Locomotor Principles: Anatomy and Physiology of Skeletal Muscles

4

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Abstract

The musculature consists of individual muscles which are mainly built up of muscle cells (muscle fibres, myocytes, myotubes), and its main function is to move and support the bones of the skeleton. In human beings, the musculature is the largest organ, consists of 640 single muscles, makes up 50 % of the body weight, moves 200 bones, and has 2,200 points of attachment. Skeletal muscles are under the control of the central nervous system, the myelon, and motor nerves. Histologically, the skeletal muscle belongs to the striated muscle type. In addition to the voluntary motor function, which is the elementary task of the organ, the muscle is also required for involuntary motor control, stabilisation of joints, and heat production, but has also immunological and endocrine functions. In addition to muscle cells, a muscle is built up of a number of other cell types and tissues. The following chapter is designated to describe and discuss basic knowledge about the anatomy and physiology of the human skeletal muscles in comparison with the skeletal muscle of other species.

4.1 Anatomy of Skeletal Muscles

4.1.1 Development of Muscle Tissue

Muscle tissue originates from the mesoderm, which is one of the three germinal layers, and develops between the amnion cave and the chorion cave. It is located in the middle between the two other germinal layers, the ectoderm and the endoderm. With progression of the embryonic development, the mesoderm forms somites along the neural tube. From there precursor muscle cells (myoblasts (developmental progenitor cells)) migrate to the sites of muscle formation in the limbs and body wall, where they give rise to muscle fibres (Partridge 2009). Migration of precursor cells is stimulated by the stimulating factor Pax3. Precursor muscle cells fuse and form a syncytium (single cell deriving from the fusion of several precursor cells), which contains hundreds of nuclei from the precursor cells and expresses the contractile apparatus. Attached to myotubes on the outside of the cell membrane are the so-called satellite cells (stem cells), which can be transformed into myotubes, whenever regeneration is necessary. Number of satellite cells and capacity of stem cells to regenerate to myotubes are limited.

4.1.2 Muscle Fibre

The muscle cell is a long, cylindrical, multinucleated, and tubular structure of up to several centimetres in length, which is surrounded by the cell membrane, called **sarcolemma**. The sarcolemma encloses the cytoplasm, which is called sarcoplasm. The sarcoplasm contains myofibrils, which are built up of the **myofilaments** actin, myosin, troponin, tropomyosin, and some other nonfilamentous proteins. Nuclei are unusually flattened and pressed against the inside of the sarcolemma. Mitochondria (sarcosoma) are located between the myofibrils. Myofibrils are surrounded by the

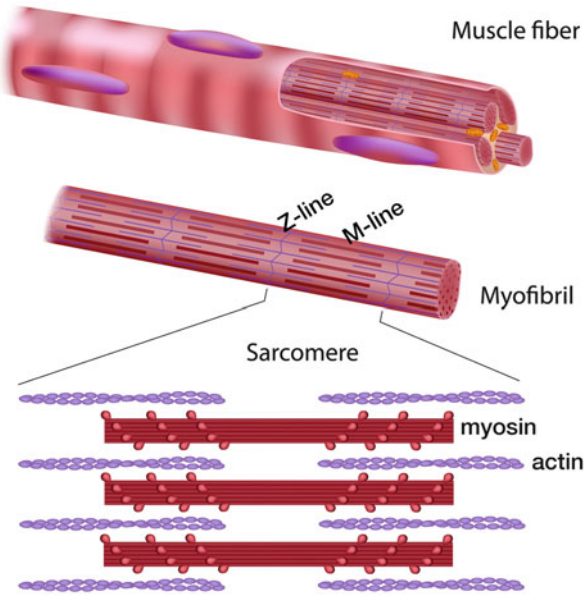

Fig. 4.1 *A muscle fibre* is composed by sarcomeres, which are the smallest contraction units. In the sarcomeres myofibrils (filaments), actin and myosin are arranged in a typical manner. Myosin filaments are connected in the Z-line; in between the M-line is a dominant characteristic. This gives the skeletal muscle a striated appearance. © [Alila Medical Images]—Fotolia.com

endoplasmatic reticulum, called sarcoplasmic reticulum, which stores calcium ions needed for muscle contraction. The sarcoplasmic reticulum ends periodically in dilated sacs, known as terminal cisterns. They cross the entire muscle fibre from one side to the other. Between two terminal cisterns, there is a tubular infolding of the sarcolemma called the transverse tubule (T-tubule). Two terminal cisterns and a transverse tubule form a structure called "triad". The T-tubule is the pathway for the excitation to signal the sarcoplasmic reticulum the release of calcium ions. Each component or compartment of a muscle cell is arranged to ensure optimal function.

4.1.3 Sarcomere

The contractile apparatus is the main morphological and functional unit of a myotube. It is build up of **sarcomeres** (single contraction units) and attached to the sarcolemma by an absorbing system (Fig. 4.1). A sarcomere is built up of the myofibrils (filaments) **actin** and **myosin**, which are arranged in a typical manner. Myosin has a diameter of about 15 nm and actin of about 5 nm. Multiple sarcomeres are arranged in a repeating manner within the myotube, resulting in the typical striated appearance of the myotubes. The term "striated" derives from this typical pattern of a myotube on histological examination. The staining best demonstrating striation of skeletal muscle cells is the phosphotungstic acid haematoxylin stain. Dark colour refers to myosin (A-band) and light colour refers to actin (I-band). All muscles moving bones (skeletal muscle), but also those responsible for mimics or ear movements, are of the striated type. A single myocyte of the biceps brachii muscle contains about 100,000 sarcomeres.

Table 4.1 Characteristics of muscle fibre types

Fibre type	Type-I MF	Type-IIaMF	Type-IIx fibres	Type-IIb MF
Contraction time	Slow	Fast	Fast	Very fast
Motor neuron size	Small	Medium	Large	Very large
Resistance to fatigue	High	Fairly high	Intermediate	Low
Mitochondrial density	Very high	High	Medium	Low
Capillary density	High	Intermediate	Low	Low
Oxidative capacity	High	High	Intermediate	Low
Glycolytic capacity	Low	High	High	High
Major stored fuel	Triglycerides	CP, glycogen	ATP, CP, low glycogen	ATP, CP
Activity	Aerobic	Long-term anaerobic	Short-term anaerobic	Short-term anaerobic
Force production	Low	Medium	High	Very high

CP creatine phosphate

4.1.4 Types of Muscle Fibres

After fusion of myoblasts to myocytes, which takes place already before birth, muscle cells continue to grow and to differentiate according to their twitch capabilities into slow-twitch fibres (type-I muscle fibres) and fast-twitch fibres (type-II muscle fibres). These fibres are differentiated by their content of proteins, content of fuel, and their functions. Concerning the fuel content, there are three sources of high energy phosphates to fill the ATP pool, creatine phosphate, glycogen (undergoes glycolysis and is degraded to lactic acid and phosphate), and glucose (used by the cellular respiration).

4.1.4.1 Slow-Twitch Fibres (Type-I Muscle Fibres, Slow Oxidative Fibres, Red Fibres)

Slow-twitch fibres have a slow speed (velocity) of contraction and a less well-developed glycolytic capacity compared to type-II muscle fibres (Table 4.1). They generate energy in the form of ATP by means of a long-term system of aerobic energy transfer (aerobic system). They are fuelled by **glycogen**, which is split into glucose molecules, as source of their energy production. The activity of the adenosine triphosphate (ATP)ase, the enzyme which splits ATP into phosphate and adenosine diphosphate (ADP), is low and its splitting rate is slow. Slow-twitch fibres contain many and large mitochondria and thus a high concentration of mitochondrial enzymes and large amounts of myoglobin (binds O_2, stores O_2), which is why they are fatigue resistant. Slow-twitch fibres contain myosin-heavy chain type 7 (MYH7). Slow-twitch fibres are supplied by many blood capillaries. Because of the high content of myoglobin, slow-twitch fibres are also termed red muscle fibres. Slow-twitch fibres render 10–30 contractions per second (10–30 Hz) (Scott et al. 2001). Type-I muscle fibres are mainly activated if a weak contraction is needed. Slow-twitch fibres are also needed for long-term exercise and for

endurance activities. Slow-twitch fibres are thus particularly found in postural muscles and are predominantly activated by endurance athletes.

4.1.4.2 Fast-Twitch Fibres (Type-II Muscle Fibres)

Fast-twitch fibres, on the contrary, are characterised by fast propagation of action potentials along the sarcolemma, the capability to split ATP very quickly, and the capability to rapidly release or uptake calcium from or to the sarcoplasmic reticulum respectively. Fast-twitch fibres rely on the short-term glycolytic system of energy transfer and contract and develop tension at two to three times the rate of slow-twitch fibres. Fast-twitch fibres render 30–70 contractions per second (30–70 Hz) (Scott et al. 2001). Type-II muscle fibres are further differentiated according to the presence of myosin isoforms. In humans, three subtypes of type-II muscle fibres are differentiated: type-IIa, type-IIx, and type-IIb fibres. Type-IIa fibres contain MYH2, type-IIx fibres MYH1, and type-IIb fibres MYH4.

Type-IIa fibres (red fibres, fast oxidative, fatigue resistant) are characterised by large amounts of myoglobin, many mitochondria, large amounts of glycogen, many blood capillaries, a high capacity to generate ATP by oxidation (reaction of oxygen and electrons to produce energy and water), very rapid rate of ATP splitting, a high contraction velocity, and fatigue resistance lower than in slow oxidative fibres. Type-IIa fibres move five times faster than type-I fibres. Type-IIa fibres are activated if a contraction stronger than provided by a type-I fibre is required and are activated at moderate strain. They are activated to assist type-I muscle fibres (Table 4.1). A similar amount of type-I and type-IIa fibres is activated by middle distance event athletes. Type-IIx fibres (fast-twitch, fast glycolytic, white fibres) are characterised by a fast contraction time, an intermediate resistance to fatigue, low myoglobin content, a medium density of mitochondria, few blood capillaries, a large amount of creatine phosphate, and quick splitting of ATP and very quick fatigability and are needed for sprinting (Table 4.1). Type-IIb fibres are mainly fuelled by creatine phosphate; have a low density of mitochondria, a low oxidative capacity, and a low density of capillaries; are innervated by very large motor neurons; have a very fast contraction time; tire easily; and are used for short-term anaerobic exercise, which lasts <1 min, but produce a high power. Type-IIb fibres are activated for maximal contractions, are always activated at last, and are used for ballistic activities. Type-IIb fibres move ten times faster than type-I fibres. Type-IIb fibres are predominantly activated by sprint athletes. Differences between muscle fibres in muscles are summarised in Table 4.1 (Larsson et al. 1991).

4.1.5 Fibre-Type Composition and Training

Individual muscles are usually composed of all four muscle fibre types (I, IIa, IIx, IIb). Most likely, in humans, there are no sex or age differences concerning fibre distribution, but the composition and proportion of fibre types varies from muscle to muscle and between individuals. Sedentary adults and young children have 55 % type-I fibres and 45 % type-II fibres. Also the number of different skeletal muscle

fibres is most probably fixed early in life and does not change in healthy subjects. Generally, the number of muscle cells is regulated by myostatin. Myostatin is a cytokine produced by muscle fibres that inhibits proliferation of muscle fibres. Since it inhibits the same type of cell in which it is produced, it is called a chalone. Whether a certain type of exercise can change the muscle fibre composition within a muscle is under debate, but there are indications that type and training alters fibre-type composition. After high-intensity endurance training, type-IIb fibres enhance the oxidative capacity such that they are capable to perform oxidative metabolism as effectively as slow-twitch fibres of untrained subjects. This would be brought about by an increase in mitochondrial size and number but not in a change in fibre type. Endurance exercise, such as running or swimming, causes gradual transformation of type-IIb fibres into type-IIa fibres. Such transformed type-IIb fibres show a slight increase in diameter, mitochondria, blood capillaries, and strength. Exercises that require great strength for short periods, such as weightlifting, increase size and strength of type-IIb fibres. The increase in size of these fibres is due to increased synthesis of actin and myosin filaments.

4.1.6 Organisation of Fascicles

A fascicle is defined as contraction unit built up of variable numbers of muscle fibres. Within the fascicle, muscle fibres are adjusted in a parallel way. Fascicles, on the contrary, can be organised in different shapes. In parallel muscles, which most of the skeletal muscles are, fascicles run parallel to the direction of the muscle. An example of a parallel muscle is the biceps muscle. In convergent muscles, fascicles fan out from a common point of attachment, allowing more versatile types of movements (Martini et al. 2008). Convergent muscles do not pull as strong as parallel muscles since not all fibres pull in the same direction, but in different directions at opposite ends (Martini et al. 2008). Examples of a convergent muscle are the pectoralis major muscle and the temporal muscle. In pennate muscles, one or more tendons run through the body of the muscle with the fascicles forming an oblique angle to the corresponding tendons, which is why fascicles in pennate muscles pull less strong on their tendons than in parallel muscles. Nevertheless, pennate muscles usually generate greater tension since they are built up of a greater amount of muscle fibres than similarly sized parallel muscles (Martini et al. 2008). Examples of pennate muscles are the rectus femoris muscle and the extensor digitorum communis muscle. The fourth type of fascicle organisation is realised in sphincter muscles. In sphincter muscles, fascicles are arranged concentrically around an opening or around a recessus (Martini et al. 2008). With contraction of a sphincter muscle, the opening gets smaller, which is why this type of muscle is usually found around entrances or exits of internal or external passageways (Martini et al. 2008). Examples of sphincter muscles are the orbicularis oculi and the anal sphincter muscle.

4.1.7 Building Up a Muscle

Though muscle cells make up the vast majority of the muscle, other specialised cells and tissues can be also found in muscles and contribute to proper muscle function. These include connective tissue forming fascia or septa within the muscle, such as the perimysium, epimysium, or endomysium; vessels, such as arteries (transport blood from the heart to other organs), capillaries (enwrap the myotube); veins (transport blood from the organs to the heart) or lymph vessels (transport interstitial fluids from the periphery to the heart), lymph nodes, tendons, and nerves (motor nerve fibres, sensory nerve fibres, vegetative nerve fibres); and receptors, such as the muscle spindles or pain receptors. Nearly every muscle is attached to a bone by bundles of collagen fibres, known as tendons.

4.1.8 Classification of Muscles, Organisation in Functional Units

Muscles are classified according to various criteria. Regarding their location between the skin and the inside of the body, superficial muscles (near to the skin) and deep muscles (inside the body) are differentiated. Skeletal muscles are predominantly located along bones and are most pronounced in size where they intensively move a part of the body. Accordingly, the largest muscles can be found at the thigh, the calves, and the shoulder girdle. Muscles, which move only the skin, like most facial muscles, or the cartilage, like the ear muscles, are thus less prominent. According to their function muscle groups are classified as facial muscles, extra-ocular muscles, chewing muscles, neck flexors, neck extensors, shoulder girdle muscles, inside- or outside rotators of the arm or hip, extensors or flexors of the arm or leg, abductors or adductors of the shoulder or hip, extensors or flexors of the elbow or knee, extensors or flexors of the hands and fingers, finger straddlers, trunk extensors or flexors, extensors or flexors of the foot or toes, or as muscles responsible for inversion or eversion of the foot. Each individual muscle has a distinct origin, a distinct attachment, a distinct movement function, and a specific motor nerve, which innervates each muscle. Each muscle has also a characteristic innervation zone, the area where motor nerves insert into the muscle via its **motor end plates** (Fig. 4.2a). To study insertion, attachment, innervation, and function of the individual muscles, the reader is referred to anatomical textbooks.

4.1.9 Innervation of Muscles

Anatomy of motor nerves, which innervate muscles, is complex and requires profound anatomical knowledge. Basically, motor nerves originate from anterior horn cells inside the **myelon**. They exit the myelon via the anterior roots to form either an individual nerve or, in the region of the cervical and lumbar myelon, trunks, which then split into divisions and thereafter cords to constitute

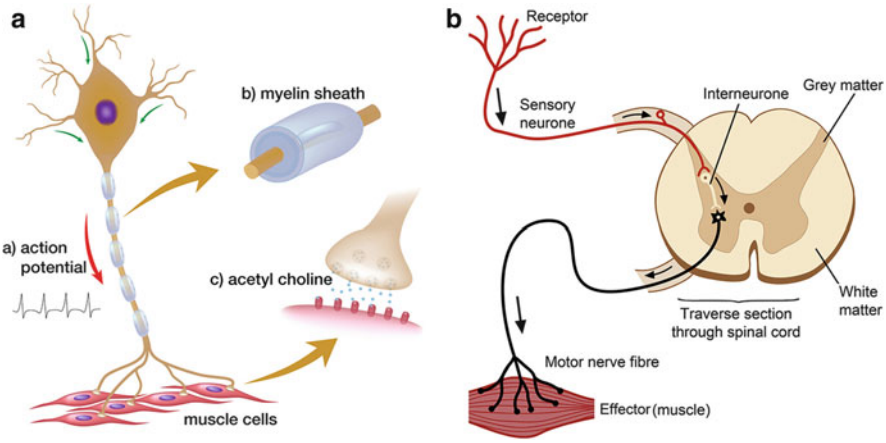

Fig. 4.2 (**a**) *The making of a neuromuscular end plate*. Motor signals to the periphery are propagated via action potentials (a) along myelinated (b) nerves. At the motor end plate, the release of neurotransmitter acetylcholine (c) leads to a depolarisation and impulse to contract muscular fibres. © [Alila Medical Images]—Fotolia.com. (**b**) *A spinal reflex arc*: sensory nerves are via interneurons connected to motor nerves in the grey matter of the myelon. The signal is forwarded thus to muscles and lead to involuntary contraction, i.e. retraction from a danger signal. This can be exploited diagnostically to test for neuronal function. © [Balint Radu]—Fotolia.com

the cervico-brachial or lumbosacral plexus. From these plexuses the main motor nerves of the arm respectively leg origin. Motor nerves originating from the brachial plexus include the median, ulnar, radial, musculocutaneous, axillary, thoracodorsal, subscapular, and lateral pectoral nerves. Motor neurons originating from the lumbar plexus include the iliohypogastric, genitofemoral, femoral, sciatic, and obturator nerves. Branches of these nerves lead to the individual muscles and split intramuscularly into subdivisions to lastly split into terminal endings shortly before arriving at the innervation zone. The innervation zone has a particular architecture and varies between muscles of a single species but also between different species.

4.2 Physiology of Skeletal Muscles

4.2.1 Physiology of Voluntary Muscle Contraction

4.2.1.1 Motor Impulse Generation and Propagation Along the Motor Nerve System

The major task of the skeletal muscle is to contract and thus to move bones. Contraction of the muscle can be voluntary or involuntary (reflectory). For voluntary contraction an impulse originating from the motor cortex of the cerebrum is propagating along the pyramidal tract to the end of the first motor neuron. There, the electrical impulse is transferred into a chemical message in form of the

neurotransmitter glutamate. The chemical message is recognised at the anterior horn cells, located in the anterior horn of the myelon, by glutamatergic receptors. Stimulation of these receptors depolarises the anterior horn cell. From there the impulse propagates along the myelinated peripheral nerves to the **neuromuscular junction** (**motor end plate**), where the electrical impulse in form of an action potential is transferred into chemical information in form of the transmitter **acetylcholine**, which then induces an action potential at the postsynaptic membrane (Fig. 4.2a). This current propagates along the muscle membrane to the T-tubule. Here, the impulse induces the release of calcium ions from the sarcoplasmatic reticulum to induce contraction of the sarcomeres.

To protect the body from damage, involuntary reflexes are important. Sensations such as pain are translated into a motor neuron reaction leading to muscle contraction and retraction from the site of danger. In this setting, the switch is made in the next spinal segment before propagating the sensation to the brain (Fig. 4.2b).

4.2.1.2 Generation and Propagation Along the Sarcolemma

Each cell membrane is charged but the type and degree of charging is determined by the cell type. Non-excitable cells establish only a membrane potential, which is defined as difference in electrical polarity between the interior and the exterior of a cell. The membrane potential is typically −60 to −80 mV in amplitude. Cells that are excitable, like neurons, muscle cells, or secretory cells, generate not only a membrane potential but, after appropriate stimulation, also an **action potential**. Membrane and action potentials are mainly determined by ion concentrations inside and outside the sarcolemma. These concentrations are mainly dependent on the selective permeability of ion channels, ion transporters, or exchangers of these ions located inside the cell membrane. Ions contributing most to the membrane and action potentials are sodium, potassium, chloride, and calcium. The resting membrane potential is stable among all species. An action potential is a short depolarisation during which the membrane potential rises and falls, following a consistent trajectory (see Fig. 4.2a; (a)). In muscle cells the action potential is a key step in the chain of events leading to muscle contraction. The action potential is generated by specific types of voltage-gated ion channels embedded in the sarcolemma (Barnett and Larkman 2007). They are shut when the membrane potential is near the resting potential, but they rapidly open in case of an increase in the membrane potential to the threshold value. After opening, channels allow an inward flow of sodium ions, which produces a further increase in the membrane potential. This causes other sodium channels to explosively open until all are open, resulting in a further increase of the membrane potential. The sodium influx causes the polarity of the sarcolemma to reverse, which in turn inactivates the ion channels. Sodium ions now have to be actively transported outwardly. Potassium channels are then activated, resulting in an outward current of potassium and in returning the electrochemical gradient to the resting state. After the action potential, a negative shift known as after-hyperpolarisation or refractory period due to additional potassium currents occurs. Sodium-based action potentials last for <1 ms (Bullock et al. 1977).

4.2.1.3 Motor Unit

A motor unit is a functional innervation unit defined as a single anterior horn cell of the myelon plus all muscle fibres innervated by this anterior horn cell (illustrated in (b) of Fig. 4.2b). The number of muscle fibres innervated by a single anterior horn cell varies greatly between different muscles. Motor units in muscles responsible for highly precise movements have only a few muscle fibres per anterior horn cell. Motor units of the muscles controlling the larynx have 2–3 fibres per motor neuron, and those controlling the extra-ocular eye muscles have ~10 fibres. Motor units, which need to produce high strength, like the lower leg muscles, have 2,000 muscle fibres per motor unit. A single motor unit contains only a single type of muscle fibre. The electrophysiological correlate of a motor unit is the motor unit action potential, which is the sum of all muscle fibre currents of a motor unit within the uptake area of a recording electrode evoked during voluntary or involuntary contraction. Activity of individual motor units follows a distinct pattern (size principle). At the beginning of a contraction, smaller motor units are activated first, but with increasing strength and duration of exercise, increasingly larger motor units are activated. The pattern of activation of individual motor units is determined by the brain and spinal cord.

4.2.1.4 Electrochemical Coupling

At the site of the T-tubule, the sarcoplasmatic reticulum is in close contact with the sarcolemma, which is why their function is closely related. After arrival of the electrical excitation at the T-tubule, **calcium ions** are released from the sarcoplasmatic reticulum, which is the storage reservoir of calcium ions within the myotube. Calcium ions are essential for muscle contraction, since it accomplishes the cyclic binding between the major **contractile elements** actin and myosin. After release from the sarcoplasmatic reticulum, calcium ions interact with the regulatory protein troponin located on the actin fibres. Calcium-bound troponin undergoes a conformational change that leads to the movement of tropomyosin, subsequently exposing the myosin-binding sites on the actin filament. This allows for myosin and actin ATP-dependent cross-bridge cycling and shortening of the sarcomere. The interaction between actin and myosin on the molecular level starts with movement of a myosin head (myosin subfragment S1) towards a neighbouring action subunit by hydrolysis of ATP. As soon as actin and myosin bind, ADP is released and the myosin head undergoes a conformational change, such that it turns down and drags the rest of the myosin filament behind. Now, another ATP is bound to myosin and the binding with actin is released. ATP hydrolysis let the myosin head return to its previous conformation and another cycle begins. According to this pattern, each myosin molecule slides along the actin filament so that the two filaments increasingly overlap. Each myosin filament carries about 500 myosin heads, which runs through the cycle five times per second.

4.2.1.5 Muscle Tone

A fundamental characteristic of each muscle is the muscle tone. Two types of muscle tone are differentiated, resting tone and dynamic tone. Resting tone (tonic

stretch reflex) is required for the muscle to be prepared to immediately respond with a contraction in case of acute voluntary innervation. Resting tone results from activation of a few motor units at all times even at rest. As one set of motor units relaxes, another set takes over. Dynamic tone (dynamic stretch reflex) is required to adapt contraction forces during movements. The dynamic tone greatly influences the degree of monosynaptic tendon reflexes. Muscle tone is regulated by the gamma motor system, which innervates the muscle spindles, which are the core of the regulatory system for the muscle tone. A muscle spindle is either built up of gamma-1 spindle fibres ("Kernsackfasern") or gamma-2 spindle fibres ("Kernkettenfasern"). Gamma-1 spindle fibres are innervated by gamma-1 motoneurons and record the tone of the fibres via so-called annulospiral endings located in the middle of the cells. Gamma-2 spindle fibres are innervated by gamma-2 motoneurons and record the tone of the fibres via so-called flower-spray endings located in the periphery of the cells. Information of the annulospiral receptors is transmitted to the myelon via 1a axons. The information of the flower-spray receptors is transmitted to the myelon via 1b axons. Muscle tone can be normal, increased, or decreased. Reduced muscle tone, also reflected as muscle hypotension, occurs in the acute stage of ischemic stroke or in peripheral nerve or myopathic lesions. Muscle tone may be increased in Parkinson's disease (rigour) or patients with lesions of the pyramidal tract (spasticity) (Bähr and Frotscher 2005).

4.2.1.6 Types of Skeletal Muscle Contraction

The skeletal muscle usually links two bones across its connecting joint. When these muscles contract or shorten, the bone moves. There are, however, also muscles which do not cross a joint but support or move structures like the shoulder, the larynx, and the diaphragm or those which have lost the ability to move a structure at all. Only few striated muscles move the skin or the cartilage, like the facial muscles, which are responsible for the mimics, or the muscles of the ear, which formerly moved the ear. Generally, a muscle may contract in a shortening, isometric, or lengthening manner (contraction with or without change in muscle length). Contraction, however, may be also classified as isokinetic or non-isokinetic (constant or variable angle velocity), static or dynamic (opposing muscles contract against each other without or with changing muscle length), concentric or eccentric, (shortening or lengthening of muscle during contraction), or incremental or constant. A contraction is called isotonic (same tension) if the muscle is allowed and not prevented to shorten. Muscle force is proportional to the physiologic cross-sectional area, and muscle velocity is proportional to muscle fibre length (Quoted from National Skeletal Muscle Research Center; UCSD, Muscle Physiology Home Page—Skeletal Muscle Architecture, Effect of Muscle Architecture on Muscle Function). The strength of a contraction, however, is determined by biomechanical parameters, such as the distance between muscle insertions and pivot points and muscle size.

4.2.1.7 Coordination of Muscle Activity

Though any of the 640 muscles can act individually, muscles usually work together with other muscles, organised in functional units. The pattern of activity and the design of a movement are determined in the CNS. According to the movement patterns, individual muscles are activated in a concerted manner. To accomplish these patterns, muscles must act in functional muscle groups in a synergistic way, as agonists or as antagonists. Muscles are generally arranged in opposition so that as one group of muscles contracts, another group relaxes or lengthens. Voluntary and involuntary innervation of involved muscles must be graded appropriately to reach the goal of an intended movement. Since voluntary or involuntary movements change the position of the body, the head, the limbs, or the trunk, nearly all muscles are affected in case of any muscle activity. Action in one muscle evokes reaction in many others. The more extensive a movement, the more extensive is the reaction of other not primarily involved muscles.

4.2.1.8 Muscle Fatigue

A main characteristic of a skeletal muscle is that it fatigues with exercise. Depending on the type of exercise, muscle fatigue develops earlier or later after onset of the exercise. Fatigue in response to exercise (exercise (-induced) fatigue) can be enhanced by mental disorders, by organic CNS abnormalities (central fatigue), or by peripheral nervous system (PNS) dysfunction or skeletal muscle disease (peripheral, muscle, contractile, or mechanical fatigue, contractile impairment, loss of force generating capacity) (Boyas and Guével 2011). Non-neurological causes of feeling tired in response to exercise include cardiac, pulmonary, haematological, renal, metabolic, neoplastic disease, chronic obstructive pulmonary disease, overtraining syndrome, or chronic fatigue syndrome (Spruit et al. 2005). The cause of muscle fatigue to exercise is largely unknown, but it can be speculated that energy production becomes insufficient or that oxidative stress occurs and disrupts cell functions. The phenomenon of muscle fatigue can be also regarded as reaction of the tissue to prevent it from damage by overuse.

4.2.2 Other Types of Muscle

The skeletal muscle is one of the three muscle types, the two others are the smooth muscle and the cardiac muscle (Fig. 4.3a). Though most processes are similar, the three muscle types act differentially.

4.2.3 Cardiac Muscle

Contrary to skeletal muscle cells, cardiac muscle cells are self-contracting, autonomically regulated, and continue to contract in a rhythmic fashion throughout life. Cardiac muscle cells are Y shaped and shorter and wider than skeletal muscle cells (Fig. 4.3a). Cardiac muscle cells are predominantly mononucleated. Contrary to the

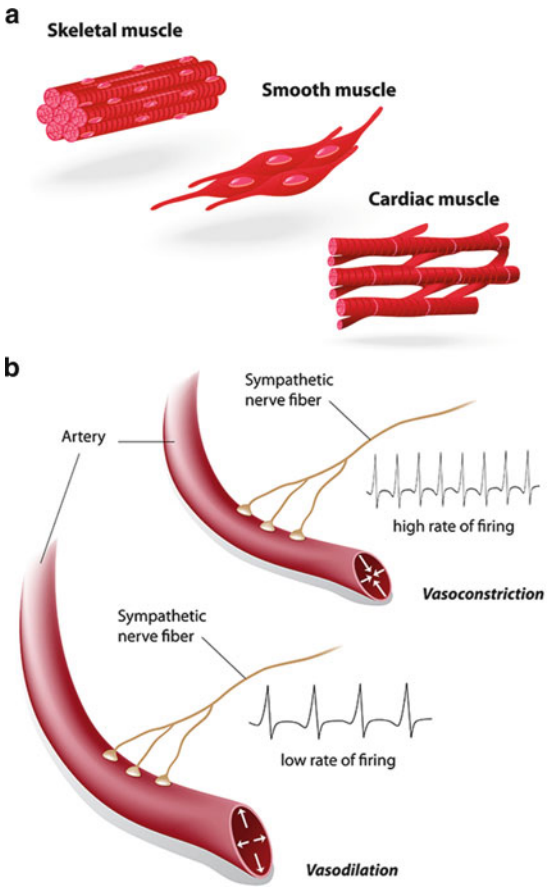

Fig. 4.3 (**a**) *The three muscle types*: skeletal muscle, smooth muscle, and cardiac muscle. © [Designua]—Fotolia.com. (**b**) *Smooth muscle function* is directed by the sympathetic or parasympathetic vegetative nervous system. Stress and activity lead to enhanced tonus of most smooth muscles, whereas parasympathetic stimuli lead to relaxation. This principle is illustrated for arteria. © [Alila Medical Images]—Fotolia.com

skeletal muscle, cardiac muscle fibres are interconnected and the sarcoplasmic reticulum is less well developed. Additionally, contraction of cardiac muscle fibres is actin regulated, meaning that calcium ions for the contraction derive not only from the sarcoplasmic reticulum but also from the extracellular space, as in smooth muscle cells. The arrangement of actin and myosin is similar to myofibres. Cardiac muscle cells are auto-rhythmic, which means that they contract without innervation by a nerve (pacemaker cells). Cardiac muscle fibres are separated by intercalated discs, which contain gap junctions to provide communication channels between the cells and to facilitate waves of depolarisation to sweep across the membranes, allowing synchronised muscle contraction. Depolarisation of cardiac muscle cells is similar to that of a myocyte, but repolarisation takes much longer to occur, why cardiac muscle cells cannot be stimulated at high frequencies and are prevented from titanic contractions. More details about anatomy and physiology of the cardiac muscle will be provided in the chapter about the heart.

4.2.4 Smooth Muscle

Smooth muscles of internal organs or vasculature cannot be stimulated voluntarily, but are controlled by the **sympathetic** and **parasympathetic** system (Fig. 4.3a, b). Contrary to myotubes, smooth muscle cells are spindle shaped, much smaller than striated muscle cells, and without striation or sarcomeres. Instead of a sarcomeric organisation of myofibrils, thin and thick filaments, corresponding to actin and myosin filaments of the striated muscle, are **organised in bundles**. Troponin and tropomyosin are absent in smooth muscle cells. Intermediate filaments, which are interlaced through the cell like a fishnet, anchor the thin filaments and correspond to Z-discs of the striated muscle. As in striated muscle, contraction of smooth muscle cells involves the formation of crossbridges between thick and thin filaments, such that thin filaments slide past the thick filaments. Contrary to striated muscle, however, shortening occurs in all directions whereupon intermediate filaments draw the cell up, like closing a drawstring purse. Calcium ions from the extracellular space bind to the calmodulin-myosin light chain, an enzyme, which then breaks up ATP and transfers phosphorus directly to myosin to activate it and to form crossbridges with actin. Both cardiac and smooth muscle can contract without being stimulated by the nervous system.

4.2.5 Comparison of Muscle Anatomy and Physiology Between Different Species

Though skeletal muscles largely function similarly among different species, there are a number of differences that need to be highlighted. Differences concern the evolution of muscles, the number of muscles, muscle size, muscle distribution, proportion of muscle to body mass, muscle types, sarcomere structure, and muscle proteins. The most obvious difference between species is the number of skeletal muscles. Whereas humans have 640 muscles, the **elephant** is equipped with 40,394 muscles. Insects are equipped with a few hundred muscles and other species with a few thousand (Triplehorn et al. 2005). Whereas the nose of the human cannot be moved at all anymore, the highly flexible trunk of the elephant is moved by about 40,000 individual muscles. Concerning the architecture and composition of muscle, there can be significant differences between vertebrates and other species. In male **salmons** or tuna fish, the amount of muscle in relation to total body weight can reach up to 70 %. Another difference between species concerns the proportion of the muscle mass to the total body weight. Whereas the proportion of muscle mass is 50 % in humans, it is much lower in bees or other insects. The proportion of muscle mass to body mass is also larger in **birds** compared to **bats** (Norberg and Norberg 2012). Differences between species refer also to the presence of other muscle types. Whereas vertebrates have both striated and smooth muscles, insects have only striated muscles. Muscle strength is also different between species, whereas an ant can lift up to 50 times its own body weight; a weightlifter lifts only three to four times his own body weight. An **ant** has a strength advantage because of the ratio

surface area to volume. The strength of a muscle is proportional to the surface area of its cross section, which is proportional to the square of its length. Volume on the other hand is three-dimensional and thus proportional to the cube of its length. Larger animals have a greater disparity between mass and strength. To lift an object, muscles of a large animal must also move a greater volume or mass of its own body. There is also a difference between species concerning the composition of contractile filaments. Whereas humans have only myosin types MYH1, 2, 4, or 7, animals have a much wider variability of myosins. Furthermore, increase in muscle mass in mice is not only achieved by an increase of the thickness of individual fibres, like in humans, but by attracting more myoblasts to fuse to a myotube. In animals not only voltage-gated sodium channels but also **voltage-gated calcium channels** contribute to the development of the action potential. In humans, action potentials last <1 ms, whereas in animals action potentials may last **up to 100 ms**.

4.2.6 Synopsis

This chapter should have helped the reader to understand basic development of muscle, anatomy and histology of skeletal muscles, and basic prerequisites of muscle function. Though statements, descriptions, and explanations were reduced to comprehensible messages, it was intended to provide an overview about all aspects of muscle anatomy and physiology using the human as example. Furthermore, it was attempted to identify differences concerning muscle organisation, architecture, function, and performance between different species. Despite these intentions, the reader is advised to collect more detailed knowledge about various aspects of the topic, if more profound insights into the world of muscles in human beings and other species are desired.

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