Journal of Bodywork & Movement Therapies (2016) **20**, 629–638

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FASCIA SCIENCE AND CLINICAL APPLICATIONS: FASCIAL PHYSIOLOGY: HYPOTHESIS

Fascial hierarchies and the relevance of crossed-helical arrangements of collagen to changes in shape; part II: The proposed effect of blood pressure (Traube-Hering-Mayer) waves on the fascia[☆]

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Received 27 October 2014; received in revised form 4 September 2015; accepted 20 October 2015

KEYWORDS
Arterial pressure waveform;
Collagen;
Cranial rhythmic impulse;
Fascia;
Helix;
Interstitial fluid flow;
Mayer waves;
Myofascia;
Traube Hering

Summary Periodic changes in arterial pressure and volume have long been related to respiratory and sympathetic nerve activity (Traube-Hering-Mayer waves) but their origins and nomenclature have caused considerable confusion since they were first discovered in the eighteenth century. However, although they remain poorly understood and the underlying details of their control are complicated, these waves do provide valuable clinical information on the state of blood pressure regulation in both normal and pathological conditions; and a correlation with oscillatory motions observed by certain practitioners suggests that they may also have some physiological value that relates to changes in the volume of fascial 'tubes'.

Part I of this paper (Scarr, 2016) described a complex fascial network of collagen-reinforced tubular sheaths that are an integral part of muscle structure and function, and continuous with 'higher-level' fascial tubes surrounding groups of muscles, the limbs and entire body. The anisotropic arrangements of collagen fibres within the walls of these tubes reflect the most efficient distribution of mechanical stresses and have been considered to coordinate changes in shape, and a proposed link between cyclic variations in arterial pressure and volume, and the behaviour of these fascial compartments is now described.

[☆] The author is an independent researcher with no funding or institutional affiliation, and there are no conflicts of interest.

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http://dx.doi.org/10.1016/j.jbmt.2015.10.008
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Introduction

The fascia

Once dismissed as a packing tissue of little consequence, the fascia is now recognized as a continuous and interconnected structural network that permeates and envelops almost every part of the body, and it has many diverse and important functional roles (Schleip et al., 2012; Tozzi, 2015a,b). Part I of this paper (Scarr, 2016) described the hierarchical structure of muscles as a complex network of collagen-reinforced tubular sheaths, which enclose the myofibres and are continuous with 'higher-level' fascial tubes (compartments) surrounding groups of muscles, the limbs and entire body (Benjamin, 2009); and this description of fascial tissues as 'tubes' naturally follows from their cross-sectional appearances (Fig. 1).

The crossed-helical tube

In 1958, Clarke and Cowey showed that changes in the relative length and diameter of nemertean and turbellarian worms were controlled by the particular alignment of tensioned fibres within their body walls, where the fibres were constrained by the crossed-helical geometry surrounding the pressurized body tube and enabled it to maintain a constant volume throughout changes in shape (Fig. 2); and this basic model has now become entrenched as a design principle in biomechanics (Wainwright, 1988; Shadwick, 2008; Kier, 2012).

A crossed-helical tube that is shortened will cause the fibre angles to increase (relative to the tube axis) while one that is extended in length will cause them to decrease; and in both cases, the tension within the fibres becomes greater as the tube shape moves away from its central resting position (Purslow, 1989; Goriely and Tabor, 2013). The shape that optimally balances both longitudinal and circumferential stresses is when the fibres are at an angle of 54.44°, i.e. the fibre orientations are reflecting the most efficient distribution of mechanical stresses and coordinating the changes in shape of the tube, as well as providing a system of elastic energy storage that assists in returning the tube to its resting state (Clark and Cowey, 1958).

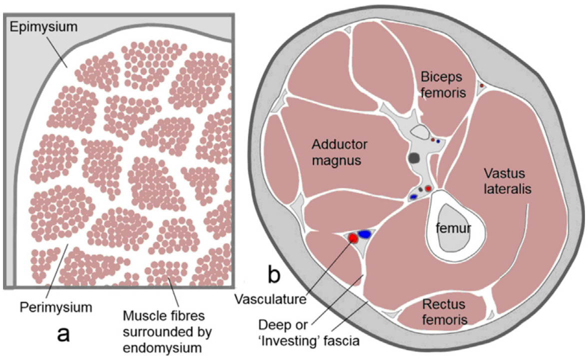

Figure 1 Schematic diagrams of (a) a transverse section of muscle showing the general hierarchical arrangement of myofascial 'tubes' surrounding the myofibres (not to scale); (b) transverse section of the human thigh showing the 'higher-level' fascial tubes consisting of muscle septa and the deep 'investing'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

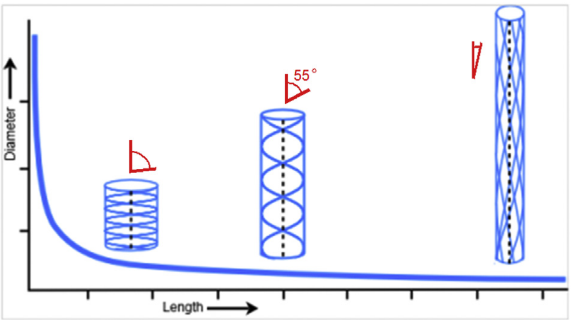

Figure 2 Graph showing the relationship between changes in length, diameter and fibre angles for a constant volume tube with crossed-helical fibres, where a 'resting' tube with fibre angles of ~55° balances both longitudinal and circumferential fibre stresses (helixes not to scale). Re-drawn with modifications from Kier and Smith (1985).

Although the functional significance of this particular arrangement is now well established in many species and in different parts of the body, it has received relatively little attention within the fascia of humans, and the theory and relevance of this pattern to changes in the shape of muscles was described in Part I (Scarr, 2016). The formation of a crossed-helical pattern is based on simple geometric principles (Pickett et al., 2000; Scarr, 2011) and its persistence is ensured because it is one of the most stable of structural configurations; and it is not surprising that such a system should predominate in compliant biological tissues because this is one of the most efficient ways of optimizing the stresses within their walls (Clark and Cowey, 1958; Wainwright, 1988; Kier, 2012).

Anecdotally, certain practitioners routinely observe an oscillatory tissue motion that is palpable on the surface of the body and provides qualitative information that contributes to the diagnosis and treatment of a wide variety of conditions (Parsons and Marcer, 2006 p 201–218; Sergueef et al., 2011) and Scarr (2013) described a potential link with crossed-helical arrangements of collagen. Nelson et al. (2001, 2006) also found a correlation with cyclic changes in arterial blood flow and it is now proposed that all these factors relate to changes in the volume of tubular fascial sheaths.

Traube-Hering-Mayer waves

While periodic changes in arterial pressure and volume have long been recognized, their physiological origins and nomenclature have caused considerable confusion since they were first described in the eighteenth century (Koepchen, 1984; Larsen et al., 2010), but they do provide valuable clinical information through the real-time monitoring of haemodynamic parameters and contribute to the decision making process within intensive care units (Lamia et al., 2005). They are also useful to research in understanding cardio-respiratory coupling (Larsen et al., 2010; Dick et al., 2014); central and baroreflex control (Julien, 2006; Morris et al., 2010); peripheral blood flow related to sympathetic nerve activity (SNA) (Barman, 2009; Fatouleh and Macefield, 2013) and changes in tissue volume and perfusion (Christ et al., 1995) under normal and pathological conditions.

Part II now explains a mechanism whereby cyclic changes in arterial pressure and volume might influence the behaviour of the crossed-helical fascial compartments surrounding them; and briefly describes the physiological implications.

Blood pressure waves

Blood pressure waves appear at various frequencies, recorded as cycles per minute (cpm) or cycles per second (Hz), and are classified into three main groups: a very-low frequency band (0.00—0.18 cpm, 0.00—0.03 Hz); low-frequency (Mayer) waves that are influenced by baroreflex activity (1.8 cpm—9.0 cpm, 0.03—0.15 Hz); and a faster Traube-Hering wave band associated with the respiratory cycle (9.0—24.0 cpm, 0.15—0.4 Hz). Although each group has traditionally implied a different mechanism of causation, the precise boundaries between each one can vary because of experimental and inter-species differences, etc (Acharya et al., 2005; Finucane et al., 2010) and the differences between them are not clear cut.

Traube-Hering waves

The appearance of Traube-Hering waves (9.0—24.0 cpm, 0.15—0.4 Hz) in the peripheral circulation is a reflection of respiratory sinus arrhythmia (RSA), a normal physiological phenomenon that reciprocally couples the respiratory rate with that of the heart, where inspiration and expiration cause momentary changes in heart rate and arterial pressure (Fig. 3), but the underlying details of their control are complex. Respiratory activity is normally monitored through mechanoreceptors (thorax) and chemoreceptors (blood gases), and this information is relayed to the brainstem and ultimately the heart through reflex changes in sympathetic and parasympathetic outflow, with cardiac activity then leading to changes in blood pressure and baroreflex stimulation that influence the respiratory centres through complex feedback loops (Larsen et al., 2010; Ben-Tal et al., 2012; Dick et al., 2014).

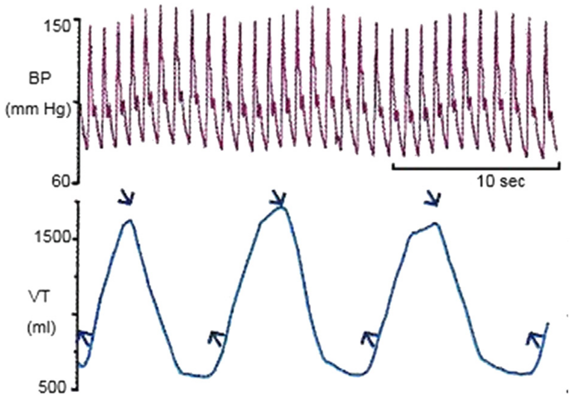

Figure 3 Synchronous tracings of brachial artery pressure (upper) and thoracic-abdominal volume (lower) showing the arterial pulse and longer-period Traube-Hering waves, and the relationship between cardiac and respiratory activity. Upward and downward arrows indicate the onset of inspiration and peak of breath, respectively, during slow deep breathing. Reproduced with modifications from Dick et al. (2014) Elsevier with permission.

Mayer waves

The origins of Mayer waves, on the other hand, have been the subject of a great deal of speculation, and Julien (2006) reviewed and summarized some of the experimental findings. The pacemaker theory "...is based on the observation that... oscillations of sympathetic nerve activity (SNA) and/or hemodynamic variables can be observed at or near the frequency of Mayer waves in the absence of sensory inputs from the periphery. Such rhythmicity is then thought to derive from the pacemaker-like activity of an autonomous oscillator located within central nervous structures generating SNA" (Julien, 2006). In other models, it was anticipated that "the numerous dynamic components and fixed time delays present in the baroreflex loop would result in the production of a resonant, self-sustained oscillation of arterial pressure" but Julien (2006) also suggested that "Mayer waves are transient oscillatory responses to hemodynamic perturbations rather than true feedback oscillations".

Dick et al (2014) showed that respiratory activity can also be modulated with the arterial pulse in humans, and Morris et al. (2010) detailed a coupling between the respiratory rhythm, vagal activity and Mayer wave-related oscillations in cats that involved "reciprocal parallel signalling paths between the pons and ventral respiratory column". These later findings thus support the presence of a central Mayer-wave oscillator that is bi-directionally coupled with respiratory oscillators, but it "remains to be shown whether the raphe-pontine network is directly involved in production of the 0.1 Hz rhythm or receives an efference copy generated elsewhere" (Morris et al. (2010).

The function of arterial pressure waves

The rather variable nature of these oscillations under different experimental conditions has led to suggestions that any perceived functions are purely incidental, particularly with Mayer-waves, although this has naturally been subject to speculation (Polosa, 1984; Miyakawa, 1984; Nelson et al., 2001, 2006). Barman (2009) noted, with respect to peripheral SNA, that "these rhythms can be entrained to inputs such as baroreceptor and lung inflation afferents and central respiratory networks, which give rise to their characteristic rhythmic pattern", and that "rhythmic activity may lead to more effective activation of sympathetic neurons than randomly occurring activity... and is important in coordinating activity in different sympathetic nerves, and... may help homeostasis". Ben-Tal et al. (2012) hypothesized that "RSA helps the heart do less work while maintaining healthy levels of blood gases" and Dick et al. (2014) even considered that "cardio-respiratory coupling is a biomarker of health"!

Regardless of their perceived 'functions', arterial pressure waves are known to reflect the state of blood pressure regulation in both normal (Julien, 2006; Fatouleh and Macefield, 2013) and pathological conditions (Christ et al., 1995; Heusser et al., 2010; Finucane et al., 2010); and a correlation with the 'cranial rhythmic impulse' (CRI) recognized by certain groups of practitioners suggests that they also have some physiological and therapeutic value that relates to changes in the volume of fascial tubes (Scarr, 2013).

A change in volume

The fascial tube

Within muscles, the perimysium and epimysium frequently contain two crossed-ply sets of collagen 'cables' aligned at about ±55° (relative to the long axis) (Rowe, 1981; Passerieux et al., 2007; Purslow, 2010), while the *apparently* isotropic alignments of collagen fibres within the endomysium appear to be random but collectively have a (numbers-weighted) mean orientation of about 59° (Purslow and Trotter, 1994). These collagen fibre angles increase with muscle contraction and become more aligned with its transverse or circumferential plane, and when the muscle is stretched the angles decrease as the fibres become aligned towards the main direction of tension, indicating that the collagen fibres are mechanically linked with each other (Fig. 2) (Purslow, 1989, 2010; Chaudhry et al., 2012).

The deep or investing fascia is a tougher tissue that surrounds and contains groups of muscles (compartments), and is continuous with aponeuroses (McCombe et al., 2001; Stecco and Stecco, 2012a,b) and the overlying 'superficial' fascia that lies beneath the skin (Benjamin, 2009; Abu-Hijleh et al., 2012); and all are involved in the transfer of tension (Maas and Sandercock, 2010; Huijing, 2012), with the loose fibre network of the superficial layer contributing to its flexibility (Iatridis et al., 2003). Although bundles of collagen fibres within the investing fascia have been found to be aligned at 0° (McCombe et al., 2001; Benjamin, 2009), Benetazzo et al. (2011) noted the mean angle *between* crossed-fibre orientations in human thoraco-lumbar and crural fascia as 78°, which indicates an average fibre angle of 39° relative to the body axis.

Hebrank (1980) showed that the dermis of eels (*Anguillidae*) contains crossed-helical arrangements of collagen fibres aligned at 45°, while Naresh et al. (1997) observed angles (50° − 70°) that varied between different parts of the skin in sharks (*Odontaspididae*); and Pabst (2000) found a similar pattern within the body walls of tuna fish (*Scombridae*), dolphins and whales (*Cetacea*: *Mammalia*). Crossed-helical alignments of muscles and connective tissues also occur within the mammalian tongue, octopus tentacles and the elephant's trunk etc (Kier and Smith, 1985), which all suggests that similar patterns are likely to occur in humans (Scarr, 2016). Whilst these examples are structural specializations whose prime function is to facilitate movement and locomotion, the alignments of muscle and investing fascial tissues that curve around the body wall and limbs are also suggestive of helical arrangements, if only in part (Fig. 4) (Benetazzo et al., 2011; Vleeming, 2012).

Part I (Scarr, 2016) concluded that these crossed-helical arrangements of collagen within muscles and 'higher-level' fascial sheaths are likely to be contributing to their dynamic behaviour, which introduces another factor into soft-tissue mechanics as these fascial tubes contain blood vessels that are continuously changing in volume.

Arteries and the fascia

Arterial walls provide reinforcement against the pressure of blood and regulate its flow by contracting and dilating under autonomic nervous system control (vasomotion), with a cyclic increase in circumference and volume (dilation) corresponding with a decrease in pressure, and vice versa (Sircar, 2008 p 302); and it should be no surprise that the collagen fibres within their walls are also arranged in crossed-helical arrangements (Holzapfel, 2006). Regular oscillations of arterial pressure and volume (Traube-Hering-Mayer waves) are then likely to influence the behaviour of the tissues surrounding them, and indeed, Christ et al. (1995) found a correspondence between cyclic increases in arterial volume and changes in the volume of the limb (<0.177 ml per 100 ml tissue).

Muscles are essentially incompressible (Baskin and Paolini, 1966) and there are no empty spaces in surrounding tissues that could absorb these changes in volume, which means that a cyclic dilation and contraction of these fascial tubes in sympathy with changes in vascular volume (both intra- and extra-muscular) might be able to influence the crossed-helical fibre configurations within their walls in a particular way.

Fig. 5a–c shows how an increase in arterial volume might cause a surrounding fascial tube with a low collagen fibre angle to increase more in diameter, one with a high angle to increase more in length, and one with an angle of

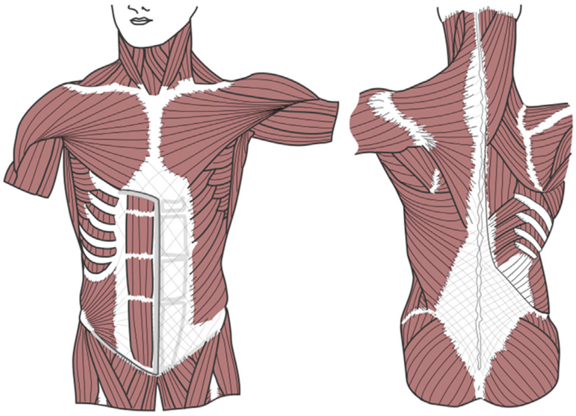

Figure 4 Schematic diagrams showing the muscles and fascia of the trunk twisting around the body wall and continuing into the neck and limbs. Reproduced from Scarr (2014) Handspring.

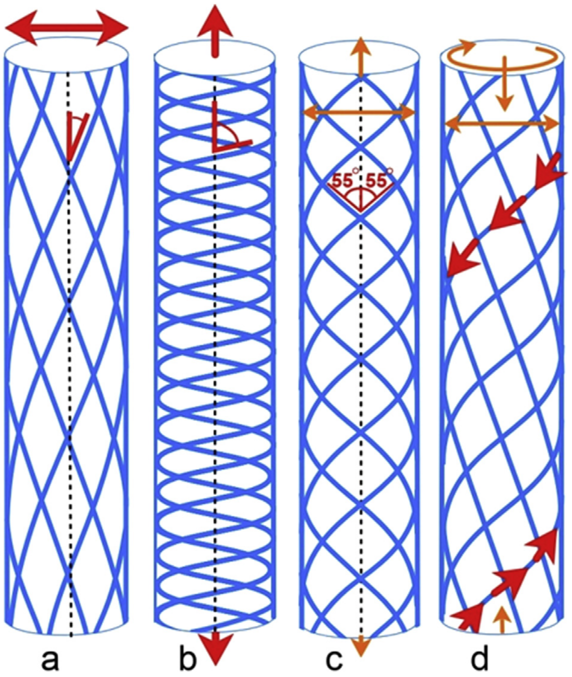

Figure 5 Schematic drawing to show how crossed-helical fibre angles of collagen might influence the response of a fascial tube to increases in volume, where: (a) a low fibre angle would preferentially increase tube diameter; (b) a high fibre angle would tend to increase tube length; (c) and the optimum fibre angle of 54.44° balances both influences; (d) left- and right-handed helixes with different angles may cause an increase in tube diameter, with shortening and torsion occurring in a direction that follows the highest fibre angle (large arrows) (see Discussion). Reproduced with modifications from Scarr (2013) Elsevier with permission.

54.44° to balance both tendencies; with even longitudinally oriented fibres (0°) that occur in some epimysial and deep fascial tissues (McCombe et al., 2001; Benjamin, 2009) leading to an expansion in tube width.

Discussion

A change in volume

While direct measurements of periodic changes in arterial blood pressure (Lamia et al., 2005; Dick et al., 2014) (Fig. 3) and flow (laser-Doppler flowmetry) are widely used, the electrical recording of sympathetic nerve activity (Barman, 2009; Fatouleh and Macefield, 2013) and plethysmographic volume changes also provide information on local tissue physiology (Gamble et al., 1993; Christ et al., 1995; Joyner et al., 2001). Plethysmography demonstrates the changes in volume that occur within an organ or limb through the direct displacement of water, or variations in its circumference (mercury-in-silastic strain gauge MSG), which is particularly relevant here because of the potential influence that cyclic changes in arterial volume have on crossed-helical fascial tubes (Fig. 5).

Christ et al., 1995 recorded (MSG) periodic volume changes of <0.177 ml per 100 ml of tissue in the lower limb of patients under positive-pressure ventilation at 9.0—19.5 cpm (0.15—0.325 Hz), whilst this author observed cyclic volume changes <0.20 ml in the whole forearm in three subjects during spontaneous breathing (water-displacement plethysmograph based on the design by Raine and Sneddon (2002)); and all appeared to correlate with the Traube-Hering wave frequencies given earlier. In this author's investigation, oscillating volume changes of less than 0.01 ml (10 μl) matched the frequency of the radial pulse, but as no continuous recording was available any slower Mayer-wave-like patterns could not be recognized. Christ et al. (1995), however, recorded low-frequency volume changes between 0.5 and 7.0 cpm (0.008—0.117 Hz) and attributed them to variations in arteriolar vasoconstriction (and possibly venous and lymphatic vessels), but excluded "Traube-Hering-*Brauer*" (sic) waves as a possible cause because they were "nearly always observed unilaterally"; but the underlying pathologies of the subjects may have influenced this finding and suggests that this conclusion might have been premature.

A note on modelling

It should be noted that the apparently continuous fibers that stretch between the ends of the crossed-helical tubes (Figs. 2 and 5) are really graphic representations of bundles of smaller collagen molecules/fibrils that are cross-linked together and transfer tensional forces between them (Avery and Bailey, 2008). These bundles are frequently wavy, or crimped, with a crimp angle of ~39° that enables them to be elastically stretched by an additional five per cent of their length; and this angle decreases as the fibres are straightened out (and tension increases) during changes in tube length and circumference. Purslow (1989) found a correlation between crossed-helical fibre angles and changes in sarcomere length, where fibre angles of 20° and 80° in the perimysium corresponded with sudden and dramatic increases in stiffness (from 0 to ~18 KPa) and set a boundary limit to further changes in shape, which also supports the predictions made by Clark and Cowey (1958) for elastic fibre systems. While muscles normally operate well within the central region between these two extremes and are thus able to change shape with ease, information on the fibre angles and behaviour of the surrounding deep/investing fasciae are less well described.

It should be emphasized that there is considerable variation in the shape and cross-sectional area of all these fascial sheaths/tubes, and that the connections and interactions between them within the overall structural hierarchy are highly complex and not completely characterized (Scarr, 2016); and the model described here merely serves as an illustration of the crossed-helical principles that may contribute to the mechanical behaviour of all these fascial tubes.

The cranial rhythmic impulse (CRI)

Anecdotally, 'cranial osteopaths' and 'cranio-sacral therapists' routinely observe an oscillatory tissue motion that is palpable on the surface of the body and provides qualitative information that contributes to the diagnosis and treatment of a wide variety of conditions (Parsons and Marcer, 2006 pp 201–218; Sergueef, 2007). Nelson et al. (2001) compared different CRI frequencies with blood velocity measurements taken on the ear lobe (laser-Doppler flowmetry), where Fourier transform and power-spectral analysis revealed distinct peaks that matched the 'very low-frequency', 'Mayer' and 'Traube-Hering' wave groups described above; although their *naming* of them was not consistent with these. Nelson et al. (2006) found that the mean palpated rate of the CRI fell within the Mayer group but then related them to Traube-Hering oscillations in a 1:2 relationship, while Nelson (2011) dispensed with these names altogether.

This frequency-domain type of analysis is widely used to isolate particular wave frequencies but can lead to misleading results on its own and does not necessarily provide useful information on the cause or regulation of these waves. The Poincaré plot would thus be valuable in future studies because it also reveals the relationship *between* consecutive wave cycles and conveniently summarizes all the information (Acharya et al., 2005; Dick et al., 2014). Scarr (2013) briefly reviewed some of the experimental evidence concerning the relationship between oscillations in blood flow and the CRI, and found that although a statistical correlation between them could be made, there was considerable confusion surrounding all these enigmatic waves.

A different pattern

Scarr (2013) also noted that the CRI and certain palpatory phenomena observed in the limbs might be explained by a *different* crossed-helical arrangement within the fascia, where a subtle sense of the limb shortening, expanding in width and rotating externally is followed by a lengthening, narrowing and internal rotation (Nelson et al., 2006; Sergueef, 2007 p 68); or in other words, a slowly oscillating (Mayer wave-like frequency), *low* amplitude helical torsioning of the entire limb. While a shortening/expansion and lengthening/narrowing oscillation resulting from changes in volume would certainly be compatible with the crossed-helical mechanics shown in Fig. 5a–c, the rotational component remains outside of this model; but a preliminary experiment showed that a crossed-helical tube with the left- and right-handed fibres oriented at *different* angles caused a shortening and torsional strain when the tube volume was increased (Fig. 5d) (see Appendix).

Whilst this experiment is very simplistic when compared with the complex structural reality of the fascia, both Wainwright (1988 p 71) and Kier (2012) depict drawings of crossed-helical tubes with fibres of different angles (although they give no examples or explanation for this particular pattern), and Goriely and Tabor's (2013) analysis of the physics underlying such an arrangement in a biological context adds support to the feasibility of this model. Scarr (2013) also suggested that a similar pattern of scales on the limbs of the pangolin (*Manis* spp) might reflect this alignment within the underlying fascial sheaths, and be an "intrinsic part of mammalian limb development", but this remains a conjecture (Fig. 6). Even so, geometric patterns do not just appear out of nowhere but because of the interactions between some basic physical principles and the constraints that underlie all self-organizing processes; and crossed-helical arrangements are a natural consequence of these (Pickett et al., 2000; Snir and Kamien, 2005; Scarr, 2011, 2014).

Figure 6 A preserved specimen of a pangolin (*Manis javanica*) showing the crossed-helical alignment of keratin scales in the limbs; compare with Fig. 5d. Reproduced with modifications from Scarr (2013) Elsevier with permission.

The tensioned tissue pump

The vascular tree

It has so far been proposed that cyclic variations in blood volume/pressure within the arteries and arterioles (Traube-Hering-Mayer waves), which are the result of rhythmic variations in sympathetic nerve activity on vessel calibre (Barman, 2009; Fatouleh and Macefield, 2013), are the driving force behind changes in the volume of the fascial tubes surrounding them; and the relevance of this model is most clear in the limbs, which consist of tubular fascial compartments containing bones, muscles, blood vessels and nerves that are generally oriented along the main limb axis. Larger arteries run within the deep investing fascia (Fig. 1b) and send one or more branches that travel within the connective tissue framework of each muscle, with smaller arteries and arterioles running parallel and ramifying in the perimysial septa before giving off capillaries that anastomose within the endomysium (Standring, 2005 p118). While propagation of the arterial pulse (systolic/diastolic pressure 120/80 mm Hg) is extremely complicated and depends in part on the distensibility of different regions of the vascular tree, mean blood pressure is considerably reduced in the arterioles (>18 mm Hg; Sircar, 2008 p251); and the pulse greatly damped by the time it reaches the capillary bed (Ethier and Simmons, 2007 p 179).

Although the measurement of *intra-muscular* pressures is notoriously difficult (Hill, 1948; Hargens et al., 1989;

Ward et al., 2007), Nakhostine et al. (1993) showed that the pressure within human anterior tibialis increases centripetally (~26 mm Hg compared to ~4 mm Hg near the muscle surface), while an extensive review by Aweid et al. (2012) found that the generally accepted normal pressure of 6–12 mm Hg at rest could rise to 141 mm Hg during activity; and should be considered pathological if it remains above 34 mm Hg after 1 min following exercise (compartment syndrome). The ability of any particular vessel to initiate changes in the volume of the fascial tube(s) surrounding it may thus depend on the local pressure differentials between them; and influence their contents.

The interstitium

The exchange of fluids within the extra-cellular matrix (ECM)/interstitial tissues is driven by the flow of plasma through the walls of blood capillaries, and its removal through the venous and lymphatic system, and it may also be that slowly oscillating changes in the volume of tubular fascial compartments are able to create a pumping action that increases the flow of fluids within them (Rutkowski and Swartz, 2007; Meert, 2012). While the local interchange of fluids is essential to the supply and removal of substances associated with cell metabolism and is greatly enhanced by muscle contraction (Sircar, 2008 p 231), a continuous low-frequency pump would ensure that this is maintained at rest; and the principle of this has already been outlined by certain practitioners as the CRI and 'primary respiratory mechanism' (Nelson et al., 2001; Parsons and Marcer, 2006 p 204; Scarr, 2013).

'Higher-level' fascial tubes are really structural continuations of the ECM/interstitial tissues that surround myofibres and virtually every other cell in the body, with the intimate connections between them and the cellular cytoskeleton, such as transmembrane proteins (Brown et al., 2012) and perimysial junction plates (Passerieux et al., 2006), enabling the transfer of tensional forces in both directions and influencing cell function in complex ways (Scarr, 2016). Changes in cytoskeletal tension, coupled with chemical signalling, cause the enzymes and substrates situated on this lattice to alter their metabolic activities and influence cellular respiration, as well as switching between different functional states such as growth, differentiation or apoptosis (Wang et al., 2009; Ingber et al., 2014).

In short, it may be that changes in fascial tension caused by cyclic variations in volume (in response to blood pressure waves) are transferrable to the ECM and cytoskeleton and thereby alter cellular activity. Oscillating changes in cytoskeletal tension and fluid flow as the result of this vascular driven fascial mechanism might then have an effect on the normal maintenance, remodelling and development of all tissues throughout the body (Nelson et al., 2005; Ingber et al., 2014).

Conclusion

The myofascia is a fibrous specialization of fascial/ECM tissues that enclose and inter-penetrate muscles as a complex hierarchy of tubes containing smaller tubes within them; and is continuous with higher-level fascial tubes that surround groups of muscles, the limbs and entire body (Fig. 1). Bundles of collagen fibres within the perimysium and epimysium are typically aligned in two distinct directions that together form crossed-helical patterns (Fig. 2), and this arrangement also appears within the deep investing fascia surrounding groups of muscles and the body wall.

Part I (Scarr, 2016) described how this particular geometric configuration might coordinate changes in muscle shape (length versus circumference) during contraction and extension, with collagen fibre tension increasing towards both these extremes and settling at an intermediate resting angle of ~55° (relative to the tube axis), and the orientation of the fibres varying between a high-angle on shortening and a low-angle when elongated (Fig. 2). In essence, the particular fibre orientations are a reflection of the most efficient distribution of mechanical stresses; and the same basic principles are likely to apply to the walls of all these tubular sheaths (Appendix).

It has thus been proposed that cyclic variations in arterial pressure and volume (Fig. 3) (Traube-Hering-Mayer waves) are likely to cause corresponding changes in the volume and shape of the tubular fascial compartments surrounding them (Fig. 5); and that the effects of this may be palpable on the surface of the body as the CRI. If this really is the case, then such rhythmic changes in volume would probably have an effect on the flow of fluids within the ECM/interstitium, with variations in tissue tension also influencing the behaviour of associated cells; and such oscillations may even play a role in the development and regulation of particular tissue shapes and patterns throughout life.

Acknowledgements

I would like to thank Emma Colley for information on the clinical value of arterial pressure waves; Stephen Dibnah and Leonid Blyum for their participation in the author's plethysmography experiment; and to the anonymous reviewer who rigorously questioned the assumptions made and provided much-needed food for thought.

Appendix

An experiment to show that an increase in the volume of a crossed-helical tube with differing fibre angles causes a torsional strain.

This demonstration is the previously unpublished 'preliminary experiment' referred to by Scarr (2013 ref 36) and omitted from that paper because the value of such a simple and apparently unique experiment was not fully appreciated at the time. It is essentially a qualitative assessment of the changes that occur following an increase in volume of a crossed-helical tube made from two sets of stretchable cords or 'fibres' with *differing* orientations (Fig. 7).

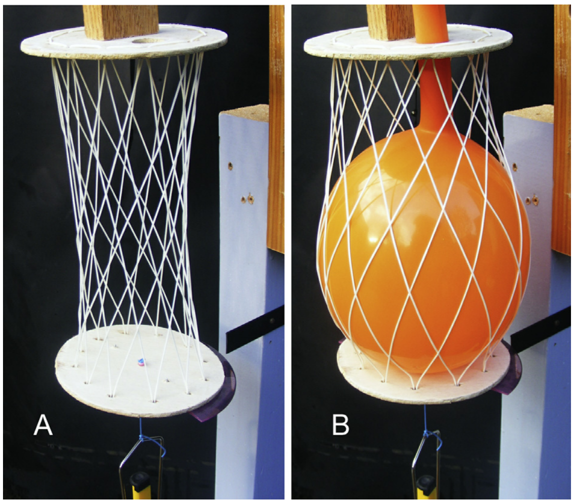

Figure 7 a) The experimental setup of a crossed-ply tube constructed from left- and right-handed 'fibres' aligned at different angles (10° and 22°, respectively, relative to the tube axis); b) an inflated balloon increases the volume within the tube and causes a shortening and torsional strain that follows the fibres with the highest angle (see Fig. 5d).

Apparatus

1. Two circular plywood plates (thickness 3 mm, diameter 100 mm) were drilled with twelve holes (2.5 mm) spaced around a circle (80 mm diameter) in preparation for the cord attachments, with similar holes drilled in the centre of each plate to allow for final stabilization of the apparatus, and a single hole (16 mm diam.) in the top plate to permit insertion of a balloon. The top plate was then screwed and fixed into position on the supporting stand.
2. A continuous length of 1.0 mm polyester cord ('Shamballa jade' as used in bead jewellery) was woven between each end plate using consecutive holes and forming a tube with a length of about 200 mm. The tension in each cord (fibre) was then equalized by rotating the lower end-plate and gently pulling down several times before securing those parts of the cords (lying on the outer face of the plywood) with a drop of *superglue* (cyanoacrylate).
3. A second length of cord was then inserted through one of the same holes of the upper plate and interwoven in a clockwise direction between five of the above cords (starting on the outside of the adjacent cord) and passed through the sixth hole of the lower plate. It was then interwoven back to the top plate, parallel with the previous cord, and the process repeated until each hole contained two 'fibres'.
4. With the wall of this crossed-helical tube now in place, the lengths of this second set of 'fibres' were now equalized and secured (as described in (1) above) so as to form a set with a distinctively higher angle (relative to the tube axis) compared to the first set. The tube had a final length of 190 mm with end diameters of 80 mm, a set of left-handed helixes at 10°, and another set of right-handed helixes at 22°.
5. Finally, a plastic protractor for measuring axial rotation was screwed onto the underside of the lower end-plate; a fixed point marker secured to the stand; and the end of a piece of string secured in the central hole in the lower plate, with the other end attached to a small mass that just removed any slack from the helical 'fibres'.

Method

The initial protractor angle was noted and a *long* rubber balloon (rather than a pear shape) was inserted through the large hole in the fixed upper end-plate and attached to a plastic hand pump. The balloon was inflated so that it pushed against all the crossed-helical tube 'fibres' and simulated an increase in tube volume; and finally tied at its end after removing the pump. The new protractor angle and length between the end-plates were then noted so as to assess the changes that followed balloon inflation.

Results

The lower end-plate was found to have rotated in a clockwise direction (viewed from below) with a change in angle from 111° to 127°, relative to the fixed upper plate, and a reduction in length between the plates from 190 mm to 180 mm. The length of the tube had thus shortened by 10 mm and the ends had twisted by 16° in relation to each other, as a result of the balloon inflation, and these changes followed the orientation of the highest fibre-angle (right-handed helix) as shown in Fig. 5d. Although the particular cord used could be stretched to almost 10% of its length, which is about twice the amount that crimped collagen fibres can be elongated to (Purslow, 1989), it is still consistent with the fibre model described by Clark and Cowey (1958).

Conclusion

This 'preliminary experiment' showed that an increase in volume of a crossed-helical tube constructed from left- and right-handed fibres with *different* angles causes a torsion that follows the orientation of the highest fibre-angle; and is consistent with the theoretical analysis of Goriely and Tabor (2013). Although the fibre angles of 10° and 22° were appreciably different from those described in the body of the text, and such an arrangement of collagen fibres within the fascia of the limbs remains speculation, it provided a qualitative demonstration of the principle and now requires more detailed analysis of fascial histology.

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