- appendages may also be modified into webbing or flippers to assist in propulsion
- generally have well-developed appendicular musculature
- can reduce pressure drag around the body by temporarily streamlining themselves when moving through water

Terrestrial locomotion

In terms of terrestrial locomotion, there are many different modes that an animal may use:

Cursorial - tetrapods that travel far or fast on the land. Cursorial animals possess a relatively elongate body, in which the vertebral column acts to increase running stride by stretching out to increase forward propulsion

Saltatorial - tetrapods that jump or hop. Saltatorial animals have bodies in which the weight is shifted to the hind legs, the legs are powerful and strongly constructed, and the center of mass is aligned with the sacrum

Scansorial - tetrapods adept at climbing. Scansorial animals have strengthened pectoral musculature and appendages, and modified phalanges for clinging to vertical surfaces

Fossorial - tetrapods that are adept at digging, and live a somewhat subterranean existence. Fossorial animals have highly flexible vertebral columns, strong pectoral musculature, and modified phalanges for digging

Each of these different modes of life requires dramatic modifications in the skeletal system (in terms of the parts of the body that receive the most stress) and the associated musculature

Animals with bipedal locomotion or that are scansorial have a foot posture that is more plantigrade, in which the soles of the feet are placed flat on the ground. In contrast, most cursorial animals have a more digitigrade posture, in which the wrist and ankle are carried off the ground and the animal walks on its digits. Or, the animal may be extremely long legged, and walk only on the tips of the digits such that the terminal end of the digit is modified to form a hoof, and other digits are lost, a posture called unguligrade.

Flight

Tetrapods that fly can do so in three different ways.

- **Parachuting** - use of limbs and body to increase overall surface area to break an inadvertent fall
- **Gliding** - use of broad membranes attached to limbs to increase surface area and travel a greater horizontal distance through the air
- **True flight** - use of wings to actively sustain movement through the air

Tetrapods that use active flight, such as birds, have pectoral appendages that are reduced to a single digit and highly developed pectoral musculature necessary to sustain active flight

In **birds**, the primary flight muscles originate on the **ventral surface of an expanded, keeled sternum:**

- pectoralis - depressor of the wing
- supracoracoideus - levator of the wing

In **bats**, the flight muscles are associated with movement of the humerus and scapula and are located **on the side of the thorax:**

- primary wing depressors:

  - pectoralis
  - subscapularis
  - serratus anterior

- primary wing levators:

    - deltoideus
    - trapezius
    - spinatus

Definitions

Abductor - moves a bone away from the midline

Adductor - moves a bone closer to the midline

Antagonistic - condition in which a muscle opposes or resists the action of another muscle

Aponeurosis - sheetlike tendon of a muscle

Cursorial - tetrapods that travel far or fast on the land

Depressor - produces a downward movement

Digitigrade - posture in which the wrist and ankle are carried off the ground and the animal walks on its digits

Epaxial - pertaining to structures that lie above or beside the vertebral axis

Extensor - increases the angle at a joint

Fascia-sheets of connective tissue that lie beneath the skin or ensheathe groups of muscles

Flexor - decreases the angle at a joint

Flight - use of wings to actively sustain movement through the air

Fossorial - tetrapods that are adept at digging, and live a somewhat subterranean existence

Gliding - use of broad membranes attached to limbs to increase surface area and travel a greater horizontal distance through the air

Hypaxial - pertaining to structures that lie ventral to the vertebral axis

Insertion - the point of attachment of a muscle that moves the most when the muscle shortens, or the most distal end of limb muscles

Levator - produces an upward movement

Origin - the end of a muscle that attaches to the more fixed part of the skeleton, which is the proximal end in limb muscles

Oscillatory swimmers - propel themselves through the water with paddle-like movements of the appendages

Parachuting - use of limbs and body to increase overall surface area to break an inadvertent fall

Plantigrade - posture in which the soles of the feet are placed flat on the ground during locomotion

Primary swimmers - species for which swimming is the sole pattern of locomotion

Pronator - turns the palm downward

Raphe - junction of two muscles at a band of connective tissue to form a line of fusion, such as linea alba

Rotator - moves a bone around its longitudinal axis

Saltatorial - tetrapods that jump or hop

Scansorial - tetrapods adept at climbing

Secondary swimmers - species which have readapted completely or partially to an aquatic mode of life from a terrestrial life

Sphincter - decreases the size of an opening

Supinator - turns the palm upward or anteriorly

Synergistic - condition in which the muscles work together to produce a common effect

Tensor - makes a body part more rigid

Undulatory swimmers - use the musculature of the fins only, or the fins in combination with the trunk and tail, to propel themselves through the water

Unguligrade - a locomotory posture used by long legged tetrapods, which walk only on the tips of the digits such that the terminal end of the digit is modified to form a hoof, and other digits are lost