



FASCIA SCIENCE AND CLINICAL APPLICATIONS: CONNECTIVE TISSUE PHYSIOLOGY

The muscular force transmission system: Role of the intramuscular connective tissue

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Summary The objective of this review is to analyze in detail the microscopic structure and relations among muscular fibers, endomysium, perimysium, epimysium and deep fasciae. In particular, the multilayer organization and the collagen fiber orientation of these elements are reported.

The endomysium, perimysium, epimysium and deep fasciae have not just a role of containment, limiting the expansion of the muscle with the disposition in concentric layers of the collagen tissue, but are fundamental elements for the transmission of muscular force, each one with a specific role. From this review it appears that the muscular fibers should not be studied as isolated elements, but as a complex inseparable from their fibrous components. The force expressed by a muscle depends not only on its anatomical structure, but also the angle at which its fibers are attached to the intramuscular connective tissue and the relation with the epimysium and deep fasciae.

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Introduction

The objective of this review is to analyze in detail the relations among endomysium, perimysium, epimysium

(Figure 1) and deep fasciae and how they may influence the transmission of muscular force.

Classically, attention is given to the connections between the muscles and the skeleton through the tendons

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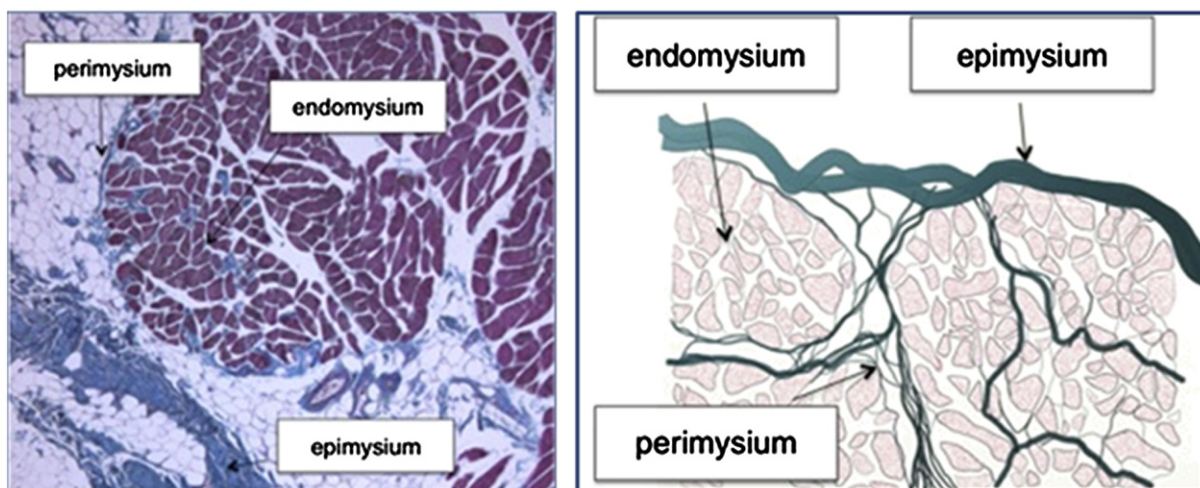


Figure 1 Connections between muscle fibers and the endo-peri-epimysium. On the left: histological preparation of a muscular section, azan-Mallory stain for collagen fibers, in blue, the muscle fibers are in red; (50× magnification). On the right: diagram of the relations between the intramuscular connective tissue components. [For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.]

of origin and insertion. The recruitment of fibers belonging to a muscle generates mechanical tension, so that the tendon connections produce the movement of the locomotor system (in case of isotonic concentric–eccentric recruitment) or the maintaining of a static position, and thus the stability of the body (isometric recruitment). At the same time, anatomical texts (Chiarugi, 1904; Testut and Jacob, 1905; Platzer, 1978; Tidball and Law, 1991; Standring et al., 2005) describe myotendinous expansions that fit on the periarticular soft tissues, with the intermuscular septum, the interosseous membranes and the neurovascular sheaths (Figure 2). Thanks to these connections, the muscles acquire additional areas to lever and generate movement (Huijing and Jaspers, 2005; Yucesoy et al., 2008). Recent studies (Stecco C et al., 2007; Huijing, 2009) highlight the connections of muscles with the dense connective tissue of the locomotor system, commonly referred to as fascia. The muscles can stretch the fascia in a longitudinal sense directly with the expansions that stem from the tendons. They can also stretch it in a transversal sense through the intramuscular connective

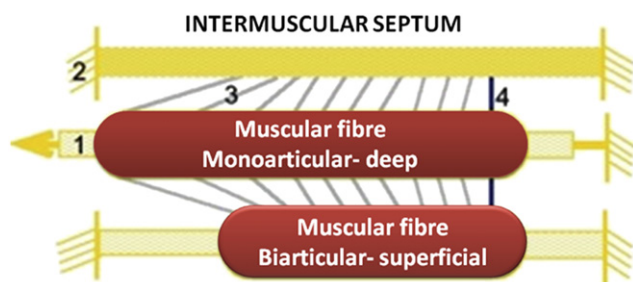


Figure 2 Aponeurotic relations between muscles arranged in series. 1, Tendons of origin and insertion; 2, aponeurosis of insertion; 3, aponeurotic expansions to septa or epimysium of the adjacent muscles; 4, neurovascular tract. Modified from Huijing and Baan, 2003.

tissue (endomysium, perimysium and epimysium) (Huijing and Jaspers, 2005; Purslow, 2010) and then through the dense connective tissue of the musculoskeletal system (such as the intermuscular septum and the neurovascular bundles). In particular Stecco et al. (2007, 2009a, b) have shown aponeurotic expansions of muscles on the fascia that surrounds the muscular groups of proximal or distal segments. Thus, we can hypothesize that every contraction generates a direct strain on the fascia arranged in series with the muscle, working according to specific spatial directions. This anatomical relation may be the basis of peripheral proprioceptive mechanisms and therefore of the mechanism that coordinates the activity of the contractile fibers.

It is also well established (Pappas et al., 2002; Finni et al., 2003) that during a muscle contraction not all of the motor units are activated simultaneously. It is also well known that the velocity of the shortening of the active sarcomeres varies depending on the location and length of the same sarcomeres inside of the muscle belly. In order to harmonize so many variables involved in the production of force (Rowe, 1981) the presence of the intramuscular connective tissue plays a vital role.

Finally, Hijikata et al. (1993, 1999) and Trotter (1993) demonstrated that only a part of the muscle fibers run the entire length of the muscle, connecting linearly with the tendons of origin and insertion, developing longitudinal forces. Such fibers are called “end-to-end”. Other muscle fibers do not have a direct relationship with the tendons and are referred to as “no-spanning”. They insert themselves on the intramuscular connective tissue (myo-tendinous) or finish on the adjacent muscle fiber (myo-musculare), exerting their action(s) on it. The “no-spanning” fibers are spindle shaped and cannot connect their extremities with the contractile elements that precede or follow them. They overlap themselves in a parallel fashion and in correspondence to this overlapping (Hijikata et al., 1993) their diameter appears to be greater. This ensures

an optimal and consistent contact surface. The connection between two contractile fibers pass through the endomysium that separates them anatomically, but couples them functionally. The importance of the connective tissue at a microscopic level has been demonstrated by observing that a myofibril can generate a tension of about 75% of the total even if disinserted by one of two extremes, due to the connections with the fibers arranged in parallel (Street, 1983).

The connections of the myofibril

The forces expressed by the contraction arise from the interpenetration of the muscle proteins, actin and myosin, organized in basic units called sarcomeres. The sarcomeres are placed in series forming a myofibril, with a cylindrical shape. They are arranged in bundles of similar chains that are transversely maintained by bridges of desmin. Then, the single muscular fiber is created, covered by a cellular membrane called sarcolemma (Denoth et al., 2002). The actin is directly connected to the cytoskeletal proteins in the Z-line. The actin of two sarcomeres in series refers to the same Z-line (at the level of the I-band) so that the contraction can transmit the force in a longitudinal direction. At the ends of the muscle fiber, in the myotendinous junction (Trotter et al., 1983), both the muscle's protein and the Z-line merge with the extracellular matrix of the tendon collagen. Observing a section at the level of the myotendinous junction the muscle fibers appear to have wavy and folded aspects, similar to the fingers of a hand separated. In this way the extracellular matrix of the tendon penetrates between the adjacent muscle fibers, increasing the interface between the muscle and connective tissue, and therefore distributing the loads over a larger area (Figure 3). This significantly reduces the mechanical stress between the contractile and the elastic elements and thus decreases the risk of myotendinous lesions.

All around the sarcomeres there is an extensive network of circular filaments that cross the space of the sarcomere and there are longitudinal filaments that completely wrap the sarcomeres (Figure 4). These types of filaments are arranged in an orthogonal fashion and consist mainly of titin and nebulin (Gautel, 2011; Ottenheijm et al., 2012). These filaments seem to form a kind of scaffolding mechanism, whose longitudinal component contributes to the static passive elasticity of the myofibril, only beyond the physiological length (Podolsky, 1964). This occurs when the strain is about 150% of its resting length. This protein network does not contribute to the transmission of the force generated longitudinally by the sarcomeres towards the myotendinous junction, but it transmits the action of the myofibril to those that neighbor it and then to the connective system placed in parallel to the contractile fibers.

At the Z-line one can note the presence of circle shaped filaments, bridges that link adjacent myofibrils (Wang and Ramirez-Mitchell, 1983) and therefore capable of transmitting force in a radial manner. These elements are composed essentially of a protein called vinculin. They are defined as costameres because at these points the sarcolemma is retracted towards the underlying sarcomeres and

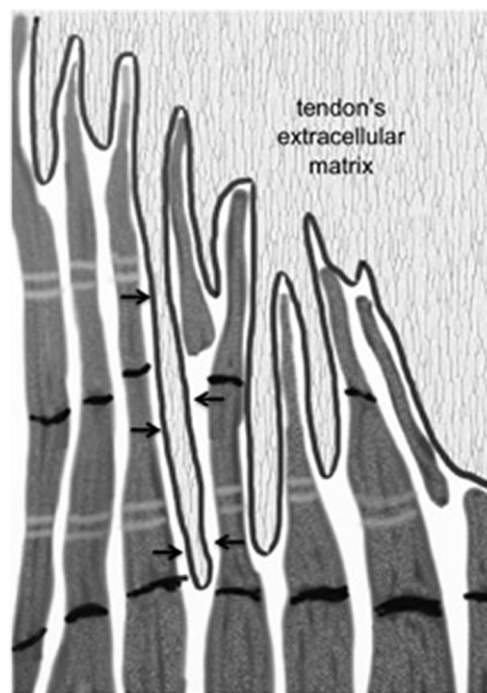


Figure 3 Diagram of the myotendinous junction; above is the extracellular matrix of the tendon, at the bottom the muscular fibers Modified from Tidball and Law, 1991.

is shaped like a group of ribs. All of these elements of connection between the extracellular matrix and the actin from the cytoskeleton allow the myofibrils to become fixed and stabilized during the corresponding movements. At the same time, an excessive enlargement of the cell membrane is prevented, as can be observed during contractions. (Pardo et al., 1983).

When a microscope is utilized (Patel and Lieber, 1997) it is possible to notice numerous proteins that cross the sarcolemma and allow a close connection between the sarcomeric chains and the basal membrane. This lamina is placed all around the cell membrane and closely linked to the endomysial connective tissue. These macromolecules allow the transmission of muscular force from the myofibril cytoskeleton towards the endomysium that covers it. It is mainly at the level of the M and Z-line that connections are verified between the sub-sarcolemmal actin and the desmin (Monti et al., 1999).

The endomysium

The endomysium is the thinner portion of the intramuscular connective tissue and it is found directly in contact with the sarcolemma and therefore with every single muscle fiber. It represents the 0.47–1.2% of the dry weight of the mass of every single muscle (Purslow, 2010). The endomysium is composed of collagen fibers type III, IV, V and in a lesser percentage of collagen type I, which is characteristic of the connective tissue of the tendons (Trotter and Purslow, 1992; Passerieux et al., 2006). There is also a fundamental substance that contains macromolecules, and elastin, while the fibroblasts are essentially absent (which are present in the remaining parts of the intramuscular

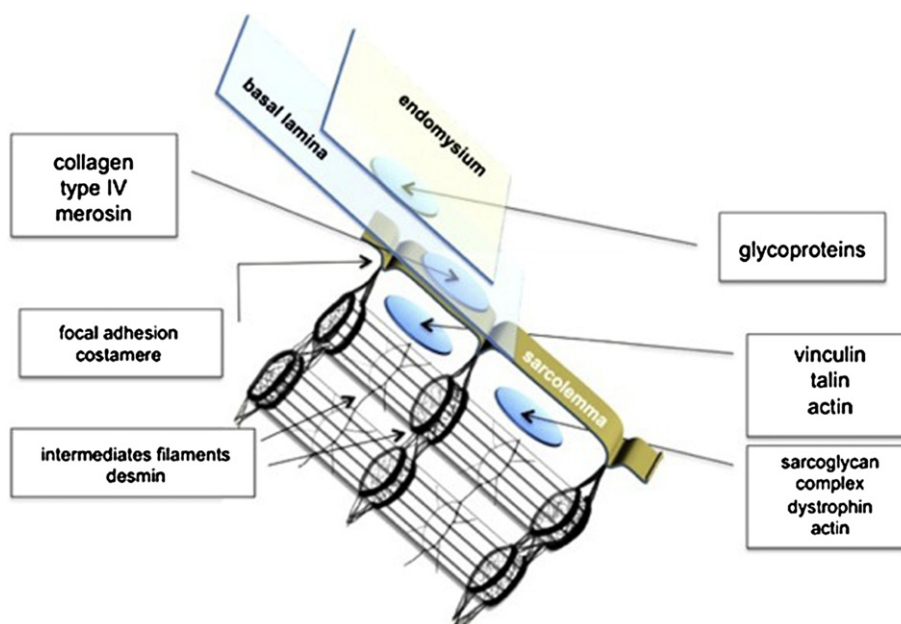


Figure 4 Diagram of the connections between the myofibrils, sarcolemma, basal lamina and the endomysium. Modified from Wang and Ramirez-Mitchell, 1983.

tissue). Covering the muscular fiber in its entire surface, it takes on a structural role, the same role as the parenchyma with the organs (Moore, 1983). The endomysium penetrates between the muscle fibers, forming a network in which the fibers lie adjacent in hexagonal shaped cells. If the thickness of this connective lamina is substantially constant, the cells assume distorted shapes or areas of variable sizes depending on the level of the section in the muscle, fitting perfectly as a tessellation. This visual finding attests that the disposition of the muscular fibers is variable (longitudinal and oblique) and that the fibers inside the belly have different lengths. The adjacent muscle fibers share the same structure of the endomysium in the two opposing surfaces. They are connected to this internal connective structure by proteins (such as dystrophin and integrin) that cross the sarcolemma. Therefore, every force generated by the muscular fiber is transmitted directly to the endomysium (Purslow, 2010; Sharafi and Blemker, 2011).

In respect to the longitudinal axis of the muscle fiber, the collagen of the endomysium appears wavy, arranged in fascicles that are predominantly oblique (Järvinen et al., 2002), performing three types of connections (Borg and Caulfield, 1980):

- Connective tissue (CT) endomysium/capillary (100/120 nm), in which the collagen fibers are disposed perpendicularly to the basal lamina of the capillaries and to the myofibrils at the level of the Z-line of the sarcomeres;
- CT myocyte/myocyte (the diameter is equal to that of the previous example), with fibers distributed perpendicularly between two muscle fibers, which penetrate their basal lamina without a solution of continuity;
- CT with fiber (diameter between 50/70 nm) in continuity with the basal lamina and parallel to the axis of each myofibril, which insert into the invaginations of the sarcolemma at the Z-line.

During a muscular contraction, the angle that the collagen fibers of endomysium form with the axis of the muscular fiber varies, allowing the endomysium to adapt itself to these changes (Purslow, 1989). Together with the sarcolemma, the endomysium resists the longitudinal deformation of the myofiber only when this has exceeded 150% of its physiological length (which is an extremely rare occurrence during normal movements). On the contrary, the endomysium is resistant if the forces of traction have a transversal pattern.

The endomysium is the only intramuscular element that, within the same fascicle, contacts the elements of the same motor unit even through muscular fibers that can be interposed but inactive. The muscle fibers that are not recruited become, thanks to the endomysium, a real tendon for the transmission of lateral force without having to change length (Trotter, 1990).

The endomysium extends itself without interruption in the perimysium's collagen.

The perimysium

The amount of perimysium inside of the muscles varies significantly in the different regions of the body: it is represented by 0.43–4.6% of the dry weight of the muscles (Purslow, 2010). This part of the connective tissue does not present a solution of continuity with the epimysium, that covers it laterally, or with the tendons of origin and insertion through specific locations defined as myotendinous joints. The perimysium divides the muscle belly in fascicles of different dimensions:

- primary fascicles (characteristics of the primary perimysium) with smaller dimensions, are composed of a well defined group of muscular fibers contained in their endomysium;

- secondary fascicles (wrapped in the secondary perimysium, thicker than the primary) composed of a group of primary fascicles.

Inside the perimysial structure we find, immersed in a matrix of proteoglycans, a smaller percentage of elastic fibers and especially collagen fibers type I, III, IV, V, VI and XII (Petibois et al., 2006; Kurose et al., 2006). The collagen type I provides the perimysium with a notable resistance to traction. It is therefore probable that this part of the intramuscular connective tissue has a fundamental role in the transmission of the force generated in the muscle towards the bone levers (type I collagen is absent from the inside of the endomysium). This function is reinforced from the presence of collagen type XII, which is able to tightly organize the elements of the extracellular matrix. The collagen type XII, in fact, is characterized by its high capacity to interact with the collagen type I, with the proteoglycans (in particular the decorin) and with the glycosaminoglycans that compose the proteoglycans (Listrat et al., 2000). The collagen fibers included in the perimysium have a diameter up to ten times greater than the collagen fibers located in the endomysium (Purslow, 1989).

Inside of the perimysium there are three recognizable layers of collagen (Rowe, 1981):

- Superficial: fibers with a smaller diameter, straight, spread out without a definite direction, they intersect with each other to form a disorganized network;
- Intermediate: larger diameter fibers, flattened, curved, they intersect in their course at variable angles in respect to the disposition of the muscular fiber;
- Deep: this soft lamina is in direct contact with the endomysium, in which it significantly increases the space between the collagen fibers, giving it a discrete laxity.

In the middle layer, the collagen fibers are arranged to form an average angle of 55° in respect to the resting muscular fiber; if the fiber is recruited, the angle increases up to the value of 80° and decreases to 20° if it is stretched. The direction of the collagen fibers therefore changes according to the state of the muscle, confirming how much this part of the intramuscular connective tissue is related to the activity of the muscle itself (Trotter and Purslow, 1992; Passerieux et al., 2006). During a passive elongation of the muscle, the collagen fibers of the perimysium become moderately straight while stretching themselves. However, the perimysium contributes to the passive resistance of the muscular fiber well beyond the values of physiological length, as occurs in the endomysium.

It therefore seems evident that the perimysium structure does not contribute to the passive rigidity of the muscle, but rather is an organized framework to transmit the forces produced in the locomotor system (Purslow, 1989).

Given its composition and its internal organization, we can identify some essential functions in the perimysium (Passerieux et al., 2007):

- structural and containment role, with the collagen arranged in a network to organize the muscular fibers in fascicles;

- connection between synergistic muscular fibers belonging to adjacent muscular fascicles, focusing the forces generated towards the same tendon;
- attachment, due to the collagen organized in fascicles of great size, to the muscular fibers that do not run through the entire length of the belly, with the tendons of origin and insertion;
- to guarantee a relative independence of the muscular fascicles during muscular contraction.

Regarding this last point, it is necessary to remember that two adjacent muscular fascicles share the opposing surfaces of the same perimysium. The physical characteristics of viscoelasticity of the perimysial connective tissue, during stretching, allow parts of the recruited muscle to shorten and modify volumetrically, moderately changing the structure of the muscular fascicles at rest (Kjaer, 2004).

The epimysium

The epimysium is thicker than the other elements of the intramuscular tissue and is formed by collagen fibers with a larger diameter (Sakamoto, 1996). It covers all the muscle bellies, forming a lamina that clearly defines the volume of each muscle. At the ends of the muscle, this connective tissue thickens before merging with the tendons of origin and of insertion (Benjamin, 2009) converging in the paratenon. In the limbs of mammals (Gao et al., 2008) the epimysium has a thickness of about $30\ \mu\text{m}$: the collagen fibers have a greater diameter in the outer portion and maintain in every part an undulating course. The collagen is arranged in superimposed layers: in the fusiform muscles with an angle of incidence of 55° in respect to the path of the muscular fibers at rest (Purslow, 2010). In fusiform muscles the collagen of the epimysium resists passive elongation to the limits of the physiological deformation of the muscle, contrary to the collagen of the tendon, which is aligned longitudinally to the axis of the muscle itself. In pennate muscles, the collagen fibers mainly reflect the progression of muscular fibers, forming a dense lamina that often acts as a superficial tendon or an aponeurosis that inserts itself into the connective tissue of the locomotor system, or in the adjacent muscles (take for example the expansion of the gluteus maximus in the iliotibial tract).

It is evident that the epimysium provides a clear resistance if the tension is along the same direction of the fiber's trend. However, it is possible to observe a discrete yielding if the traction occurs in an orthogonal manner (Purslow, 2010).

Where the epimysium of two muscles connects, there is frequently a connective tissue membrane that transports the vessels and the nerves destined to reach these muscles. This, on the one hand prevents the two bellies from separating, and on the other hand it facilitates a discrete sliding of the muscles in all directions. At the same time, this provides the vessels and the nerves with an important autonomy to adapt themselves to the changes in the form of the muscles during movement (Sakamoto, 1996).

The presence of a constant basal tone of the muscle fibers maintain all of the elements of the intramuscular connective tissue in a state of permanent tension, more or less elevated. The internal pressure generated from the

mass of the muscle (especially from the liquids inside it) and the modification of the volume of the belly due to the type of contraction and shortening are additional considerations (Van Leeuwen and Spoor, 1992).

Primarily the epimysium is subjected to mechanical tension and to forces that act orthogonally on its internal and outer surface.

The epimysium therefore takes on a role of:

- containment, limiting the expansion of the muscle with the disposition in concentric layers of the collagen;
- transmission of forces, that are received from the perimysium and from the direct insertion of the fibers into some parts of the muscle; these forces come directly to the tendons or to the aponeurotic expansions;
- sliding surface, of the muscle in respect to the surrounding structures and vice versa;

Between the collagen fibers, fundamental substances, rich in hyaluronic acid can be recognized (McCombe et al., 2001). This allows the collagen fibers to slide with little friction when a demand exists, providing relative mobility. The fundamental substance is a lubricant and is simultaneously a binder for the diverse elements of the extracellular matrix of the intramuscular dense connective tissue (Hukins and Aspden, 1985). The presence of hyaluronic acid in the fundamental substance of the epimysium is what gives each muscular belly a relative independence from the surrounding elements. This occurs everywhere except areas in which the epimysium collagen is shared between two muscles, between a muscle and a neurovascular tract line or with the deep fascia.

The relationship between muscular fibers and the connective tissue of the deep fascia

Within the muscle, the contractile fibers have a longitudinal, transversal and oblique disposition (Savelberg et al., 2001; Finni et al., 2003; van Donkelaar et al., 1999). During a contraction forces are generated in multiple directions, which express themselves in the bone levers, and simultaneously in the connective tissue of the muscle itself. Huijling et al. (2003, 2005, 2007) have demonstrated how 30–40% of the force generated from a muscle is transmitted not along the tendon but rather to the connective tissue outside of the muscle.

Ultrasonography actually can show demonstrates how the fibrous skeleton of the muscle moves and comes into tension before it is possible to measure a traction performed by the proximal or the insertion tendon. Therefore, this occurs before it can be observed in an articular movement. The muscular belly deforms itself in the three planes of space simultaneously and the change in volume and in the form of the belly anticipates its longitudinal shortening.

In vivo experiments have demonstrated how muscle recruitment and relative change in its form can significantly affect the activity of synergistic adjacent muscles (Trotter, 1993; Huijing, 2009; Purslow, 2010). For this reason special attention has been given to the possible connections among

muscular fibers, through that muscle's deep fascia, in the connective component of the proximal-distal muscles and the adjacent muscles that are in the same osteofibrous compartments (Eldred et al., 1993; Hijikata et al., 1993; Hijikata and Ishikawa, 1999).

The deep fascia is a whitish and semitransparent lamina, and it is obvious that the disposition of collagen fibers are well organized, densely adhered and oblique in respect to the axis of the underlying muscles (Benjamin, 2009).

It covers continuously all of the locomotor system with a variable thickness depending on the body region. The average size is 1 mm in thickness (Stecco et al 2009a,b, 2010):

- $297 \pm 37 \mu\text{m}$ in the pectoral region;
- $944 \pm 102 \mu\text{m}$ in the thigh (fascia lata);
- $924 \pm 220 \mu\text{m}$ in the leg (crural fascia).

In the anterior region of the trunk, the thickness is greater in the abdominal region when compared with the pectoral zone. As a general rule, the deep fascia increases from the proximal-distal direction, creating in the extremities highly specialized areas such as the retinacula of the wrist and ankle. In the limbs the intermuscular septa are formed as expansions of the deep fascia, introducing themselves deeply through the different muscular bellies and attaching firmly to the skeleton. The osteofibrous compartments are formed in this way, filled with synergistic muscle groups. Between the deep fascia and the epimysium of the muscles there is a layer of loose connective tissue interposed, that makes it very easy to separate these two sheets, allowing the muscles to slide easily on the dense connective tissue membrane that covers and defines them. Only in selective points does the deep fascia stick to the underlying epimysium.

Conclusions

From this review it appears that muscular fibers should not be studied as isolated elements. They are closely associated with the connective component of the muscle, in particular at the myotendinous junction in a longitudinal way, and at the entire length of the myofibrils through the elements of lateral connection between the muscular fiber and the endomysium. Since the area of the surface of contact with the endomysium is clearly greater along the horizontal axis of the myofibril, compared to that of the myotendinous junction, the force generated during a contraction converges especially in the intramuscular connective tissue.

It is not possible to analyze the structure and the properties of a muscle without keeping in mind the disposition of its fibers and the relationships of the same myofibrils with the aponeurosis and tendons (Finni et al., 2003). The force expressed by a single muscle depends (Van Leeuwen and Spoor, 1992) on its anatomical structure, on the angle at which its fibers are attached to the epimysium and to the tendon's components and on the pressure generated during the muscle recruitment in respect to the internal pressure of the internal structure of the muscle (muscular tissue and blood). Above all, it

depends on the balance of the tension expressed by the basal tone of the muscle that counteracts the tension of the epimysium itself and the surrounding tissues through the epimysium/deep fascia.

It is evident that the muscular connective tissue and the fascia determine the structural and functional characteristics of muscle. Muscle contraction stretches the tendon and simultaneously moves the intramuscular connective tissue.

The functional significance of this relationship between the activity of the muscle and the movement of the connective tissue intra- and extra-muscular needs further study, especially taking into account the presence of numerous receptors that may affect the peripheral coordination of movement.

References

- Benjamin, M., 2009. The fascia of the limbs and back—a review. *Journal of Anatomy* 214 (1), 1–18.
- Borg, T.K., Caulfield, J.B., 1980. Morphology of connective tissue in skeletal muscle. *Tissue & Cell* 12 (1), 197–207.
- Chiariugi, G., 1904. Milano. Istituzioni di Anatomia dell'uomo, vol. 1. Società editrice libraria.
- Denoth, J., Stüssi, E., Csucs, G., Danuser, G., 2002. Single muscle fiber contraction is dictated by inter-sarcomere dynamics. *Journal of Theoretical Biology* 216 (1), 101–122.
- van Donkelaar, C.C., Willems, P.J., Muijtjens, A.M., Drost, M.R., 1999. Skeletal muscle transverse strain during isometric contraction at different lengths. *Journal of Biomechanics* 32 (8), 755–762.
- Eldred, E., Ounjian, M., Roy, R.R., Edgerton, V.R., 1993. Tapering of the intrafascicular endings of muscle fibers and its implications to relay of force. *The Anatomical Record* 236 (2), 390–398.
- Finni, T., Hodgson, J.A., Lai, A.M., Edgerton, V.R., Sinha, S., 2003. Mapping of movement in the isometrically contracting human soleus muscle reveals details of its structural and functional complexity. *Journal of Applied Physiology* 95 (5), 2128–2133.
- Gao, Y., Kostromina, T.Y., Faulkner, J.A., Wineman, A.S., 2008. Age-related changes in the mechanical properties of the epimysium in skeletal muscles of rats. *Journal of Biomechanics* 41 (2), 465–469.
- Gautel, M., 2011. The sarcomeric cytoskeleton: who picks up the strain? *Current Opinion in Cell Biology* 23 (1), 39–46.
- Hijikata, T., Ishikawa, H., 1999. Functional morphology of serially linked skeletal muscle fibers. *Acta Anatomica* 159 (2–3), 99–107.
- Hijikata, T., Wakisaka, H., Niida, S., 1993. Functional combination of tapering profiles and overlapping arrangements in non-spanning skeletal muscle fibers terminating intrafascicularly. *The Anatomical Record* 236 (4), 602–610.
- Huijing, P.A., Baan, G.C., 2003. Myofascial force transmission: muscle relative position and length determine agonist and synergist muscle force. *Journal of Applied Physiology* 94 (3), 1092–1107.
- Huijing, P.A., Jaspers, R.T., 2005. Adaptation of muscle size and myofascial force transmission: a review and some new experimental results. *Scandinavian Journal of Medicine & Science in Sports* 15 (6), 349–380.
- Huijing, P.A., Van De Langenberg, R.W., Meesters, J.J., Baan, G.C., 2007. Extramuscular myofascial force transmission also occurs between synergistic muscles and antagonistic muscles. *Journal of Electromyography and Kinesiology: Official Journal of the International Society of Electrophysiological Kinesiology* 17 (6), 680–689.
- Huijing, P.A., 2009. Epimuscular myofascial force transmission: a historical review and implications for new research. *Journal of Biomechanics* 42 (1), 9–21.
- Hukinsa, D.W.L., Aspden, R.M., 1985. Composition and properties of connective tissues. *Trends in Biochemical Sciences* 10 (7), 260–264.
- Järvinen, T.A., Józsa, L., Kannus, P., Järvinen, T.L., Järvinen, M., 2002. Organization and distribution of intramuscular connective tissue in normal and immobilized skeletal muscles. An immunohistochemical, polarization and scanning electron microscopic study. *Journal of Muscle Research and Cell Motility* 23 (3), 245–254.
- Kjaer, M., 2004. Role of extracellular matrix in adaptation of tendon and skeletal muscle to mechanical loading. *Physiological Reviews* 84 (2), 649–698.
- Kurose, T., Asai, Y., Mori, E., Daitoku, D., Kawamata, S., 2006. Distribution and change of collagen types I and III and elastin in developing leg muscle in rat. *Hiroshima Journal of Medical Sciences* 55 (3), 85–91.
- Listrat, A., Lethias, C., Hocquette, J.F., Renand, G., Ménissier, F., Geay, Y., Picard, B., 2000. Age-related changes and location of types I, III, XII and XIV collagen during development of skeletal muscles from genetically different animals. *Histochemical Journal* 32, 349–356.
- McCombe, D., Brown, T., Slavin, J., Morrison, W.A., 2001. The histochemical structure of the deep fascia and its structural response to surgery. *Journal of Hand Surgery* 26 (2), 89–97.
- Monti, R.J., Roy, R.R., Hodgson, J.A., Edgerton, V.R., 1999. Transmission of forces within mammalian skeletal muscles. *Journal of Biomechanics* 32 (4), 371–380.
- Moore, M.J., 1983. The dual connective tissue system of rat soleus muscle. *Muscle & Nerve* 6 (6), 416–422.
- Ottenheijm, C.A., Granzier, H., Labeit, S., 2012. The sarcomeric protein nebulin: another multifunctional giant in charge of muscle strength optimization. *Frontiers in Physiology* 3, 37.
- Pappas, G.P., Asakawa, D.S., Delp, S.L., Zajac, F.E., Drace, J.E., 2002. Nonuniform shortening in the biceps brachii during elbow flexion. *Journal of Applied Physiology* 92 (6), 2381–2389.
- Pardo, J.V., Siliciano, J.D., Craig, S.W., 1983. A vinculin-containing cortical lattice in skeletal muscle: transverse lattice elements (“costameres”) mark sites of attachment between myofibrils and sarcolemma. *Proceedings of the National Academy of Sciences of the United States of America* 80 (4), 1008–1012.
- Passerieux, E., Rossignol, R., Chopard, A., Carnino, A., Marini, J.F., Letellier, T., Delage, J.P., 2006. Structural organization of the perimysium in bovine skeletal muscle: junctional plates and associated intracellular subdomains. *Journal of Structural Biology* 154 (2), 206–216.
- Passerieux, E., Rossignol, R., Letellier, T., Delage, J.P., 2007. Physical continuity of the perimysium from myofibers to tendons: involvement in lateral force transmission in skeletal muscle. *Journal of Structural Biology* 159 (1), 19–28.
- Patel, T.J., Lieber, R.L., 1997. Force transmission in skeletal muscle: from actomyosin to external tendons. *Exercise and Sport Sciences Reviews* 25, 321–363.
- Petibois, C., Gousspillou, G., Wehbe, K., Delage, J.P., Délérès, G., 2006. Analysis of type I and IV collagens by FT-IR spectroscopy and imaging for a molecular investigation of skeletal muscle connective tissue. *Analytical and Bioanalytical Chemistry* 386 (7–8), 1961–1966.
- Platzer, W., 1978. Locomotor system. In: Kahle, W., Leonhardt, H., Platzer, W. (Eds.), *Color Atlas and Textbook of Human Anatomy*, first ed. Georg Thieme Publishers, Stuttgart.
- Podolsky, R.J., 1964. The maximum sarcomere length for contraction of isolated myofibrils. *The Journal of Physiology* 170, 110–123.
- Purslow, P.P., 1989. Strain-induced reorientation of an intramuscular connective tissue network: implications for passive muscle elasticity. *Journal of Biomechanics* 22 (1), 21–31.

- Purslow, P.P., 2010. Muscle fascia and force transmission. *Journal of Bodywork & Movement Therapies* 14 (4), 411–417.
- Rowe, R.W., 1981. Morphology of perimysial and endomysial connective tissue in skeletal muscle. *Tissue & Cell* 13 (4), 681–690.
- Sakamoto, Y., 1996. Histological features of endomysium, perimysium and epimysium in rat lateral pterygoid muscle. *Journal of Morphology* 227 (1), 113–119.
- Savelberg, H.H., Willems, P.J., Baan, G.C., Huijing, P.A., 2001. Deformation and three-dimensional displacement of fibers in isometrically contracting rat plantaris muscles. *Journal of Morphology* 250 (1), 89–99.
- Sharafi, B., Blemker, S.S., 2011. A mathematical model of force transmission from intrafascicularly terminating muscle fibers. *Journal of Biomechanics* 44 (11), 2031–2039.
- Standring, S., Ellis, H., Healy, J., Johnson, D., Williams, A., 2005. *Gray's Anatomy*, 39th ed. Churchill Livingstone, London.
- Stecco, C., Gagey, O., Macchi, V., Porzionato, A., De Caro, R., Aldegheri, R., Delmas, V., 2007. Anatomical study of myofascial continuity in the anterior region of the upper limb. Tendinous muscular insertions onto the deep fascia of the upper limb. First part: anatomical study. *Morphologie* 91 (292), 29–37.
- Stecco, A., Macchi, V., Masiero, S., Porzionato, A., Tiengo, C., Stecco, C., Delmas, V., De Caro, R., 2009a. Pectoral and femoral fasciae: common aspects and regional specializations. *Surgical and Radiologic Anatomy* 31 (1), 35–42.
- Stecco, C., Pavan, P.G., Porzionato, A., Macchi, V., Lancerotto, L., Carniel, E.L., Natali, A.N., De Caro, R., 2009b. Mechanics of crural fascia: from anatomy to constitutive modelling. *Surgical and Radiologic Anatomy* 31 (7), 523–529.
- Stecco, C., Macchi, V., Porzionato, A., Morra, A., Parenti, A., Stecco, A., Delmas, V., De Caro, R., 2010. The ankle retinacula: morphological evidence of the proprioceptive role of the fascial system. *Cells, Tissues, Organs* 192 (3), 200–210.
- Street, S.F., 1983. Lateral transmission of tension in frog myofibers: a myofibrillar network and transverse cytoskeletal connections are possible transmitters. *Journal of Cellular Physiology* 114 (3), 346–364.
- Testut, J.L., Jacob, O., 1905. *Précis d'anatomie topographique avec applications medico-chirurgicales*, vol. III. Gaston Doin et Cie, Paris.
- Tidball, J.G., Law, D.J., 1991. Dystrophin is required for normal thin filament-membrane associations at myotendinous junctions. *The American Journal of Pathology* 138 (1), 17–21.
- Trotter, J.A., Purslow, P.P., 1992. Functional morphology of the endomysium in series fibered muscles. *Journal of Morphology* 212 (2), 109–122.
- Trotter, J.A., Eberhard, S., Samora, A., 1983. Structural domains of the muscle-tendon junction. 1. The internal lamina and the connecting domain. *The Anatomical Record* 207 (4), 573–591.
- Trotter, J.A., 1990. Interfiber tension transmission in series-fibered muscles of the cat hindlimb. *Journal of Morphology* 206 (3), 351–361.
- Trotter, J.A., 1993. Functional morphology of force transmission in skeletal muscle. A brief review. *Acta Anatomica* 146 (4), 205–222.
- Van Leeuwen, J.L., Spoor, C.W., 1992. Modelling mechanically stable muscle architectures. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 336 (1277), 275–292.
- Wang, K., Ramirez-Mitchell, R., 1983. A network of transverse and longitudinal intermediate filaments is associated with sarcomeres of adult vertebrate skeletal muscle. *The Journal Cell Biology* 96 (2), 562–570.
- Yucesoy, C.A., Baan, G., Huijing, P.A., 2008. Epimuscular myofascial force transmission occurs in the rat between the deep flexor muscles and their antagonistic muscles. *Journal of Electromyography and Kinesiology: Official Journal of the International Society of Electrophysiological Kinesiology* 20 (1), 118–126.