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Fascial hierarchies and the relevance of crossed-helical arrangements of collagen to changes in the shape of muscles☆

Graham Scarr, CBiol., FRSB., FLS., DO*

60 Edward Street, Stapleford, Nottingham, NG9 8FJ, UK

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Summary Muscles are composite structures consisting of contractile myofibres surrounded by complex hierarchies of collagen-reinforced fascial sheaths. They are essentially flexible cylinders that change in shape, with the particular alignment of collagen fibres within their myofascial walls reflecting the most efficient distribution of mechanical stresses and coordinating these changes. However, while the functional significance of this crossed-helical fibre arrangement is well established in other species and in different parts of the body, relatively little attention has been given to this within the fascia of humans; and the relevance of this geometric configuration to muscles and surrounding fascial tissues is described.

Introduction

The fascia

The importance of the fascia to normal function has been recognized by 'hands-on' practitioners for more than a century (Still, 1899; Findley and Shalwala, 2013) but it is only recently that it has emerged as a significant contributor to mainstream orthopaedic knowledge (Schleip et al., 2012). Once dismissed as a packing tissue of little consequence, the fascia is now recognized as a continuous interconnected network that permeates and envelops almost every part of the body and is now taking its rightful place at the 'top table' of anatomical and physiological research.

The term 'fascia' refers to dense planar tissue sheets such as the 'deep' or 'investing' fascia (fascia profunda), septa, aponeuroses, joint and organ capsules, the epimysium that surrounds muscles; and the softer 'superficial' fascia beneath the skin, the intra-muscular endomysium that surrounds individual muscle fibres; and perimysium that surrounds bundles of these fibres. It also includes the dura mater, periosteum, neurovascular sheaths and abdominal mesentery etc, and is continuous with 'non-

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* Tel.: +44 115 9491753.
E-mail address: gscarr3@ntlworld.com.

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fascial' densifications in the form of ligaments, tendons (Benjamin, 2009; Schleip et al., 2012), periosteum and bone (Aaron, 2012).

The internal structure of these fascial sheets consists of an extra-cellular matrix (ECM) containing highly hydrated proteoglycan complexes ('ground substance') and a variety of cells and interlinked fibres (Gillies and Lieber, 2011), and is continuous with the ECM that surrounds virtually every cell in the body. A fibrillar collagen and elastin network also encloses proteoglycan 'microvacuoles', which surround and blend with tendons, aponeuroses, skin, nerves and blood vessels etc so that at the *microscopic* level there is no distinct boundary between where one ends and another begins (Guimberteau, 2005, 2012).

Unfortunately, it is this anatomical continuity and the pervasiveness of fascial tissues at every size scale that has confounded anatomists over the centuries and maintained this connective tissue matrix as the "Cinderella of orthopedic science" (Schleip et al., 2012 p xv); but a new and all encompassing classification system based on density and fibre alignment is now able to relate them all together in a useful way (Schleip et al., 2012 p xvii). The myofascia is then just a fibrous specialization that is intimately connected with muscle, and the crossed-helical orientation of collagen fibres within it and the surrounding fascia play important functional roles that deserve wider recognition.

The fascia

Myofascia

The myofascia is traditionally classified into three different regions (Turrina et al., 2013), which together form a hierarchical network of fibrous tubes or sheaths enclosing smaller tubes within them, and is continuous with 'higher-level' fascial tubes (compartments) that surround groups of muscles, the limbs and entire body (Fig. 1). Although some authors consider that the myofascia should no longer be considered as a collection of 'tubes' or 'sheaths', as it is really a "three-dimensional matrix that is continuous throughout the entire organ" (Purslow and Delage, 2012 p 5) and "tremendously complex compared with other connective tissues" (Gillies and Lieber, 2011 p 318), a comparison with crossed-helical 'tubes' in other parts of the body and in different species suggests that an appreciation of this pattern is important to furthering our understanding of muscle mechanics (Clark and Cowey, 1958; Kier and Smith, 1985).

Endomysium

The endomysium is a delicate tissue that surrounds individual muscle fibres (myofibres) and links them all within a continuous honeycomb arrangement that extends laterally across each fascicle and over the entire length of the muscle (Purslow and Trotter, 1994; Nishimura et al., 1996) (Fig. 2). It consists of a basement membrane that covers the sarcolemma (plasma membrane) and contains mostly type IV collagen, and a thicker felt-like reticular layer of collagen fibres of predominantly types III, V and VI with only small amounts of type I.

This network forms an intimate connection with the myofibril and enables the transfer of contractile force (Huijing, 2012a; Turrina et al., 2013), and because the tubular wall of this endomysial sheath is shared between adjacent myofibres, the tensional force generated by contraction can be efficiently transmitted to *adjacent* tubes through what is described as trans-laminar shear (Purslow and Trotter, 1994; Purslow, 2002). Even the terminations of serially arranged myofibres, which are often staggered by about a quarter of their length with respect to adjacent myofibres, must transmit their force in the same way (Gaunt and Gans, 1992; Sharafi and Blemker, 2011) as this endomysial network is the only structure that continuously links them all together within a fascicle (Purslow, 2010; Turrina et al., 2013). Such lateral load sharing

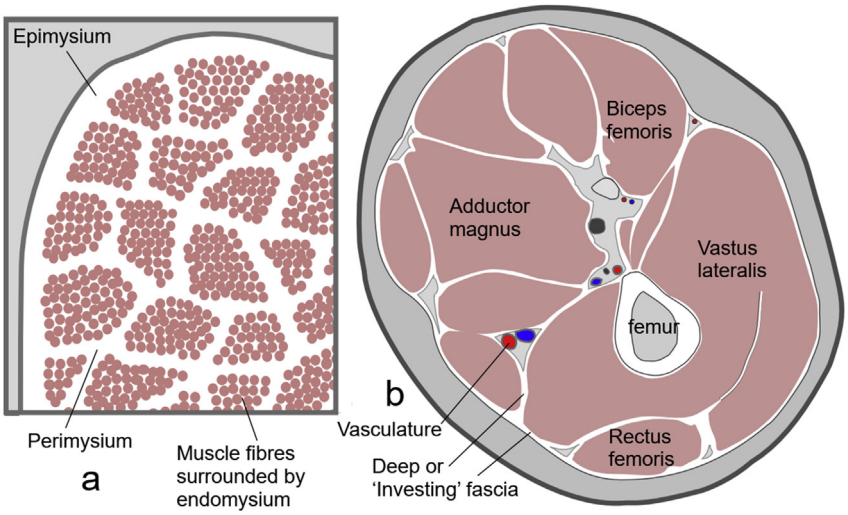

Figure 1 Schematic diagrams of (a) a transverse section of muscle showing the general hierarchical arrangement of myofascial 'tubes' surrounding the myofibres (not to scale); (b) transverse section of the human thigh showing the 'higher-level' fascial tubes consisting of muscle septa and the deep 'investing' fascia surrounding individual muscles and the entire limb. Reproduced with modifications from Scarr (2014) Handspring.