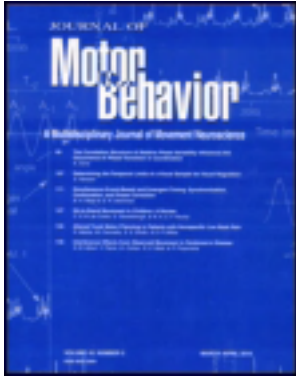


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The Medium of Haptic Perception: A Tensegrity Hypothesis

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MAIN ARTICLE

The Medium of Haptic Perception: A Tensegrity Hypothesis

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ABSTRACT. For any given animal, the sources of mechanical disturbances inducing tissue deformation define environment from the perspective of the animal's haptic perceptual system. The system's achievements include perceiving the body, attachments to the body, and the surfaces and substances adjacent to the body. Among the perceptual systems, it stands alone in having no defined medium. There is no articulated functional equivalent to air and water, the media that make possible the energy transmissions and diffusions underpinning the other perceptual systems. To identify the haptic system's medium the authors focus on connective tissue and the conjunction of muscular, connective tissue net, and skeletal (MCS) as the body's proper characterization. The challenge is a biophysical formulation of MCS as a continuum that, similar to air and water, is homogeneous and isotropic. The authors hypothesized a multifractal tensegrity (MFT) with the shape and stability of the constituents of each scale, from individual cell to whole body, derivative of continuous tension and discontinuous compression. Each component tensegrity of MFT is an adjustive-receptive unit, and the array of tensions in MFT is information about MCS. The authors extend the MFT hypothesis to body-brain linkages, and to limb perception phenomena attendant to amputation, vibration, anesthesia, neuropathy, and microgravity.

Keywords: haptic system, fascia, connective tissue, multifractal tensegrity, ecological approach

In Bernstein's (1996)¹ functional characterization of the vertebrate movement system, the ability to mobilize hundreds of muscles in a coherent, harmonious fashion, as in standing, running, jumping, and swimming, is primarily the responsibility of the level of muscular-articular links or synergies supported by the basement level of tone. Underpinning the proficiency of these functional levels in coordinating movements at the scale of the whole body is a perceptual capability involving mechanoreceptors that infuse skin, muscles, tendons, ligaments, and fascia. Bernstein referred to this capability as the muscular-articular sense. Other labels are kinesthesia and proprioception.

Bastian (1880) suggested the term *kinesthesia* or sense of movement in recognition of the complexity of contributions from skin, muscles, tendons etc. in generating sense impressions of weight, effort, resistance, limb positions, and limb movements (Boring, 1942). For Bastian, the foregoing were sensations available for introspection. Sherrington (e.g., 1906) promoted the term *proprioception* (meaning self-perception) to address a similar but smaller inventory of concerns from a physiological rather than introspective viewpoint.

Use of the term *haptic* is comparable in age to the uses of *kinesthesia* and *proprioception* but its origin is less certain due in part to its variable interpretation (see historical summaries in Grunwald, 2008). It is said to be derivative of the Greek *haptesthai* (able to lay hold of; e.g., Revesz, 1950).

Haptic, therefore, is a most appropriate term for the nonvisual perceiving that occurs in the everyday context of laying hold of something for the purpose of doing something. Figure 1a provides an example of the four kinds of mechanically based awareness accompanying the laying hold of an object. Their designations are general, and two are familiar. The extension beyond the familiar proprio- and exteroception stems from Lee's (1978, 1980) investigations of the perceiving made possible by the optic flow field and Shaw's (2001) elaboration of them with an eye to a theory of intentionality. Lee (1978, 1980) added exproprioception to the classical terminology of exteroception and proprioception in order to give emphasis to information available in optic flow about the environment relative to the organism. He intended this new term to also cover the availability of information about the organism relative to the environment (personal communication to R. E. Shaw). In clarification, Shaw (2001) equated Lee's exproprioception with perceiving the environment relative to self and introduces proexteroception for perceiving self relative to environment. Following Shaw (2001), the four kinds of perceiving depicted in Figure 1a can be schematized, most generically, as four modes of reference, two reflexive and two symmetric. Through the algebraic properties of reflexivity and symmetry, Figure 1b expresses the intentionality of perception—haptic and otherwise.

Perceptual Systems and Media

The key to all functions of the haptic perceptual system is the temporary deformation of tissue. Differential pressure counts but uniform pressure (e.g., air pressure) does not. Uniform pressure is not deforming, not mechanically stimulating. A considerable body of research suggests that humans respond in specific ways to specific deformations (Carello & Turvey, 2000; Turvey & Carello, 1995, 2011). Surprisingly, there is a related and likewise considerable body of research that shows that individual cells exhibit specificity of response when subjected to specific deformations (Chen & Ingber, 1999; Ingber, 1993, 2000, 2006). Cell, similar to human, is a haptic system. A connective tissue cell shares with the human the exteroceptive activities of dynamic or effortful touching to negotiate and manipulate its microenvironment during migration—activities such as pushing, pulling, probing, prodding, bending, stretching, and tugging. The question posed in the present article is that of what constitutes the medium of haptic perception. We expect the preceding

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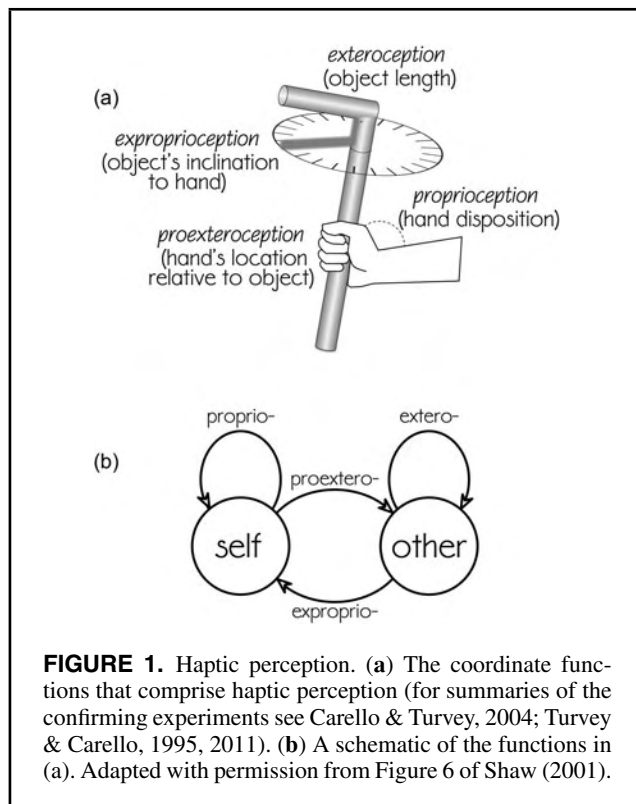


FIGURE 1. Haptic perception. (a) The coordinate functions that comprise haptic perception (for summaries of the confirming experiments see Carello & Turvey, 2004; Turvey & Carello, 1995, 2011). (b) A schematic of the functions in (a). Adapted with permission from Figure 6 of Shaw (2001).

identity to play an important role in our efforts to draft an answer. The starting point is an examination of life's media (Denny, 1993).

Haptic and auditory perceptual systems share a common basis: each is grounded in mechanical forces, tissue deformation, and mechanosensitivity. The commonality is most obvious in insects. Research has shown that, uniformly, the ears of insects located on legs, wings, or mouths, are organs comprising mechanoreceptors that originated in insect haptic systems (Yager, 1999). The evolutionary physiological relation between insect auditory and insect haptic systems is an intimate one. There are, however, significant divergences. Unlike the many instantiations of auditory systems, the many instantiations of haptic systems have no circumscribed sense organ (no anatomical equivalent to the ear). The organ permeates the whole body. They also have no identified physical medium for the propagation and distribution of mechanical disturbances (no functional equivalent to air or water in respect to conveying sound). Tradition on this matter defers to Aristotle (in *De Anima*; see Polansky, 2007): For animals, flesh is the medium of touch (and not the organ of touch).²

At the ecological scale—the scale of organisms and their environments—air and water are the primary media (Denny, 1993; Gibson, 1979). Their compressibility allows the transmission of sound arising from mechanical events, their transparency allows the transmission of light reflected from surface layouts, and their diffusivity allows the transmission of substances from chemical interactions. Air or water are the

necessary conditions for auditory, visual, olfactory, and gustatory perceptual systems. For an auditory perceptual system immersed in a vibration field, the wave fronts and the invariants of the wave trains are potential information about distal mechanical events (Gibson, 1966, 1979). For any such wave-producing event, a key ecological requirement of a medium is that information about the event be available at any arbitrary location, in any arbitrary direction, and at any arbitrary distance relative to the event within the limits of propagation and the attenuating effects of degree and density of absorbing materials. Continua of water and air fulfill this requirement by virtue of their symmetries. They are homogeneous (their physical properties are place invariant) and isotropic (their physical properties are direction invariant). The foregoing suggests that if a medium is to be defined for haptic perceptual systems, it will have to be in terms of a continuum description of the body that is homogeneous and isotropic. Understanding how such a continuum can be instantiated in the body is not without major challenges. Foremost, perhaps, is the necessary condition that the invariances of place and direction hold for each and every individual haptic system within any given species despite the fact that, by definition, each is different. Individuality is synonymous with uniqueness (no extant duplicates), which means, in the present context, that each individual haptic system differs (e.g., anatomically, biochemically) from all others (cf. Bergman, Afifi, & Miyauchi, 2012; Williams, 1956). A primary challenge to be addressed at some point, therefore, will be to comprehend and articulate the conception of invariance above heterogeneity (Elsasser, 1998), that is, how the haptic medium is functionally the same in each of its indefinitely many instantiations.

Fibroblasts, Extracellular Matrix, and Forms of Connective Tissue

Standard inquiry into the biology of the haptic perceptual system is focused primarily on nerve cells (for simplicity, cells that are best at conducting) and secondarily on muscle cells (for simplicity, cells that are best at contracting). Our inquiry will be more expansive. It will include, and give larger consideration to, connective tissue cells of the fibroblast family (chondroblasts, osteoblasts, and fibroblasts). The speciality of these cells is creating a mechanically supportive and regulatory framework for all other cells (Alberts et al., 2002; Cooper, 1997; Silver, 2006; Silver, DeVore, & Siperko, 2003). This framework is the extracellular matrix (ECM) schematized in Figure 2. In animals it is constituted by two main classes of macromolecules, produced locally and primarily by the fibroblasts within the matrix. One class comprises fibrous proteins (collagen, elastin, fibronectin, and laminin). The other class comprises polysaccharide chains that yield a gel-like substance (ground substance; see Oschman, 1984) that embeds the fibrous proteins. With qualifications (see Silver, 2006; Silver et al., 2003), the gel resists compressive (C) forces and collagen fibrils of fixed

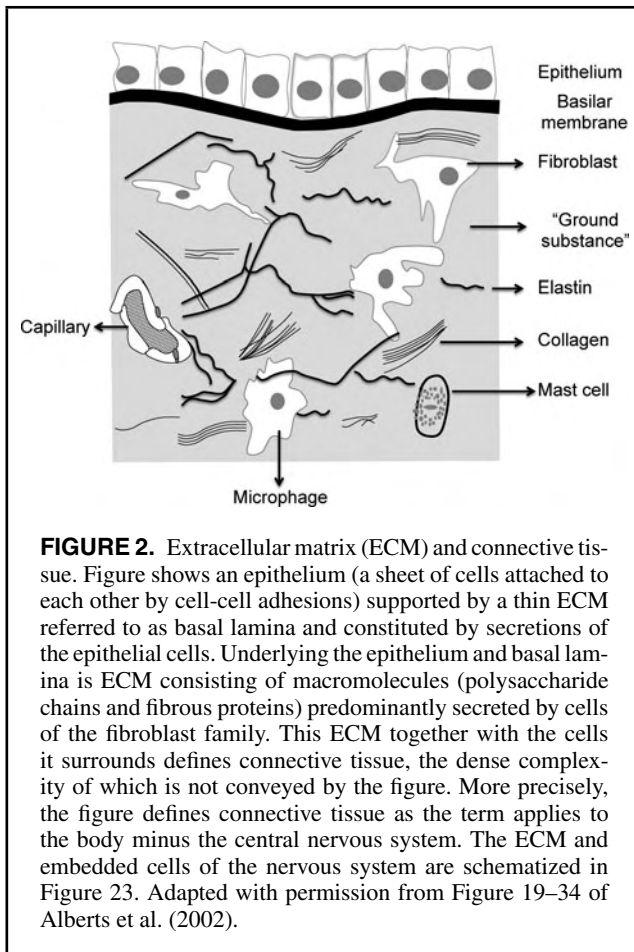


FIGURE 2. Extracellular matrix (ECM) and connective tissue. Figure shows an epithelium (a sheet of cells attached to each other by cell-cell adhesions) supported by a thin ECM referred to as basal lamina and constituted by secretions of the epithelial cells. Underlying the epithelium and basal lamina is ECM consisting of macromolecules (polysaccharide chains and fibrous proteins) predominantly secreted by cells of the fibroblast family. This ECM together with the cells it surrounds defines connective tissue, the dense complexity of which is not conveyed by the figure. More precisely, the figure defines connective tissue as the term applies to the body minus the central nervous system. The ECM and embedded cells of the nervous system are schematized in Figure 23. Adapted with permission from Figure 19–34 of Alberts et al. (2002).

length form structures that resist tensile (T) forces. Elastic fibers give the ECM the resilience needed to recoil after a transient stretch. The extent to which they stretch, however, is limited by interwoven collagen fibrils. Although the gel's weight is less than 10% the weight of the fibers the gel fills most of the ECM space. It is connective tissue's primary mechanical support (Alberts et al., 2002).

A variety of forms of connective tissue follow. In each case the ECM may be identified with the sum total of extracellular substance within the connective tissue (that is, Figure 2 minus the varied cells). In each case the ECM is not a static collection of macromolecules but a dynamical system, continuously responsive to the conditions in its microenvironment (Rutka, Apodaca, Stern, & Rosenblum, 1988). Its components move and deform continuously (Sivakumar et al., 2006). At the aggregate scale of a sheet of connective tissue, indices of structural variation resemble frozen turbulence (Schmitt & Kumar, 1996). These coordinate images of continuous change and frozen turbulence have bearing on the hypothesized haptic medium. In preview, we will eventually come to characterize the medium in terms of a turbulent-like, cascade-like, organization, more changeable at its smaller scales, more invariant at its larger scales.

The kind of connective tissue that typifies most ligaments and tendons (and aponeuroses) is referred to as dense regular connective tissue. This tissue is apparent where functional demands require that tensile loading occur predominantly in one direction or just a few directions. The collagen strands composing the connective tissue are arranged in parallel along the direction of the imposed loads. The multiple other kinds of connective tissue, that which can be termed fascia, are identified in Table 1 (Langevin & Huijing, 2009). Many of them differ from ligaments and tendons primarily in the irregularity (the multidirectionality) of the collagen strands that compose them. In respect to the skin, for example, the dermis that lies beneath the epidermis (the true outer layer of skin) is irregular, moderately dense connective tissue. Pre-saging upcoming themes, the receptive elements of the skin are largely housed in the dermis (Shepherd, 1988). Free nerve endings permeate the middle dermis. Pacinian corpuscles lie deep in the dermis. Meissner corpuscles, Merkel's discs, and Ruffini endings reside in the dermis-epidermis junction.

The major concern motivating Table 1 should be noted:

We do not recommend that the term "fascia" be given such a wide meaning that it also includes all tendons and ligaments, for that is simply acknowledging that tendons and ligaments are forms of connective tissue and equates "fascia" with connective tissue in general. (Langevin & Huijing, 2009, p. 7)

The potential uniting function of connective tissue, especially fascia, should be emphasized given our current goals. Connective tissue binds muscle fibers to muscle fibers, muscles to muscles, and muscles to bones (Kjaer, 2004). Connective tissue binds every cell in the body to its neighbors and, arguably, the internal mechanics of each cell to the mechanical state of the body as a whole (Ingber, 2006; Silver, 2006).

Returning to the desired continuum, the base requirement is met by the supportive structure of connective tissue but only crudely. The problem in large part is that a characterization in terms of the compositions of connective cells and ECM is too detailed and at too low a level of abstraction for revealing how this continuum might satisfy the signature media properties of homogeneous and isotropic. A relatively macroscopic functional characterization is needed. Significant help in this respect is provided by the previously noted extensive inquiry into the mechanosensitivity of individual cells, to which we now turn. Prior to doing so, however, we underscore that—for purposes of developing the biological basis of haptic perception—focusing on the nervous system will not suffice. Nerves and connective tissue must be considered jointly, on equal theoretical footing. Myers (2001) suggested the terminology neural net and fascia net. With regard to the latter, the designations ECM, collagenous, and connective tissue are suggested as potential (but not fully equivalent) substitutes for fascia. Abiding Langevin and Huijing's (2009) concern, we preserve the term *fascia* for the forms of connective tissue identified in Table 1 and use connective tissue as the umbrella term for ligaments, tendons, cartilage,

TABLE 1. Recommended Use of Terms Regarding Fascial Structures

Dense connective tissue	Connective tissue containing closely packed, irregularly arranged (i.e., aligned in many directions) collagen fibers.
Nondense (areolar) connective tissue	Connective tissue containing sparse, irregularly arranged collagen fibers.
Superficial fascia	Enveloping layer directly beneath the skin containing dense and areolar connective tissue and fat.
Deep fascia	Continuous sheet of mostly dense, irregularly arranged connective tissue that limits the changes in shape of underlying tissues. Deep fasciae may be continuous with epimysium and intermuscular septa and may also contain layers of areolar connective tissue.
Endomysium	Fine network of irregularly arranged collagen fibers that form a tube enveloping and connecting each muscle fiber. Adjacent muscle fibers share a wall of the tube (similar to the cells of a honeycomb).
Perimysium	A dense multi-layered, irregularly arranged collagen fiber sheet that envelopes muscle fascicles. Adjacent fascicles share a wall of the tube (similar to the cells of a honeycomb).
Epimysium	A multilayered, irregularly arranged collagen fiber sheet that envelops muscles and that may contain layers of both dense and areolar connective tissue.
Intermuscular septa	A thin layer of closely packed bundles of collagen fibers, possibly with several preferential directions predominating, arranged in various layers. The septa separate different, usually antagonistic, muscles groups (for example, flexors and extensors), but may not limit force transmission.
Intra- and extramuscular aponeurosis	A multilayered structure with densely laid down bundles of collagen with major preferential directions. The epimysium also covers the aponeuroses, but is not attached to them. Muscle fibers are attached to intramuscular aponeuroses by their myotendinous junctions.
Neurovascular tract	The extramuscular collagen fiber reinforcement of blood and lymph vessels and nerves. This complex structure can be quite stiff. The diameter and, presumably, the stiffness of neurovascular tracts decrease along limbs from proximal to distal parts. Their stiffness is related to the angle or angles of the joints that they cross.
Periost	Surrounding each bone and attached to it is a bilayered collagen membrane similar in structure to the epimysium.
Interosseal membrane	Two bones in a limb segment can be connected by a thin collagen membrane with a structure similar to the intermuscular septa.

Note. Adapted with permission of Langevin and Huijing (2009).

and fascia. The benefit of doing so is that we can approach the nonmuscular aspect of the haptic perceptual system as the mesh of the nonmuscular neural net and the connective tissue net (for brevity, the connective net). We can define our immediate goal as that of determining whether, and in what sense, the connective net can be understood as homogeneous and isotropic.

Functional Characterization of Connective Tissue: Insights From the Cell

By cell in the discussions and research summaries that follow, we mean mammalian cell and, in most cases, of a connective tissue type, usually fibroblast. Our calling on the cell for insight into the desired functional characterization of connective tissue proceeds in two steps. In the first step we

identify phenomena at the level of cell and ECM that demonstrate the cellular capability to sense, and to respond adaptively to, mechanical forces. In the second step we identify a theoretical abstraction from these phenomena—the notion of tensegrity architecture—that promises the homogeneity and isotropy required of the sought after medium for haptic perception.

Step 1: Cell Mechanosensitivity (or the Cell as a Minimal Haptic Perceptual System)

Cells adhere to the ECM via integrins (proteins so named because they integrate the cell’s function with the ECM) and, in general, are not viable in the absence of being an attachable-to solid (whether soft or rigid). It should be underscored that the individual cell is not attached to the ECM

uniformly, all of apiece, but locally, here and there. It has points of adhesion, so called focal adhesions. This fact bears significantly on the understanding of cell shape, cell architecture, and cell behavior.

Given focal adhesions to a substrate, individual cells exhibit controlled motility. The canonical case is the directed cell migration that is a leading determinant of tissue morphology (e.g., migration of neural cells during the formation of the embryonic nervous system). The motility subserving migration—a kind of locomotion by crawling (Abercrombie, 1980; Stossel, 1993)—involves a coordinated cycle of 3–5 events (depending on the study). Here is a four-event version. First, forming lamellipodia and filopodia, actin-rich membrane processes that extend outward from the cell's leading edge. Second, forming attachments of these extensions to the substrate. Third, developing traction at the attachment points. Fourth, dissociating the trailing edge from the substrate and retracting it into the cell body (Cooper, 1997; Lauffenburger & Horwitz, 1996).

Central to all aspects of the cell's locomotion cycle is a network of protein filaments, the cytoskeleton (CSK). It provides a structural framework for the cell, determining the cell's shape and the general organization of the cell's cytoplasm (Alberts et al., 2002; Cooper, 1997). Arguably, the structure of CSK is entailed by the aforementioned fact that cells are not glued evenly to ECM but unevenly by spot weld-like attachments (Chen & Ingber, 1999). The CSK structure enables a concerted cell response to these ever-changing local sources of tension. When the details of CSK dynamics and ECM's involvement are spelled out, the number of distinguishable events comprising one cycle of crawling is 12 (see Ingber, 1993).

In exhibiting directionally controlled crawling a cell expresses forms of mechanosensitivity that are analogues of the exteroceptive and proprioceptive capabilities exhibited by the kingdom Animalia (Margulis & Schwartz, 1982/1998). These capabilities are manifest as a forceful probing—alias dynamic (effortful) touching (see Turvey & Carello, 1995, 2011)—of the substrate by means of the lamellipodia and filopodia. In approximate terms, and in respect to the substrate's ability to support the cell's locomotion, the probing can be said to comprise (a) anchoring to and pulling on the substrate and (b) organizational changes in CSK in response to the detected rigidity (stiffness) of the substrate (e.g., Discher, Janmey, & Wang, 2005). Enacting (a) amplifies tension at the adhesion points. Effecting (b) cannot be once only. CSK must, presumably, reconfigure per each repetition of (a) so as to render detectable what is not changing with each probe, and what is not dependent on its own current configuration. We assume that cell locomotion, paralleling animal locomotion, can be reliably successful only if perception ensures contact with the facts of ECM, facts of the cell ecology (e.g., Michaels & Carello, 1981; Turvey, 2013; Turvey & Carello, 2011; Turvey, Shaw, Reed, & Mace, 1981). Registering one substrate's ability to support locomotion as better than another substrate's ability requires de-

tecting substrate stiffness as an invariant measure over the variations in tension at the focal (integrin) attachments to the substrate and over the variations in CSK organization (cf. Lo, Wang, Dembo, & Wang, 2000). This variation to reveal nonvariation is, seemingly, the *modus operandi* of the dynamic (effortful) touch subsystem of the human haptic perceptual system (Carello & Turvey, 2000; Turvey & Carello, 1995, 2011), albeit at a different scale. If such an instance of functionally specific variability were not the case in cell locomotion then, as Pelham and Wang (1997) remarked, “cells will simply deform soft substrates to an increasing extent until they experience a similar resistance as on stiff substrates” (p. 13655).

Selectivity with respect to surface rigidity deserves much further comment.³ Given a substrate so divided as to have a sharp border between two levels of stiffness (say, firm and soft), a cell approaching the transition from the soft side proceeds readily to the firm side, with an increase in traction forces and in body area, and with the lamellipodia that initiated the firm contact assuming the leading haptic role. In contrast, approaching from the firm side is marked by arresting forward crawling and either (a) rotating so as to crawl parallel to the transition, or (b) retracting the contacting lamellipodia (Lo et al., 2000). The general relevance of this apparent preference for stiffer substrates has been revealed through the use of surfaces composed of a dense array of flexible micro-fabricated posts (Ghibaudo et al., 2008). Varying post height across surfaces (with fixed within-surface post height) introduces variation in global surface resistance to deformation by traction forces. Further, composing surfaces with posts that are either all elliptical or all circular in cross section introduces a contrast between global anisotropic stiffness (when elliptical) and global isotropic stiffness (when circular). The height manipulation reveals a systematic increase in traction forces with rigidity up to a plateau, perhaps indicative of a CSK tendency to keep substrate deformation constant (Ghibaudo et al., 2008). The cross-section manipulation reveals directional crawling when substrate stiffness is anisotropic versus random-like crawling when substrate stiffness is isotropic, perhaps indicative of a general tendency for migration paths to be oriented in the stiffest direction, implying a correlation of direction with maximal traction forces. An observed correlate of direction was actin polarization in the CSK (Ghibaudo et al., 2008). It is notable that in the few studies conducted to date in three-dimensional ECM, migration is found to be more persistent in direction than would be observed in two-dimensional ECM where spontaneous direction changes are not uncommon (Even-Ram & Yamada, 2005). It is also notable that these 3D ECM studies, absent the dorsal-ventral polarization induced in 2D ECM, reveal focal adhesions over the entire cell body (Even-Ram & Yamada, 2005). Despite the different CSK organizations entailed by the latter fact, the indications are that CSK's contribution to contractility and ECM reorganization in 3D is the same as in 2D (Kraning-Rush, Carey, Califano, Smith, & Reinhart-King, 2011).

Cell locomotion benefits not only from an ability to register the stiffness of substrata (natural or cultured ECM) but also from an ability to register the spatial properties of substrata (for a review, see Dalby, 2005). Certain spatial arrangements seemingly support adhesion configurations, and hence probing and locomotion opportunities, better than others (e.g., Charest, Eliason, Garcia, & King, 2006; Curtis & Wilkinson, 1997). Weiss (1945, 1958) conducted the original inquiry into such matters, labeling the phenomena contact guidance (also known as topological guidance). He observed that cells prefer to crawl on fibers and grooves. The question has become in current form: Why should the substrate difference of grooved versus planar give rise to large differences in cell behavior?

The guidance envisioned by Weiss includes the possibility that certain spatial arrangements detectable by cells might be indicative of nearby regions that are more supportive of directional crawling than others, regions that invite preferential probing. Individual cells can be cultured on substrates constituted by ECM adhesion molecules. The substrates are ECM islands. Each is surrounded by a surface to which cells cannot adhere. Brock, Chang, Ho, LeDuc, Jiang, Whitesides and Ingber (2003) examined the effects of equal-area ECM islands that differed in aspect ratio and geometric shape (square, triangle, pentagon, hexagon, trapezoid, various parallelograms). Through the configuration of their focal (local points of) adhesion, the cells assumed the shape permitted by the specific geometry and specific aspect ratio of the substrate. A significant observation was that for each ECM-island form the cells probed the island's corners more so than its noncorners. The disproportionate growth of new lamellipodia and new fibrils toward (and confined within) the corners suggest a mechanosensitivity to edges (Brock et al., 2003) or, more broadly, to discontinuities (Curtis, 2004). Discontinuities in ECM would have bearing on the orientation of cell migration. How might a cell be informed about the presence and direction of structural discontinuities in ECM? A possible answer is implicit in arguments of Parker et al. (2002), namely, that discontinuities and their directions are specified by the cell deformation pattern induced by the tractional forces arising from the cell's focal adhesions to, and modulation of, ECM.

A final point is that ECM mechanics can foster tissue formation by altering the relative motion between cells, promoting the formation of cell-cell contacts. Cells seemingly have the ability to interrelate mechanically through the ECM (Reinhart-King, Dembo, & Hammer, 2008). That this ability may have large-scale (whole body) implications is suggested by observations that fibroblasts form a cellular network, with extensive interconnection of their cytoplasmic processes (Langevin, Cornbrooks, & Taatjes, 2004).

This summary of the haptic capabilities manifest at the cellular level is not exhaustive. It is sufficient, however, to motivate the question of the basis for a cell's mechanically based ability to relate adaptively to its surroundings, to which we can now turn.

Step 2: Cell Architecture (or the Cell as an Exemplary Tensegrity System)

In Step 1 we provided a number of examples of the specificity of cell behavior to cell deformation in the context of locomotion. In part, its purpose was to highlight the parallels between cell mechanosensitivity and the Animalia haptic subsystem of dynamic (effortful) touch. In Step 2 we need to highlight parallels between the organization of CSK when anchored to the ECM and a particular kind of architecture known as tensegrity (a contraction of tension and integrity; Fuller, 1975).

The CSK is (a) a molecular framework, composed of interconnected microfilaments (also known as actin filaments), microtubules, and intermediate filaments within ground substance (Alberts et al., 2002; Cooper, 1997), and (b) a system that is generative of, and resistant to, forces. Arguably, (a) is entailed by the fact of local rather than global adhesion and the consequent need for unifying forces of different origin in the cytoplasm (Chen & Ingber, 1999). Feature (a) ensures that forces applied locally to the cell are distributed globally across the cell. In seeking a mechanical understanding of CSK—an understanding that would speak to phenomena of the kind surveyed in Step 1—Ingber initiated the conceptual integration of (a), (b) and tensegrity system (Ingber, 1993; Ingber & Jamieson, 1982, 1985; Ingber, Madri, & Jamieson, 1981, 1985).

We can introduce the concept of tensegrity in the manner of Skelton and de Oliveira (2009), using Figure 3 and beginning with the definition of a tensegrity configuration of rigid bodies.

In the absence of external forces, let a set of rigid bodies in a specific configuration have torqueless connections (e.g., via frictionless ball-joints). Then this configuration forms a tensegrity configuration if the given configuration can be stabilized by some set of internal tensile members, i.e., connected between the rigid bodies. The configuration is not a tensegrity configuration if no tensile members are required and/or no set of tensile members exist to stabilize the configuration.

Figure 3b is a tensegrity configuration. Figure 3a is not a tensegrity configuration. Whereas the parts in Figure 3a cannot be stabilized by any set of tensile components (e.g.,

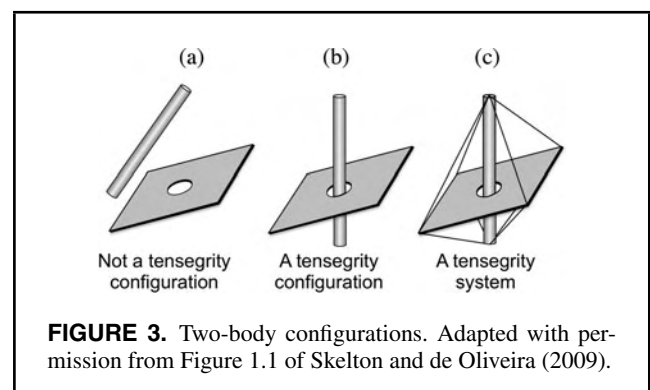


FIGURE 3. Two-body configurations. Adapted with permission from Figure 1.1 of Skelton and de Oliveira (2009).

strings) as the providers of internal forces, the same parts in Figure 3b could be (as Figure 3c shows). Thus, the definition of tensegrity configuration depends only on the existence of a set of tensile members of constant length that could stabilize the configuration in the absence of external forces (Skelton & de Oliveira, 2009).

Figure 3c is a stable embodiment of the tensegrity configuration in 3b. It is a tensegrity system defined by Skelton and de Oliveira (2009) as follows: A tensegrity system is composed of any given set of strings connected to a tensegrity configuration of rigid bodies.

The foregoing is consonant with how Snelson (n.d.; www.kennethsnelson.net/faqs/faq.htm) chose to describe his originally termed floating compression:

... a closed structural system composed of a set of three or more elongate compression struts within a network of tension tendons. The combined parts are mutually supportive in such a way that the struts do not touch one another, but press outwardly against nodal points in the tension network to form a firm, triangulated, prestressed, tension and compression unit.

It remains to define a tensegrity system's stability and, thereby, the central notion of prestress identified in the prior quotation. Skelton and de Oliveira (2009) did so in terms of the null solution, that is, the solution closest to the specified configuration.

The null solution of a tensegrity system (specified by a given tensegrity configuration, a given string connectivity, and a given set of external forces) is a stable equilibrium if the structure returns to the original configuration after the application of arbitrarily small perturbations anywhere within the configuration. (p. 2)

Given the obvious practical value of a singular characterization of a topic of inquiry, we introduce the carefully worded definition of tensegrity system advanced by (Motro, 2003):

A tensegrity system is a system in a stable self-equilibrated state comprising a discontinuous set of compressed components inside a continuum of tensioned components. (p. 19)

The rationale for the word choices of system, self-equilibrium, stable, components, compressed, tensioned, discontinuous set, continuum, and inside is spelled out by Motro over several pages.

An immediately intuited benefit of tensegrity as a form of stable system architecture is its potential economy with respect to mass (roughly, fewer heavy compression-bearing materials) and, relatedly, its high strength to weight ratio. Further, a tensegrity system exhibits nonlinear increases in stiffness (strain hardening) when subject to stresses, with relatively big stiffness changes for relatively small displacements—properties that follow from its geodesic and triangular organization (Fest, Shea, Domer, & Smith, 2003;

Oppenheim & Williams, 2000). Of larger significance for our present purposes, however, is a less obvious intuition, namely, that nature is inclined toward tensegrity whenever large controllable changes in a system's configuration are needed (Skelton & de Oliveira, 2009). Exemplary instances of such a need are cellular behavior and animal behavior.⁴

In promoting the hypothesis that the cell (e.g., a mammalian fibroblast) is a tensegrity system, the initial charge is to identify candidates for what would function as the strings and the rigid bodies (synonymously, cables and struts) and to identify the conditions of cell and ECM that would prestress the assemblage of these candidates.

The Cables and Struts

At the core of Ingber's tensegrity conceptualization of the cell is the identification of CSK microfilaments as a continuous network of tension resisting (actin microfilaments) and tension generating (actomyosin microfilaments) structures (e.g., Ingber, 1993, 2003a, 2003b, 2006). The proposal is favored by the following observations. First, actin microfilaments are frequently organized in stiff bundles that can act as mechanical guides for stress propagation within the cell. Second, actomyosin microfilaments generate active contractile forces that are continuously transmitted to the whole cell. Third, intermediate filaments, such as the microfilaments, can function as tension guide-wires that act to stabilize the cell. The intermediate filaments are connected to cell-cell and cell-ECM sites, as well as to other CSK structures, to form a system that strengthens the entire internal structural network. Fourth, microtubules play a compressive load-bearing function. Wang and Suo (2005) and Wang, Tytell, and Ingber (2009) suggested that microtubules, stiffened by intermediate filaments together with actin bundles, function as an integrated mechanical unit that serves to propagate forces within the cell and over long distances.

The Origin of Prestress

Following Skelton and de Oliveira's (2009) definition, a cell's prestress is a function of its tensegrity configuration, its string connectivity, and the external forces. In Ingber's cell-as-tensegrity system, the parts comprising the tensegrity configuration in Figure 3b are stiffened microtubules, the string connectivity of Figure 3c is supplied by actomyosin microfilaments and intermediate filaments, and the external forces are those arising from the attachments to ECM. An expression of the latter feature, however, is absent from Figure 3c. Another image of similar simplicity is required—the camping tent. In Figure 4, the focal adhesions to the ECM have their analogues in the tent's external tethers (to the ground). Patently, the tent will not stabilize in a tent-like form in the absence of the tethers, just as the cell will not stabilize in a cell-like form in the absence of its ECM adhesions.⁵

The internal tent poles in Figure 4 are the analogues of the stiffened microtubules. The figure makes apparent the complementary load-bearing functions of the tethers

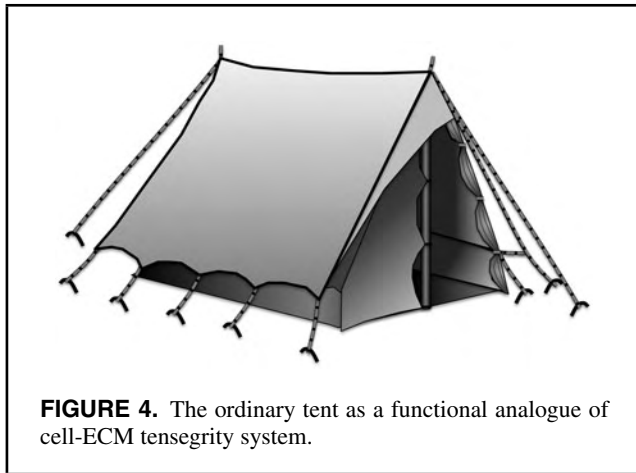


FIGURE 4. The ordinary tent as a functional analogue of cell-ECM tensegrity system.

and poles: they both resist the inward-directed forces exerted by the tent membrane, the analogue of the actomyosin microfilaments and intermediate filaments. In its simplicity, Figure 4 gives full expression of the central notion that prestress is the unifying principle behind cell shape stability. Mirroring Ingber (2003a), stabilization of the tent's (cell's) form is through a mechanical force balance in which the tent poles (CSK struts) and tethers (focal adhesions to ECM) resist and balance the pull of the tent's (cell's) contractile membrane (CSK), thereby placing the entire network in a tensionally prestressed state of isometric tension.

Tensegrity's Other Format

Of considerable significance to theory development in respect to the haptic perceptual system are the following: (a) What is essential to shape stabilization is continuous transmission of tensional forces (isolated cables and struts are one way to satisfy this requirement); and (b) the specifics of the components, for example, their material properties and individual shapes, though important, are less important than how the components are organized. Geodesic structures exemplify both.

Geodesic structures are an alternative realization of (a) (Ingber, Bojanowski, Chen, Huang, & Maniotis, 1996; Levin, 2002). Their components are stiff struts that (1) can resist either tension or compression as loading conditions demand, and (2) do not need to be in direct contact with each other (e.g., they can be pin-connected). This form of tensegrity without strings constrains movement geometrically by means of fully triangulated struts oriented along minimal paths (geodesics). Geodesic tensegrity and prestressed tensegrity contrast in respect to flexibility and stiffness (Chen & Ingber, 1999). Prestressed is preferable when flexibility is the performance criterion. Geodesic organization is preferable when stiffness is the performance criterion. Despite the connection between stiffness and prestress (Wang et al., 2001), amplifying prestress is not the most effective means for sustaining stability (Canadas, Laurent, Oddou, Isabey, & Wendling, 2002). Adjusting the spatial relations among com-

ponents is a better means, and more economical (see also Skelton & de Oliveira, 2009). A noteworthy observation is that a tensegrity system, in which struts are connected into triangles, pentagons, and hexagons, has the potential to exhibit disproportionately large stiffness increases for relatively small displacements (cf. Oppenheim & Williams, 2000).

Empirical evidence suggests that geodesic tensegrities are integral to CSK in the form of actin geodesic domes, referred to, alternatively, as polygonal actin nets and geodomes (e.g., Entcheva & Bien, 2009; Heuser & Kirschner, 1980; Lazarides, 1976; Mochizuki, Furukawa, Mitaka, Yokoi, & Kodama, 1988; Rafferty & Scholz, 1985). The existence of these distinct and highly organized CSK microarchitectures in a large variety of cell types suggests a universal CSK property—one that is sensitive to ECM topography and, perhaps, CSK's tensioned state (Entcheva & Bien, 2009)

A Nesting of Tensegrity Systems and a Generalized Thermodynamic View

Figure 5 is a tensegrity model of the deformation of the cell induced by ECM deformation. It shows the CSK deforming and—more importantly for our immediate purposes—it shows the nucleus deforming, in parallel. This tensegrity model casts the cell as two tensegrity systems, that of the CSK tethered to the ECM and that of the nucleus tethered to and nested in the CSK tensegrity system. For Pienta and Coffey (1991), Figure 5 exemplifies the nature of what they termed generically the tissue tensegrity matrix. ECM is contiguous with intermediate filaments of CSK, which in turn are contiguous with the nuclear matrix. These three components interact to form the tissue matrix system—the dynamical system that coordinates cell function.

The conceptual inspiration for Figure 5 is Fuller's notion of tensegrity systems as structural hierarchies (Fuller, 1961). A tensioned or compressed component of a tensegrity system at one level is itself a tensegrity system at the level below, constituted by tensioned (T) and compressed (C) components. In the larger structure of Figure 5—specifically, the cell-ECM system—the nucleus is a tensioned component. It is shown as a tensegrity system. This extended architectural feature is not limited to the cell. It applies, ex hypothesi, to all scales of an organism, both above and below the cellular scale (Ingber, 2003b). Figure 6 shows a cascade of tensegrity systems (indexed by C and T) from the knee joint to contractile microfilaments and microtubules of a CSK and local regions of ECM.

Figure 6 can do valuable work for us. It contrasts two images. One image is of scale-dependent morphological descriptions requiring scale-dependent (special) lines of scientific inquiry. The other image is of a scale-independent functional description requiring a scale-independent (general) line of scientific inquiry. Emphasis on the first image encourages an orthodox form of physics, one in which reductionism is to entities (e.g., molecules). Emphasis on the second image encourages a heterodox form of physics, one

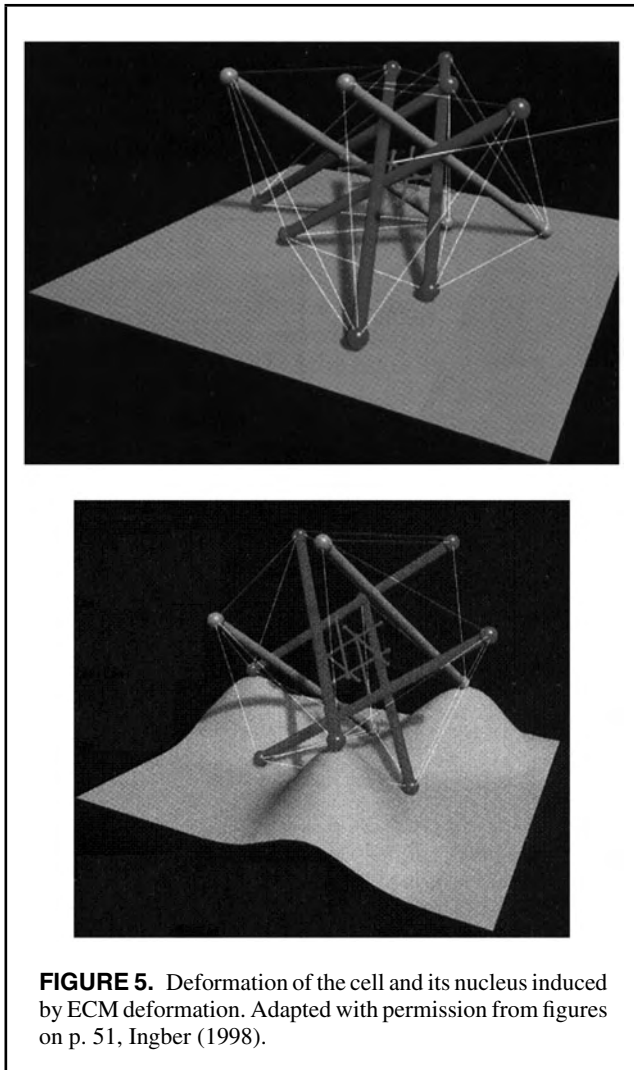


FIGURE 5. Deformation of the cell and its nucleus induced by ECM deformation. Adapted with permission from figures on p. 51, Ingber (1998).

in which reductionism is to principles. The latter emphasis, we contend, is needed for the theory of the haptic medium as homogeneous and isotropic.

Fuller's (1961) thesis of a scale-invariant architecture can be wedded to Iberall's (Iberall, 1977, 1978) thesis of a scale-invariant thermodynamics. The wedding is scientifically commendable. The conception of nested tensegrity systems requires a corresponding conception of nested thermodynamics for its fulfillment. Indeed, the foundational argument for biological tensegrity systems suffers to the extent that the concept is equated with well-defined deterministic structures advanced in engineering and mathematics (Shen & Wolynes, 2005). Nonequilibrium (irreversible) thermodynamics is the physics of systems (Kondepudi & Prigogine, 1998).

The departure point for Iberall and colleagues (e.g., Iberall, 1977, 1978; Soodak & Iberall, 1978, 1987; Yates, 2008) is the causal linkage between architecture (or structure) and process. Process is guided and constrained by architecture (as repeatedly argued in biological tensegrity theory), and archi-

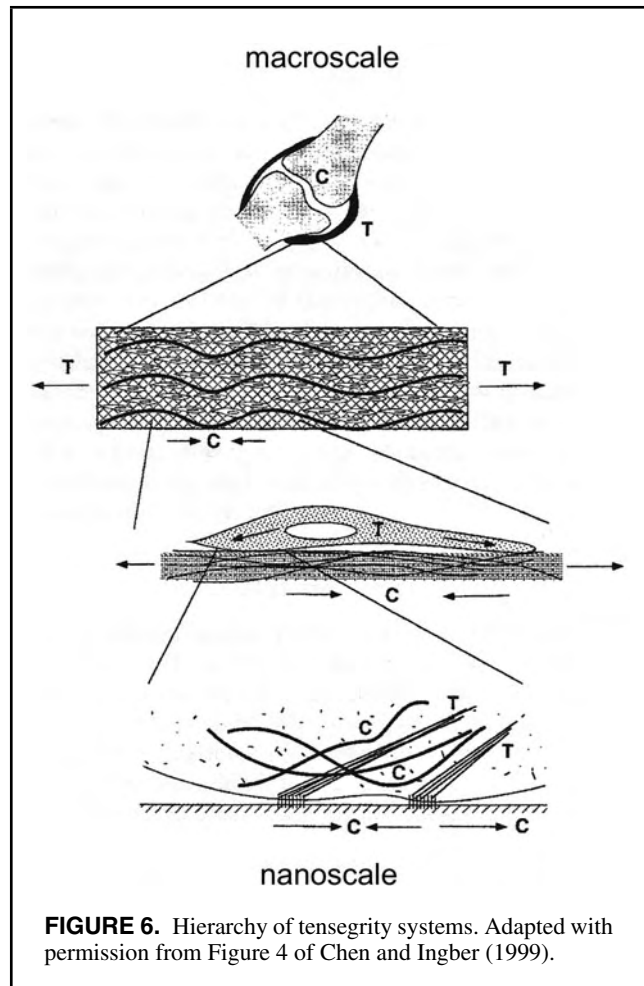


FIGURE 6. Hierarchy of tensegrity systems. Adapted with permission from Figure 4 of Chen and Ingber (1999).

ture is laid down, maintained, changed, and degraded by process (as often implied in biological tensegrity theory). At its base, the generalized thermodynamic view is nonequilibrium, irreversible thermodynamics applicable to near equilibrium conditions, those in which thermostatic description holds locally. A succinct but thorough summary of the view follows (Soodak & Iberall, 1987, pp. 460–461). It can be read with an eye to the cascade of macroscopic systems indexed by C and T in Figure 6 and their microscopic underpinnings.

At each level stereotypic activities within the individual atomistic units and among units as they interact in small numbers, determine the dynamic behavior of a system formed from many units. The kinetic behavior is described in terms of the microscopic coordinates of the units. The macroscopic behavior of the system is governed by laws representable as a continuum or field equations in terms of macroscopic coordinates, which are integrals or averages over appropriate microscopic quantities. These macroscopic coordinates and their interrelations are to be regarded in a dual fashion: they are emergent properties, arising from the kinetic behavior; and they represent set measures or constraints on the kinetic behavior. Thus the micro and macro levels are mutually linked. The kinetics at the micro-level determines the continuum field mechanics and is the source of internal macroscopic

fluctuations. In turn, that kinetics is constrained by the macrostate. Finally, the behavior of the macrosystem, as described by its field equations, is constrained by boundary conditions from outside the system. These outside constraints (which may be fixed or variable) often originate from a higher level system of which the macroscopic system is itself simply one of the atomistic units.

We therefore regard thermodynamics as addressing systems at any level, including their relation to the levels immediately below and above them.

In Figure 6, the most important property of the tensegrity system at each depicted scale is prestress, emergent from the mutualism of inter-component interactions and summarized by C and T. At each scale C and T must be generated by nonequilibrium thermodynamics. Shen and Wolynes (2005) gave a preliminary example of the possible thermodynamics of prestress assembly at the scale of the cell, where C and T involve polymerizations and movements of motor proteins. Across the scales of Figure 6, the components comprising C and T differ but the thermodynamic means of prestress assembly are likely to be the same.

The major goal of the present section has been to establish reasonable grounds for interpreting the body, in particular, the connective net, as a homogeneous, isotropic medium. If, as argued, the body in all of its parts, at all of its scales, is constituted by the same kind of system under a common scale-independent thermodynamics, then the grounds for the interpretation can be considered reasonable. The next steps to be taken are steps toward affirming that the architecture of Bernstein's (1996) level of synergies, the level of musculoarticular links, is that of tensegrity. Affirmation is needed because it is at this level that animal haptic perception plays its most substantive role.

Concerted Response of Tensegrity Architecture

A frequently expressed intuition about the tensegrity architecture of cells is that it ensures a concerted response in the face of the many multifarious degrees of freedom that comprise cell dynamics. To do so it must provide the apposite degrees of constraint, in form and number. It is a good biological model for Bernstein's level of synergies.

Dictionary definitions of *concerted* are mutually contrived, planned, or arranged. A close semantic relative of concerted response is concinnity, a harmonious arrangement of parts, the adaptive fit of parts of a system to each other and to the system as a whole. Implicit in these definitions is (a) self-organization and self-integration and (b) a special relation between degrees of freedom and degrees of constraint. Arguably, in the abstract, the latter must relate as duals, for example, as an octohedron (degrees of freedom) embedded in a cube (degrees of constraint) as depicted in Figure 7. Every symmetry of the cube is a symmetry of the octohedron. And by further argument, again in the abstract, the degrees of freedom of cell-as-tensegrity and the degrees of constraint of cell-as-tensegrity should relate continuously, not as a cycle of

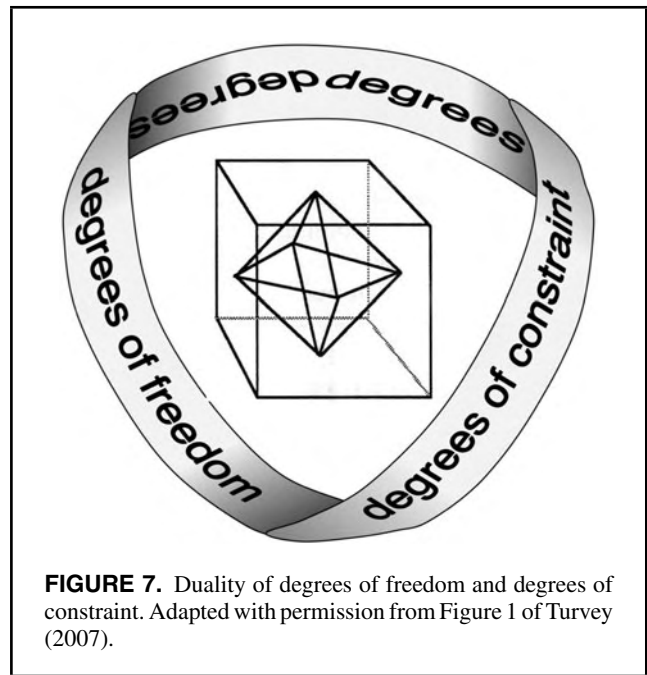


FIGURE 7. Duality of degrees of freedom and degrees of constraint. Adapted with permission from Figure 1 of Turvey (2007).

separate events, but as the functional equivalent of a Möbius band, as depicted in Figure 7. Prestress seems to demand that it be so. The abstractions in Figure 7 have been advanced as a necessary perspective on the degrees of freedom problem that is central to movement science (Turvey, 2007).

On Natural and Artifactual Construction

A brief contrast, between things constructed by humans and things constructed by nature (i.e., the dynamics of evolution), makes transparent the challenges of simulating the concerted response of biological tensegrity. The human style of construction is fashioning components that are then assembled into a system without firm comprehension of the assembly rules for producing an efficient system with a prescribed set of functional capabilities. Nature's systems arise through general physical principles that generate materials and topologies that are optimal in respect to function (cf. Skelton & de Oliveira, 2009). Whereas law constrains natural constructions (e.g., Bejan, 2000, 2005; Denton, Dearden, & Sowerby, 2003), educated reason constrains human constructions.

For the engineer and roboticist, finding the right prestressed tensegrity system is a form-finding problem (Motro, 2003; Paul, Lipson, & Cuevas, 2005). It entails minimally determining (a) a connectivity pattern that will enable a stable form to exist and (b) the lengths of the compressed and tensioned elements for a given connectivity pattern that will result in a stable form. The methods at hand include heuristic guidelines, hierarchical design based on known components, mathematical methods directed at a subset of the tensegrity space, and evolutionary algorithms constrained by choice of a fitness criterion (see Connelly & Back, 1998; Motro, 2003;

Paul et al., 2005; Rieffel, Valero-Cuevas, & Lipson, 2010; Tibert & Pellegrino, 2003).

Adjustive-Receptive Architecture: A Lesson From the Mammalian Auditory System

The cochlear dynamics of mammalian ears exhibits an exemplary concerted response, one that is grounded in the connective net. Cochlear dynamics interface acoustic wave fronts and wave trains with spatially and temporally patterned neural activity. These dynamics are not those of a simple (passive) frequency analyzer, as once thought, but of a nonlinear filter in which the responsiveness of the primary receptive elements (inner hair cells) is modified by forces generated by motile elements (outer hair cells) of the basilar membrane (e.g., Corey et al., 2004; Nobili, Mammano, & Ashmore, 1998). The system exhibits its own kind of tonus, in that eardrum and middle ear are stabilized by muscle-like microcomponents that place them under isometric tension, rendering them responsive to mechanical stress with minimal delay.

Simply put, the registering of sound at the level of the cochlea is not an achievement of receptors. Rather it is an achievement of an architectural organization that includes specialized connective tissues, notably basilar and tectorial membranes, and motoric modes of tensing, notably the stapedius and tensor tympani (Ingber, 2006). The receptors, the inner hair cells, are themselves functionally defined through their highly particular connective tissues, notably tip-links, and the motoric modes of tensing them, most significantly the motor that lowers or raises the upper attachment of a tip-link along a hair thereby changing its stiffness (Pickles & Corey, 1992). The registering of sound at the level of the cochlea is an achievement of receptive components and adjustive components.

This cursory examination of cochlear dynamics makes explicit a conception that was only implicit in our examination of the cell. It is the functional conception of a responsive architecture constituted by components of reception and components of adjustment. In his pioneering work *The Senses Considered as Perceptual Systems*, Gibson (1966) referred to such a responsive architecture as an organ of sensitivity and suggested how the hierarchy arising from the nesting of smaller within larger organs of sensitivity constitutes a system of sensitivity. Gibson emphasized that the adjustive and receptive aspects of an organ of sensitivity need not be in the same place. The cochlear architecture provides microscale examples of the separation. At the macroscale, whereas the receptive part of the olfactory organ, the nose, is deep in the facial bones, the adjustive part is in the chest muscles and manifest as acts of sniffing and breathing (Gibson, 1966). Returning to Figure 6, we should now suppose that at each depicted scale, from nano to macro, C and T comprise adjustive-receptive architectures in the preceding sense.⁶

By way of a reprise, we note that in the textbook theory of proprioception the emphasis has been on the nervous

system, with a persistent emphasis on local signs and linear signaling pathways (law of isolated conduction; Helmholtz, 1868/1968). In the textbook theory, the morphology of the body, its architecture, is notable by its absence. The basic lesson taught by the mammalian ECM, the mammalian cell and the mammalian auditory system is that understanding the mammalian haptic system will entail a detailed appreciation of its mechanosensitive architecture.

The Flow of Muscular Force

The musculoskeletal system is regarded conventionally as a mechanical linkage of bones achieved through joints and adjusted by the action of specific muscle groups. Bones are viewed as compression support structures, muscles as force-generating actuators, and joints as bone-bone relations fixed by connective tissue (ligaments and capsules), and by the muscles and fascia that go across them. On the understanding that the ligaments, capsules and muscles have definite origin and insertion points related to their major attachments in the bones, connective tissue associated with a joint is considered as independent of (a) the muscles that cross it and (b) the connective tissues associated with other joints. In overview, bones are global compressive supporting structures that are helped locally by the tensile support of tendons, ligaments, capsules, fascia and muscles. Expressed differently, the musculoskeletal system, on the conventional view, is a system that sustains global continuous compression and local discontinuous tension. In what follows, we present evidence and argument contrary to the conventional view.

A common assumption about muscles parallels that about nerves, specifically, that they are functionally independent of the connective tissue that embeds them. We argued previously that understanding the biology of haptic perception cannot come from a focus on nerves alone. Nerves and connective tissue must be considered jointly, on equal theoretical footing. Here we will argue, in similar vein, that understanding the biology of movement cannot come from a focus on muscles and nerves alone. Muscles, nerves and connective tissue must be considered jointly, on equal theoretical footing.

Derivative of the muscles-and-nerves-alone perspective are two assumptions: (a) that muscles function independently of each other and (b) that for any given muscle, all of its force is transmitted via its tendon to the bone (see Figure 8, upper panel). These assumptions change when the analyses are fully inclusive of the connective net (Huijing, 2003). To be fully inclusive is to recognize explicitly the content of Table 1: that fascia encases individual muscle fibers, encompasses bands of muscle fibers, surrounds individual muscles, binds muscles together, attaches muscles to other tissues, and fixes muscles to bones. The experimentally manifest form of muscle's primary function—to generate and transmit force—varies with how muscle is separated, and the degree to which it is separated, from its attendant fascia. Transmission from muscle via tendon (myotendinous force transmission)

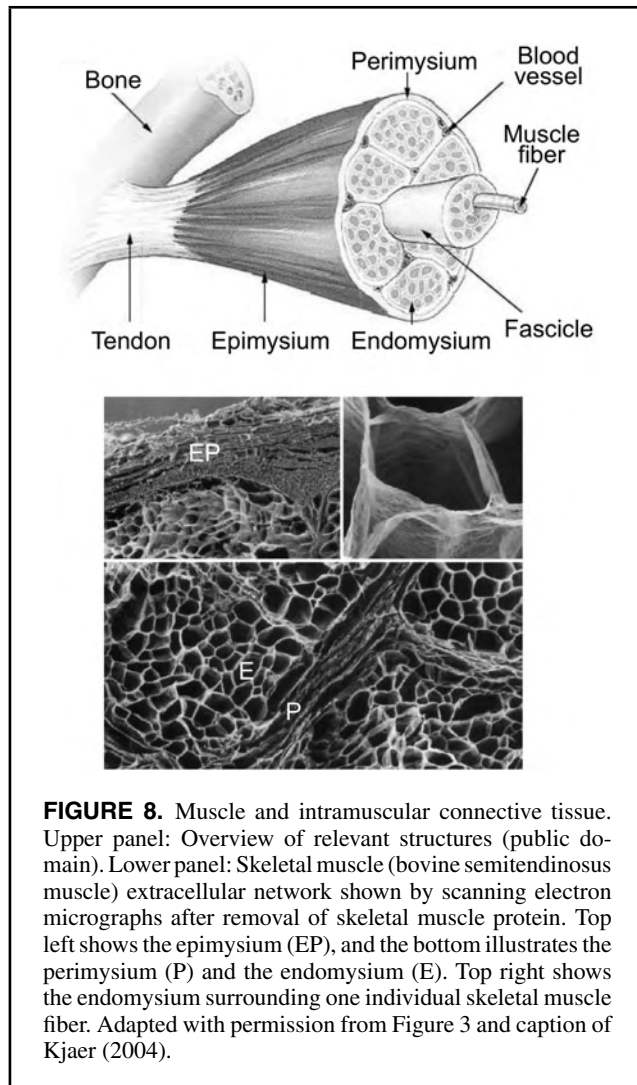


FIGURE 8. Muscle and intramuscular connective tissue. Upper panel: Overview of relevant structures (public domain). Lower panel: Skeletal muscle (bovine semitendinosus muscle) extracellular network shown by scanning electron micrographs after removal of skeletal muscle protein. Top left shows the epimysium (EP), and the bottom illustrates the perimysium (P) and the endomysium (E). Top right shows the endomysium surrounding one individual skeletal muscle fiber. Adapted with permission from Figure 3 and caption of Kjaer (2004).

is manifest experimentally when muscle is freed as much as possible from fascia. However, as will become evident, other forms of force transmission are made manifest when the separation of muscle from its attendant fascia is more selective.

A common image of a muscle is that of long, parallel fibers spanning from its tendinous origin to a tendinous insertion. Contrary to the image, large numbers of muscle fibers, in association with their specific motor units, either terminate within the muscle or decrease gradually in area, or both (Eldred, Ounjian, Roy, & Edgerton, 1993; Monti, Roy, & Edgerton, 2001; Purslow & Trotter, 1994). The consequence of these latter features is that the force produced by the fibers in question cannot be transmitted linearly to the muscle's attachments (Young, Paul, Rodda, Duxson, & Sheard, 2000). The complex connective tissue network within muscle, however, seemingly guarantees efficacy of transmission (Monti et al., 2001; Trotter, 1993). A continuous three-dimensional array of collagen fibers connects muscle fibers and provides a mode by which force can be effectively transmitted among

motor units. This fascia-based facility for lateral transmission allows the forces from multiple fibers to be functionally integrated and distributed to the muscle attachments (Monti et al., 2001; Street, 1983).

The complex integration of muscle fibers and the fascia kinds identified in Table 1 allows unexpected patterns of muscle force distribution. As noted previously, conventional understanding has been that muscle-generated force is transmitted exclusively from the muscle's fibers to the muscle's tendinous connection (myotendinous force transmission). This conventional understanding has been contradicted, however, by a steady flow of experimental results from Huijing and colleagues (e.g., Huijing, 1999, 2009; Huijing & Baan, 2001, 2003; Huijing & Jaspers, 2005; Jaspers, Brunner, Pel, & Huijing, 1999; Rijkelijhuizen, Baan, de Haan, de Ruiter, & Huijing, 2005). The base finding is that the simultaneous measurement of forces at a muscle's proximal and distal tendons shows the distal to be consistently less in magnitude than the proximal. This force difference occurs because most of the force generated by muscle fibers is transmitted via intramuscular fascia, which can transmit forces in many forms.⁷

Individual muscles are organized hierarchically into fibers encased by fascia (Purslow, 2002). Thus, the sarcomeres of a muscle are connected to one another by means of their CSK to form the muscle fiber, which is surrounded by the endomysium. Groups of muscle fibers form fascicles, which are covered by the perimysium. The fascicles are grouped to form the muscles, which are encased by the epimysium. As opposed to the conventional thinking that the endomysia, perimysia, and epimysium are the parallel elastic elements of a muscle, they are arranged in series with the sarcomeres to form the muscle's internal framework of connective tissue (Huijing, Baan, & Rebel, 1998; Purslow, 2002). This hierarchy or nesting means that the force produced by individual muscle fibers necessarily flows into the intramuscular fascia network.⁸ This flow is called myofascial force transmission and it comes in three main varieties.

Intra-, Inter-, and Extramuscular Force Transmission

The internal network of connective tissue inside muscles allows the forces produced by the sarcomeres to be transmitted to the muscle's collagenous ECM. These sarcomere-produced forces that affect the collagenous structure of muscles may be conveyed over pathways other than the myotendinous pathway. The alternate paths for force transmission are termed intramuscular, intermuscular, and extramuscular (e.g., Huijing & Jaspers, 2005). Appreciating these alternate paths is facilitated by inspection of Table 1. The evidence for them is summarized subsequently. This evidence was obtained, unsurprisingly, in vitro—that is, within laboratory settings and under experimental conditions that are not necessarily those that mimic natural force production and force transmission. Experimental investigations of alternate paths within settings closer to reality have

emerged with the focal issue being that of the degree of myofascial transmission. A first impression that the *in vivo* contribution might be small or nonexistent (Herbert, Hoang, & Gandevia, 2008; Maas & Sandercock, 2008) has given way to the understanding that it is likely to be as significant as the *in vitro* findings would imply (Bojsen-Moller, Schwartz, Kalliokoski, Finni, & Magnusson, 2010; Huijing, Yaman, Ozturk, & Yucesoy, 2011; Yucesoy & Huijing, 2007).

In intramuscular force transmission, the forces produced by the sarcomeres are transmitted to their associated endomysium, which may be longitudinally transmitted to its continuous tendon or laterally to neighboring endomysia within the same fascicle. Because the endomysia are continuous with the perimysium (see Figure 8, lower panel), forces propagate to the perimysial network, allowing force redistribution to other endomysia and their associated tendon fibers. Thus, intramuscular force transmission offers an effective means of force distribution within the muscle (Huijing, 2009; Huijing & Jaspers, 2005).

As the epimysial structure is also continuous with the perimysium and endomysium, some of the force generated by the sarcomeres is transmitted to the epimysium. The forces reaching the epimysium of one muscle may be transmitted to the epimysium of another. This force transmission between the intramuscular connective tissue of two muscles is intermuscular force transmission (Huijing, 2009; Huijing & Jaspers, 2005). Thus, forces generated within one muscle may propagate (or be distributed) to neighboring muscles within the same anatomical compartment (see Windhorst, Stuart, & Hamm, 1989, for definition and a review).

The practical significance of this mode of force transmission is the light it sheds on efforts to treat individuals with spastic cerebral palsy by transferring rectus femoris from its extensor to a flexor site of the knee. The individuals in question walk with stiff-knee gait; the surgery's intended purpose is to convert rectus femoris from a knee extensor to a knee flexor so as to increase knee-flexion during the swing phase. However, contrary to expectation, stimulation of transferred rectus femoris continued to result in a knee extension moment for more than a year after surgery (Riewald & Delp, 1997). Transmission of rectus femoris forces to the patella seemingly occurs via epimuscular myofascial pathways and/or scar tissue linking rectus femoris to neighboring knee extensors (Huijing, 1999; Maas et al., 2003). Subsequent experiments with rats have confirmed, extended and clarified the phenomenon and its interpretation (Maas & Huijing, 2012).

The forces reaching intramuscular fascia can also be transmitted to extramuscular fascia, such as the neurovascular tract (see Table 1), ligaments, and capsules, providing a mode of extramuscular force transmission (Huijing, 2009; Huijing & Jaspers, 2005). Potential force transmissions to antagonist muscles, if they occurred, could only do so extramuscularly. Evidence indicates that they do occur (Rijkkelijkhuizen et al., 2005) and are suggestive of extramuscular force transmission influencing joint complexes at some remove from

the segment of experimental interest (Huijing & Jaspers, 2005).

Multiplicity of Muscle Functions

The variety of force transmission dovetails with the observed variety of muscle function. Acting as a motor is not muscle's only role. Within biological movement's many contexts, a muscle can function as a brake, a strut, a tuner, a meter, and a spring (Dickinson et al., 2000). It can also function in ways that are as yet unlabeled (e.g., redistributing moments or finely tuning the ground reaction force; Jacobs & van Ingen Schenau, 1992; Kargo & Rome, 2002). One especially significant implication is that muscles in a single anatomical group (e.g., the muscles that swing a leg) do not necessarily share a common mechanical function (Ahn & Full, 2002). In more general terms, the implication is that redundancy in a multiple-muscle group may represent diversity in muscle function (Dickinson et al., 2000). If such is the case, then coordination may be with respect to roles (i.e., context-dependent muscle functions) rather than individuals (i.e., muscles; Turvey, 2007; Turvey & Fonseca, 2009).

The Muscular, Connective Net, Skeletal System

In respect to theory, one primary goal of the present section was to foster appreciation for the following tenet: to understand the functional design of the mammalian musculoskeletal system one must put connective tissue on a par with muscles and nerves. The evidence surveyed in support of the tenet counters the conventional assumption about the nature of force propagation within the musculoskeletal system (global compression and local tension) and opens the door for the conjecture that the musculoskeletal architecture is that of a nested tensegrity system. But the tenet and the evidence in its favor enforce an even more fundamental rethinking, namely, that the system under inquiry in the present section has not been the musculoskeletal system but the system comprising muscles, connective net, and skeleton, the system shown in Figure 9. The classical terminology is in arrears. It neglects to make conceptual payment on the full complement of ways that sarcomere-based forces are transmitted. Our inquiry now moves to this system of muscles, connective net, skeleton and the issue of its fit to tensegrity architecture.

Is the Muscular, Connective Tissue, Skeletal System (MCS) a Tensegrity System?

How might the structural continuity of MCS be likened to that of a tensegrity system? Our focus is the scale of MCS depicted by the upper level of Figure 6.

The likeness sought is morphological (roughly, are they alike structurally) and functional (roughly, do they behave similarly). Functional likeness, in the form of prestress, is our primary concern. Its realization should provide insight into the hypothesized haptic medium.

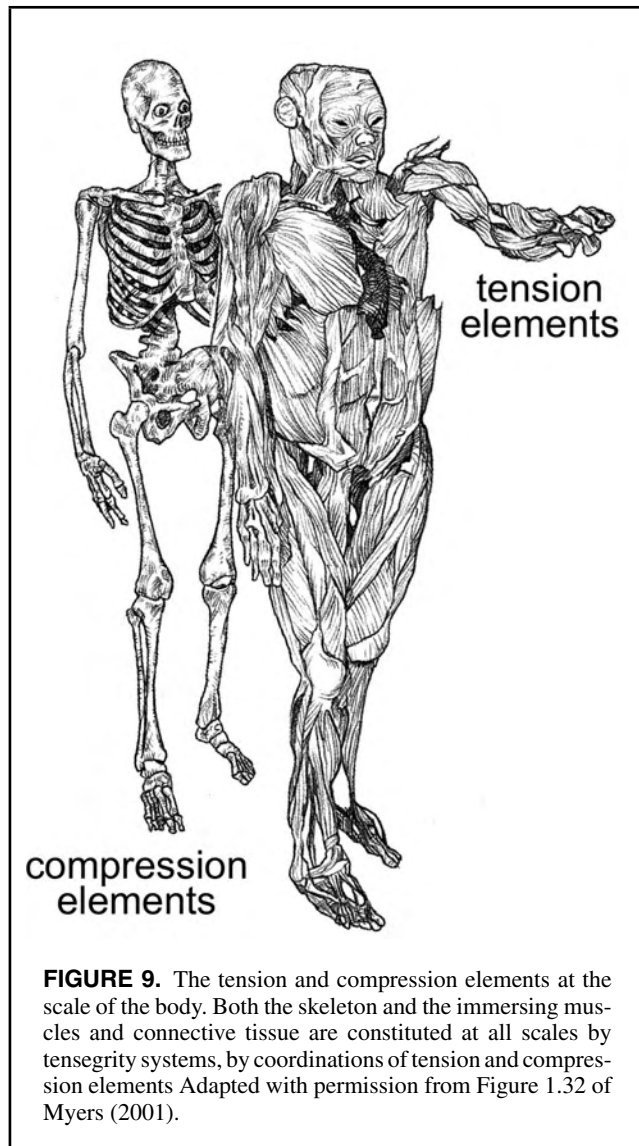


FIGURE 9. The tension and compression elements at the scale of the body. Both the skeleton and the immersing muscles and connective tissue are constituted at all scales by tensegrity systems, by coordinations of tension and compression elements Adapted with permission from Figure 1.32 of Myers (2001).

Tensegrity Classes

A familiar perspective on a tensegrity system is as a truss. It implies a ball joint (de Jager & Skelton, 2005) or a flexible (even frictionless) hinge (Levin, 2002). In this perspective, a tensegrity system can be classified according to the number of compressive components that are in contact at the joint or hinge (Skelton & de Oliveira, 2009).⁹ We can readily apply this classification to MCS, allowing that contact is in the sense of convergent to a fat point. Consider the elbow. At the elbow, the tendons (primarily) bring into contact the humerus, ulnar, and radial bones. The elbow is a Class 3 tensegrity system. At this level of description (absent fascia as identified in Table 1) MCS can be seen as a multimodular tensegrity system. Whereas the elbow is Class 3, the shoulder and individual joints of a toe are Class 2 (Skelton & de Oliveira, 2009). Amplifying this variety by class is the variety within a class following from

differences in number of tensioned components, differences that may bear on the flexibility of the equilibria of tensegrity systems (Skelton & de Oliveira, 2009). How the tensioned components are organized may further amplify the differences. The tendons of a finger of the human hand are organized as a longitudinally symmetric rhombus, a triangular architecture that seems to play a critical role in torque redistribution (Valero-Cuevas et al., 2007). The likelihood of numerous anatomical variations in the tendons to the fingers (e.g., Zilber & Oberlin, 2004, for the extensors) suggests that if the symmetric rhombus were the governing organization it would be an exemplar of invariance over heterogeneity.

Consonant with the tensegrity class formulation are analyses of the shoulder by Levin (1997, 2005) and the elbow by Scarr (2012). They constitute departure points for future in-depth quantitative studies (anatomical and biomechanical) evaluating agreement with or difference from the engineering conception of tensegrity and the presumed roles of fascia. Comments by Van der Helm and Gupta (2005) and Stecco and Dupare (2011) highlight the need for such studies.

Long-Range Connectivity

There are notable circumstances in which muscles act locally and also share important functional relations with anatomically nonadjacent areas (Myers, 2001). In the human musculoskeletal system the sacrotuberous ligament of the sacroiliac joint is a case in point. Due to its continuous relation to the biceps femoris muscle, it is linked to movements at the ankle joint through the insertion of this muscle at the fibula (Snijders, Vleeming, & Stoeckart, 1993; Vleeming & Stoeckart, 2007). A further case in point is the coupled action of the contralateral latissimus dorsi (LD) and the gluteus maximus (GM) muscles on the superficial thoracolumbar fascia (Vleeming, Pool-Goudzwaard, Stoeckart, van Wingerden, & Snijders, 1995). An hypothesized connectivity between LD and the contralateral hip joint via GM and the thoracolumbar fascia has been confirmed through an evaluation of the effects on the hip (its resting position and its passive stiffness) produced by tensioning LD (both actively and passively; Carvalhais et al., 2013). The hip variables were affected by LD tensioning, providing evidence of long-range connectivity and myofascial force transmission in vivo. This observation suggests a linkage of shoulder, spine and hip. If one considers the insertion of the gluteus maximus on the iliotibial tract and the relation of this structure to the lateral patellar retinaculum (Merican & Amis, 2009; Vieira et al., 2007), then the flow of tensional stress from the knee to the shoulder is a real possibility.

The spine is a prime example of the interconnectivity among structures (e.g., Levin, 2002). Figure 10 shows the fascial organization of the tissues of the lower back, in particular, the triangular pattern assumed by the several muscles and connective tissues of the thoracolumbar fascia. The four

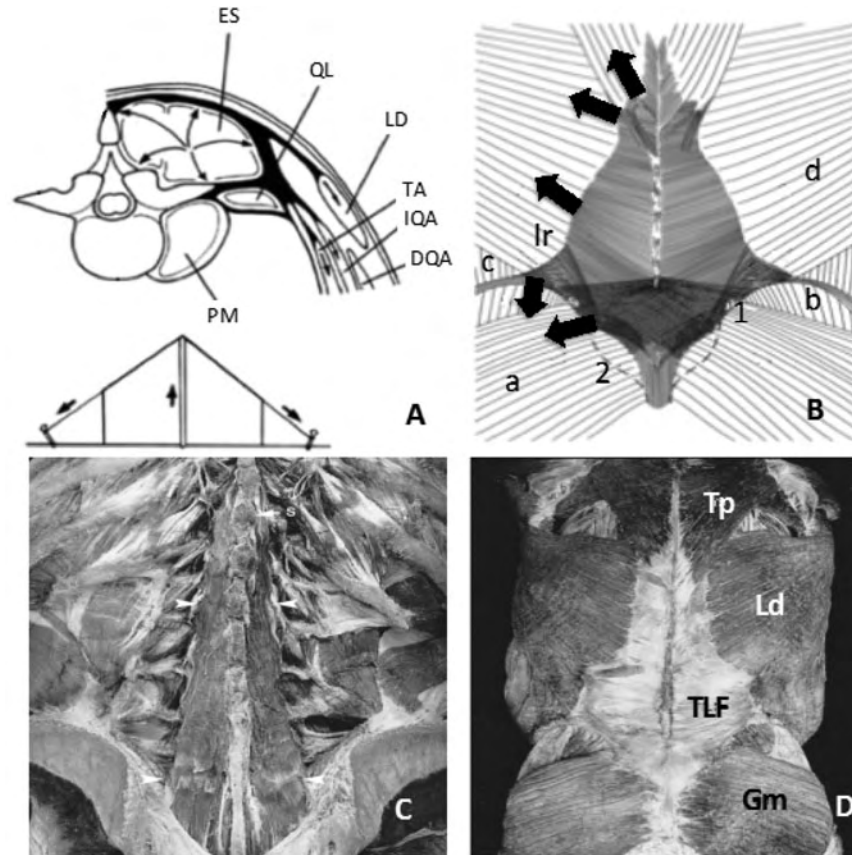


FIGURE 10. Fascial organization around the spine. (A) Cross-sectional view of the thoracolumbar fascia and associated muscles. Letters index muscles that attach to the fascia. Their organization is tent-like. Adapted with permission from Figure 3–13 of Porterfield and DeRosa (1998). (B) Pictorial representation of the fiber alignment of the thoracolumbar fascia with a the fascia of gluteus maximus, b the fascia of gluteus medius, c the fascia of external oblique, d the fascia of latissimus dorsi, 1 the posterior superior iliac spine, 2 the sacral crest, lr part of the lateral raphe. Letters and numbers hold for both sides of the figure. Arrows indicate, from cranial to caudal, the direction of traction of the trapezius, cranial, and caudal parts of latissimus dorsi, gluteus medius, and gluteus maximus muscles, respectively. Same arrow arrangement applies to right side of figure. Adapted with permission from Vleeming et al. (1995). (C) Frontal plane dissection of the deep thoracolumbar fascia and related muscles. (D) Anatomical arrangement of latissimus dorsi (Ld) and gluteus maximus (Gm) connecting to the superficial thoracolumbar fascia (TLF). (C) and (D) are adapted with permission from Figures 1.3a and 1.23 of Willard (2007).

panels demonstrate the patterned organization of the superficial and deep thoracolumbar fascia. Central interest lies in how muscles and fascia (connective tissue) are organized in series to provide mechanical support for the lumbar area. Willard (2007) demonstrated that when the bones of the spine are removed, and the dense and nondense connective tissue is preserved, the connective net maintains the anatomical continuity that would be coordinate with that of the intact spine. Willard's demonstration allows speculation that the connective tissue and muscles of the spine share an intrinsic anatomical relationship that could support the transmission of tensional forces from one area to other, distal areas. The interconnectivity of the musculoskeletal system accords with suggestions that fascia act as stress transmitting structures arranged in series with muscles (van der Mameren & Drukker, 1984).

Neutral Posture and Prestress

To reiterate, the defining functional property of a tensegrity system is prestress. The leading question, therefore, is whether the MCS system possesses this property. A point of entry into this question is neutral posture or loose packed position. In orthopedics and ergonomics, a joint's neutral posture (loose packed position) is that resting posture in which the tension in muscles, tendons, capsule and ligaments is minimized (Magee, 2007). For example, an elbow is in a neutral position when forearm and upper arm form an angle close to 90°, and a resting forearm is in neutral position when the thumb is up and the forearm is subject to neither pronation nor supination. In short, in neutral posture the connective tissues of a joint are under the least amount of stress and the joint capsule is at its greatest capacity (e.g., to hold synovial

fluid). In addition to this well known orthopedic term, another related concept is widely used to describe the position and stability of a joint: neutral zone. Neutral zone refers to a joint position in which the measurable net resistance torque against motion provided by the joint and the muscle's connective structures is zero (Panjabi, 2003). In this position, it is assumed that all connective structures are maximally loose and the joint is intrinsically unstable (Panjabi, 1992). Neutral zone, as defined, contradicts the tensegrity principle of prestress. An experiment testing for the presence of prestress at the ankle counters the definition and its implication (Souza, Fonseca, Goncalves, Ocarino, & Mancini, 2009).

The plantar flexors and dorsal flexor of the ankle can be modeled as two simple springs acting in opposite directions. These springs can be prestrained producing a state of co-tension, in accord with tensegrity. Stretching one spring (increasing its prestress), increases stiffness in both directions, not just the stretched direction. The experiment of Souza et al. showed that when the knee joint was moved passively (without muscular contraction) from flexion to extension—thereby stretching only the biarticular gastrocnemius muscle that produces plantarflexion—the stiffness of the ankle was increased in both (plantarflexion and dorsiflexion) directions (see Figure 11). The ankle joint proved to be prestressed, in agreement with the expected behavior of a tensegrity system.

Equating Tonus With Prestress

In his treatise on dexterity and development, Nikolai Bernstein (1996) observed that a prerequisite for dexterity is good motor coordination, and a prerequisite for good motor coordination is properly functioning tonus. Within the human MCS, severe malfunctioning of the level of tonus is manifest as either a general constrained rigidity of the whole body (with an inability to make anything more than the smallest of movements) or its opposite—a state of “excessive looseness and relaxation” (Bernstein, 1996, p. 120) encompassing all joints. When properly functioning, tonus is implicit, operating in the background and rarely assuming a leading role in movement assembly and performance.¹⁰

As Bernstein (1996) strongly emphasized, good coordination of the multisegmented body is founded upon the capabilities of the level of synergies or musculoarticular links, a level that is orchestrated through haptic proprioception. Good coordination, properly functioning tonus, and the haptic perceptual system, are intimately connected, suggesting that understanding tonus and its conceptual relation to prestress is of importance to our current goals.

Any inquiry into tonus must be conducted with some degree of circumspection. The historical and contemporary usage of the term suffers from ambiguity of reference (as underscored by Walsh [1992] and earlier by Fenn and Garvey [1934]). Here, we let the present focus on tensegrity systems dictate the definition: tonus is tautness or resistance to stretch of MCS under resting conditions (cf. Lakie, Walsh,

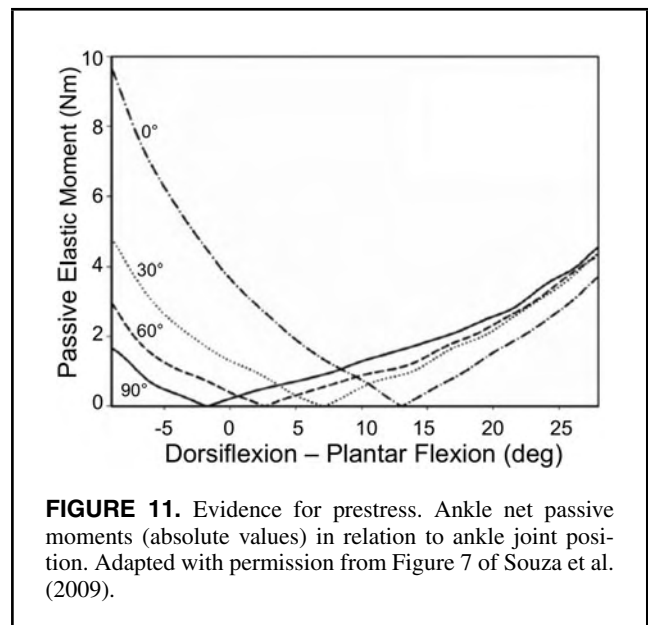


FIGURE 11. Evidence for prestress. Ankle net passive moments (absolute values) in relation to ankle joint position. Adapted with permission from Figure 7 of Souza et al. (2009).

& Wright, 1984; Walsh, 1992). This definition is consonant with prestress. Further, the substitution of MSC for muscle (the common qualifier of tone) is consonant with the understanding reviewed previously that the in vivo resistance of muscles to stretching cannot be independent of the resistance of their associated connective tissue to stretching. In proposing the equivalence of prestress and tonus, it is of special note that under the defining resting conditions the manifest form of tonus is without contractile (electromyographic) activity, persists in the presence of general anesthesia and neuromuscular blocking agents, and is dissociable from so-called stretch reflexes (Walsh, 1992). Similar to the tensioned cables or strings (prestress) of a tensegrity system, MCS tonus is strictly a property of the material nature of the body's cables (the soft tissues) and their relation to the body's compressed components (the bones) that the body's cables link. The continuous tonus is not a product of neural activity.

Behind the definition of tonus are experiments involving two complementary measures of stiffness—one derived from resonant frequency and one derived from the effects of a force applied slowly through a given distance. Resonant frequency of a limb segment about a joint is measured by applying a constant torque in flexion and extension at a frequency that is changed logarithmically with time, so as to sweep smoothly through a chosen range of frequencies. The resultant peak displacement and velocity of the limb segment increase to a maximum and then decline progressively, demonstrating a resonance (Lakie et al., 1984; Walsh, 1992). A stiffness k expressed through the resonant frequency ω_0 follows from $\omega_0 = 1/2\pi(k/I)^{1/2}$, where I is the moment of inertia of a limb segment (for the hand in motion about the wrist, see Lakie et al., 1984; for the foreleg in motion about the knee, see Douglas, Walsh, Wright, Creasey, & Edmond, 1991).

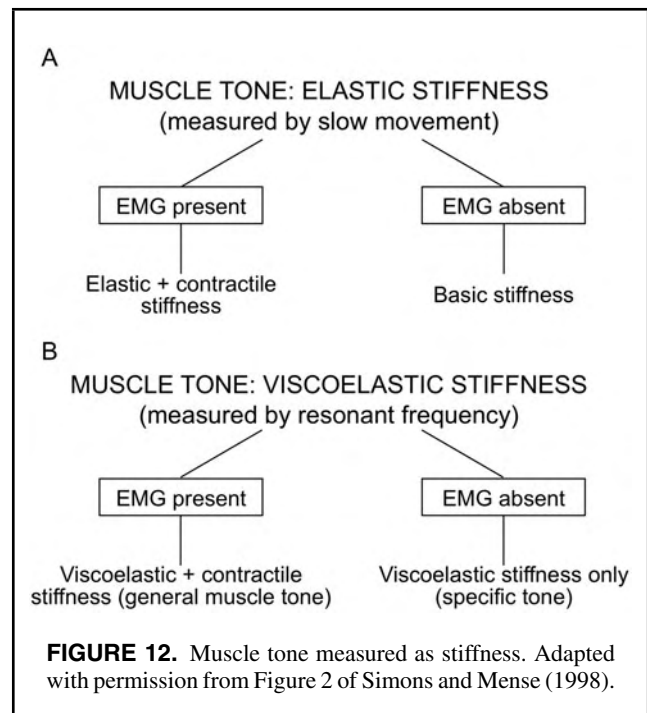
Larger k is reflected in higher ω_0 . The complementary stiffness measure of tonus is derived from single movements in response to a torque applied as rectangular waves of very low frequency (about 0.1 Hz). A limb segment is pushed into flexion or extension and then settled to a resting position before being moved in the opposite direction (e.g., Douglas, Walsh, Wright, & Edmond, 1989; Walsh, 1992). This variant of stiffness is calculated over a succession of recordings of flexions and extensions as the torque τ divided by the resulting angular displacement θ .

The simple linear form of the dynamics in the resonance-based method is given by $m\ddot{x} + c\dot{x} + kx = F_0 \sin \omega t$, with the limb segment represented as a point mass. The right-hand side is the external periodic forcing. The left hand side is the corresponding inertial, damping or frictional, and spring-like forces of the limb segment proportional to acceleration, velocity, and displacement, respectively (Den Hartog, 1956/1985). The significant feature of these dynamics for present purposes is that “At low speeds the external force overcomes the spring force; at high speeds the external force overcomes inertia, while at resonance it balances the damping force” (Den Hartog, 1956/1985, p. 50). At resonance, the spring force and the inertia force are equal and opposite, cancelling one another. Only damping (friction, viscosity) determines the motion for a given periodic forcing (Lakie et al., 1984; Walsh, 1992).

The latter observation is worth dwelling on. The measure of tonus made through the resonance-based method is inclusive of both the displacement dependent and velocity dependent responses of MCS. In contrast, the measure of tonus made in the displacement-based method reflects only the displacement dependent response. The contrast can be stated more usefully as follows: the resonance-based measure identifies MCS tonus as a viscoelastic property; the displacement-based measure identifies it as an elastic property. Following the lead of Simons and Mense (1998; see Figure 12) we give priority to the viscoelastic definition of tonus in virtue of its inclusiveness and fit to the material properties of MCS, as will become apparent subsequently.

Viscoelasticity and Thixotropy

What does it mean for MCS to be viscoelastic? Viscous material is material that resists flow when subjected to forces. Viscoelastic material is viscous material that exhibits, in addition, elastic properties, such as the ability to store the energy of deformation. In the measurement context, viscoelastic stiffness is revealed as a time-dependent relation between stress (a material structure’s internal response expressed as force per unit area) and strain (roughly, a change in the distances among the parts of a material structure induced by an external force relative to the original distances). For elastic materials subject to loading, strain is a constant function of time. For viscoelastic materials subject to loading, strain is an increasing function of time.



When a weight is placed on viscoelastic material, there is an instantaneous elastic response and a time-dependent viscous response. In viscoelastic behavior, the time-dependent response can markedly outweigh the time-independent response. Within MCS there is, fortunately, a means to rein in the time-dependent response (Silver, 2006).

Among the properties of a viscoelastic material is thixotropy—broadly defined as a history-dependent change in fluid viscosity. The more prolonged the applied shear stress, the lower the viscosity. The longer the time delay since applied shear stress, the higher the viscosity. Familiarity with thixotropy is provided by the experience with tomato ketchup. Following a period of nonuse, it resists movement when initially subjected to pouring. After a little shaking, the ketchup pours freely. It is similarly the case for paint. Stirring is initially resisted but is enacted easily following agitation and a few successful stirs. Experiments with the resonance-based method have demonstrated thixotropy in the MCS system (e.g., Lakie & Robson, 1988, 1990; Lakie et al., 1984).

The low rotational inertia of the finger facilitates the delivery of accurately defined pulses or taps of force. In the experiments of Lakie and Robson (1988) the finger was shaken (or stirred) through 15 s of vigorous movement produced actively by the participant or by a sinusoidal 3 Hz oscillation applied by a motor. Different periods of rest or nonuse (1 s to 30 min) then followed the agitation of this segment of MCS. Subsequent to a period of inaction, the finger was subjected to a brief tap that induced a transient mechanical disturbance in the form of a decremting train of oscillations. Figure 13A shows the train of oscillations. Most importantly, it shows through power spectra the increase in

the resonant frequency ω_0 and, perforce, stiffness k , with increase in the period of inaction. Stiffness doubles in approximately 60 s and continues to do so at an exponentially declining rate as shown in Figure 13B. The sharpness of tuning Q , equal to $\omega_0/(\omega_1 - \omega_2)$ where ω_1 and ω_2 identify power at half the peak, similarly increases with inaction—an outcome that calculation reveals to be due to magnification of k , not c (damping; Lakie & Robson, 1988). The implication, in sum, is that the stiffness of MCS revealed through the index finger is labile and increases steadily as time elapses following active or passive movement. MCS is thixotropic. It becomes more fluid-like with activity, and more solid-like with inactivity. It acts similar to ketchup and paint.

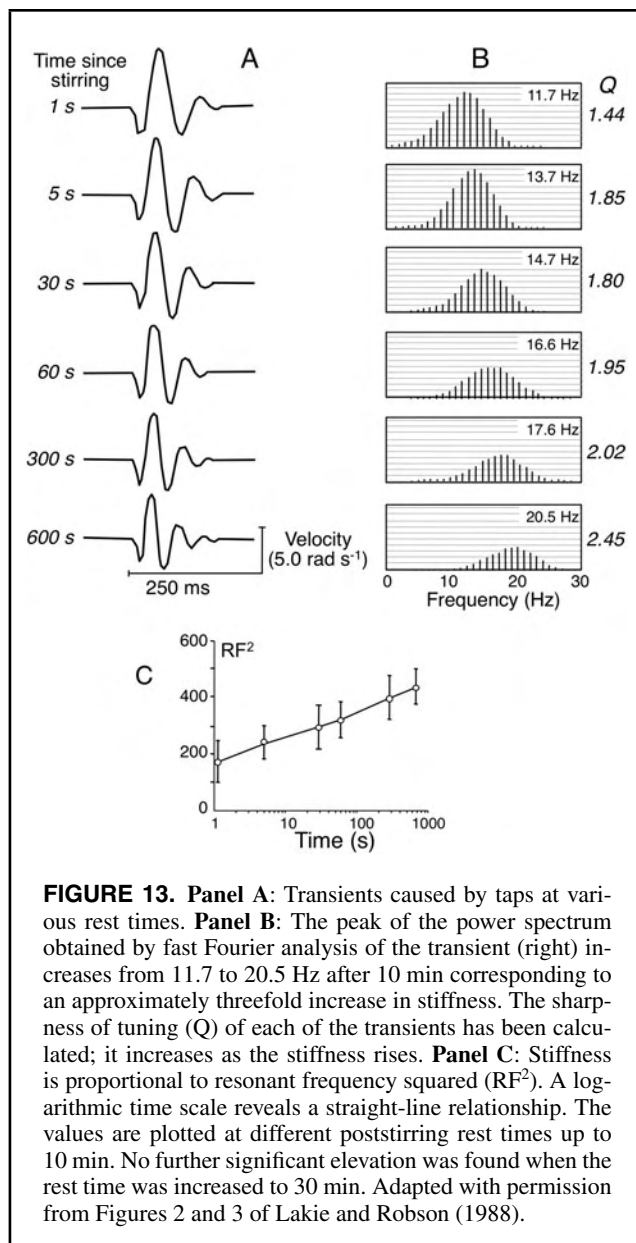


FIGURE 13. Panel A: Transients caused by taps at various rest times. Panel B: The peak of the power spectrum obtained by fast Fourier analysis of the transient (right) increases from 11.7 to 20.5 Hz after 10 min corresponding to an approximately threefold increase in stiffness. The sharpness of tuning (Q) of each of the transients has been calculated; it increases as the stiffness rises. Panel C: Stiffness is proportional to resonant frequency squared (RF^2). A logarithmic time scale reveals a straight-line relationship. The values are plotted at different poststirring rest times up to 10 min. No further significant elevation was found when the rest time was increased to 30 min. Adapted with permission from Figures 2 and 3 of Lakie and Robson (1988).

Viscoelastic Tensegrity Systems

Picturesquely, Walsh (1992) remarked that “the bones are embedded in a stiff jelly: the postural system is ‘fixed in aspic’” (p. 101). He conjectured that a system that automatically stiffens when not in use, but which can be instantly loosened, may be of considerable value in postural stabilization. From a tensegrity perspective, Walsh is painting a picture of a viscoelastic system that finds thixotropy a useful design feature (see Warner & Wiegner, 1990).

The viscoelastic nature of the cell’s CSK has motivated investigations of viscoelastic tensegrity systems (Canadas et al., 2002; Canadas, Wendling-Mansuy, & Isabey, 2006). They warrant a brief comment. The system proposed by Canadas et al. (2006) consists of six bars and 24 cables (an icosahedral tensegrity; see subsequent discussion), with each cable modeled by a Voigt body—a spring and dashpot (elasticity and viscosity) in parallel (for an overview of the conventional trio of mechanical models of viscoelasticity, see Fung, 1993; for the conceptual problems associated with them, see Zhang, 2005). The modeling is in respect to the system’s frequency behavior under the imposition of low amplitude oscillatory loading. A specific frequency-dependent contribution of elastic and viscous effects is revealed that is responsible for a significant change in the model’s dynamical properties. Namely, the contribution of the system’s spatial rearrangement (its deformation) declines from low to high frequency as elastic dominance gives way to viscous dominance. An initial frequency-dependent hardening-like process transitions to a subsequent frequency-dependent watering-like process (an analogue of a gel-sol transition).

Metering MCS

We return once again to Figure 6 and the proposal that, at each scale, the compressed component and the tensioned component compose a responsive (adjustive-receptive) architecture. The charge here is to detail the receptive components of responsive architectures within MCS—their location and their kind. We make two (reasonable) assumptions about the receptive detail in question: (a) it reflects the structural complexity that mediates the forms of myofascial force transmission (Huijing, 2007) and (b) it parallels the multifariousness of individual muscle, that is, the muscle’s regional and context dependent variations in activation level, mechanical action, fiber type, architecture and strain (Higham & Biewener, 2011; Loeb, 1985).

The perspective to be taken on the receptive components is not conventional. It follows from rejection of the classical understanding of the functional architecture of joints, a rejection that evolved from sustained inquiry into the elbow of man and rat. Its foundation is a heterodox dissection procedure, one that preserves the continuity of the connective tissue. In the procedure—developed by anatomists at Maastricht University (most prominently, Drukker, van der Mameren, and Wal)—regular arrangements of dense

(collagenous) connective tissue are exposed rather than removed.

By the classical understanding, muscles play an active role, and the connective tissue of the joint capsule a passive role, in stabilizing the elbow, with their distinctly different roles organized in parallel (Figure 14, Panel A). The contrary understanding is that muscular and joint tissues are, for the most part, organized in series (Figure 14, Panel B), with the joint-capsule tissue continuous with the periosteum, a dense membrane composed of fibrous connective tissue that closely wraps or invests all bone (apart from articulating surfaces enveloped by a synovial membrane). Within the Maastricht conceptualization (e.g., Drukker, van der Mameren, & Wal, 1983a, 1983b; van der Mameren & Drukker, 1979, 1984; Wal, 1988, 2009), ligaments are not truly separate entities and the bones framing a joint are not linked by collagenous structures (contrary to the top panel of Figure 8). Connective tissue spans the periosteal aspects of the bones and the fascicles of the muscles to form one stability system in which muscular tissue and connective tissue function in series (Strasman, Wal, Halata, & Drukker, 1990).

The latter formulation changes the perspective on the receptive components of responsive architectures within MCS. Rather than developing the receptive detail in terms of classical anatomical divisions—muscles, capsules, and ligaments—it is developed in respect to the architecture of force transmission. For any given joint, the charge is to develop the receptive detail in respect to the regions conveying tensile stresses (Wal, 2009). To pursue this charge in earnest is to be skeptical of divisions of the kind muscle receptors

versus joint receptors and respectful of the implied mutuality between receptor detail and MCS architecture.

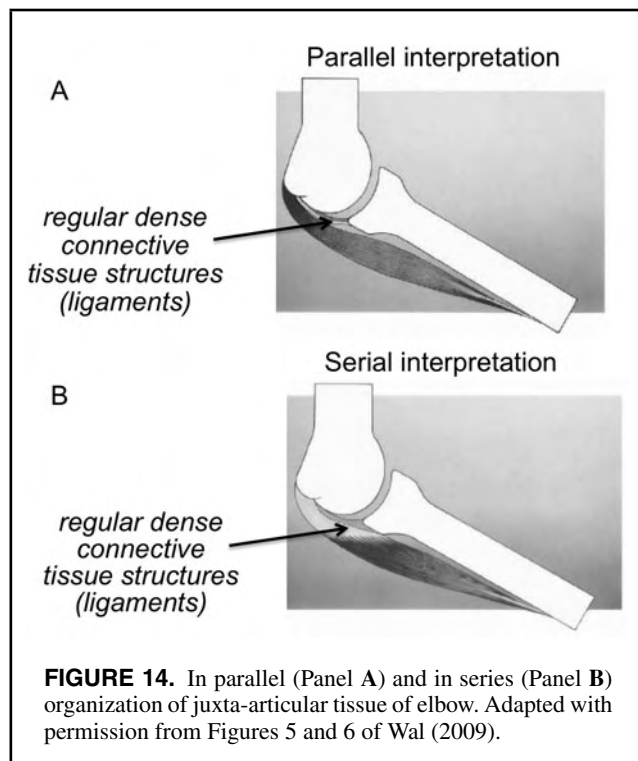
The Issues of Spindles Per Muscle, Spindles Per Region

A pronounced theoretical blind spot is the inability to relate the number of spindles to a given muscle, be it attempted a priori or a posteriori. It is, as Banks (2006) remarked, “an inability that reflects... an incomplete kinematic and dynamic theory of motor control” (p. 270). For Kokkrogiannis (2004, 2008), the fact of different muscle spindle densities across skeletal muscles makes it difficult to justify the spindle’s traditional length-monitoring function. He notes that the repertoire of fine movements participated in by the human gluteus maximus muscle is seemingly much smaller than that of the intrinsic muscles of the hand, but its endowment of muscle spindles is considerably larger, ranking among the largest spindle endowment of all the skeletal muscles. The paradox here is the traditional classification that high spindle densities index muscles involved in fine movements and Vernier contractions, low spindle densities index muscles involved in gross movements (e.g., Barker, 1974).

The topographic distribution of receptors within muscles is similarly perplexing. They are plentiful in some regions and sparse or even nonexistent in others (for summaries see Botterman, Binder, & Stuart, 1978; Kokkrogiannis, 2004; Wal, 1988). The functional significance and principles behind these regional variations in the distribution of mechanoreceptors have not been self-evident. The histological distribution shows that muscle spindles tend to be located in regions where slow oxidative (Type I) muscle fibers predominate. Conversely, these receptive components of MCS are scarce in superficial areas and in muscle regions where there is a predominance of fast Type II muscle fibers. On the basis of this “common and striking feature of intramuscular design” (p. 147), Botterman et al. (1978) ventured that a function of spindles, and a possible basis for their regional distribution, is preferential monitoring of oxidative fiber activity (cf. Kokkrogiannis, 2004, 2008).

Abiding the charge to develop the receptive detail in respect to the architecture of force transmission, we make note of the fact that oxidative fibers concentrate in the deeper and central portions of muscles, close to neurovascular tracts (see Figure 15). Neurovascular tracts are collagen fiber-reinforced structures, containing the major blood vessels as well as nerves. As identified previously, they are so situated within MCS as to serve as extramuscular myofascial conveyors of force (Yucesoy, Baan, & Huijing, 2008; Yucesoy, Koopman, Baan, Grootenboer, & Huijing, 2003). Perhaps the common and striking feature for spindles to concentrate in proximity to oxidative fibers is owed more to the copresence of tensile stresses than to the oxidative fibers as such.

The conjecture, if correct, carries implications for the issues at hand, those of why spindle distributions differ as they do across muscles of different sizes, and differ as they do between regions of individual muscles. For both issues, the



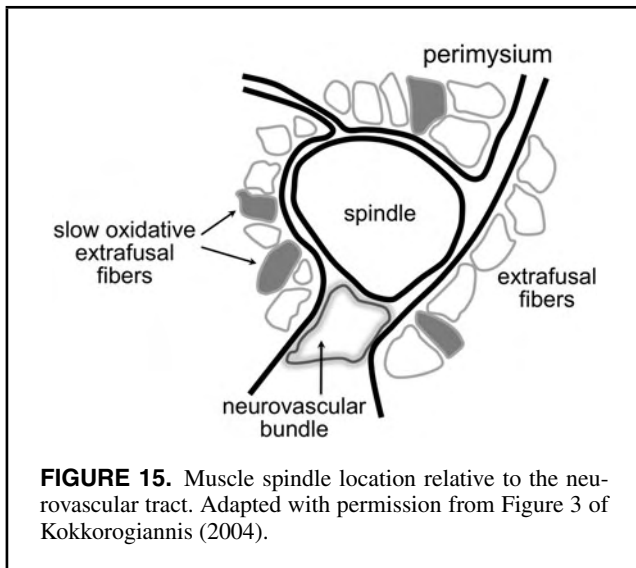


FIGURE 15. Muscle spindle location relative to the neurovascular tract. Adapted with permission from Figure 3 of Kokkrogiannis (2004).

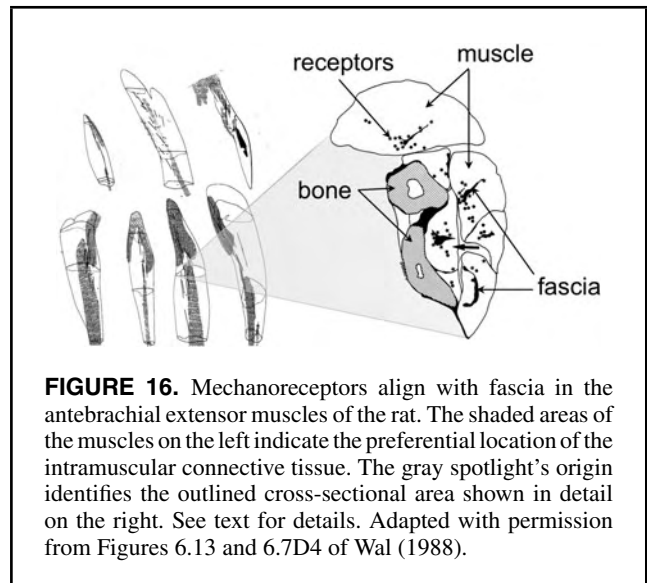


FIGURE 16. Mechanoreceptors align with fascia in the antibrachial extensor muscles of the rat. The shaded areas of the muscles on the left indicate the preferential location of the intramuscular connective tissue. The gray spotlight's origin identifies the outlined cross-sectional area shown in detail on the right. See text for details. Adapted with permission from Figures 6.13 and 6.7D4 of Wal (1988).

conjecture intimates that explanation should be sought, not in the topography of muscles, but in the functional architecture of connective tissue in relation to muscles.¹¹

Lessons on Adjustive-Receptive Architecture From Rat Antebrachial Extensors

The functional units of the elbow in the serial interpretation depicted in Figure 14 (Panel B) are MC units within MCS that transmit tensile stresses over the elbow joint. In respect to the haptic perceptual system at the scale of the body, these functional units would comprise the adjustive aspect of the adjustive-receptive systems primarily involved in, for example, dynamic touching by exploratory wielding of a handheld object (see Turvey & Carello, 1995, 2011).

Figure 16 displays the arrangement of muscle spindles and Golgi tendon organs for the antibrachial extensor muscles of the rat (those in the foreleg area between elbow and paw; see Wal, 1988; Wal & Drukker, 1988; Wal, Strasmann, Drukker, & Halata, 1988). There seems to be no common organizing principle when considered from the perspective of individual muscles but such a principle is suggested when a perspective is taken relative to connective tissue. Figure 16 shows a strong spatial correlation between the morphological substrate of receptive components, specifically spindles and Golgi tendon organs, and the muscle-connective tissue architecture (Wal, 1988, 2009). As the figure reveals, the primary location of mechanoreceptors—of both the muscle and the joint types—is the transitional zones between regular dense (collagenous) connective tissue and muscle tissue. In these transitional zones, between tissues of different stiffness, tissue deformation would be expected to be most pronounced, and the deformation's field-like structure to be most richly patterned.

The metering of MCS qua deformation field will have to be a primary aspect of our effort to identify the haptic medium. Important prefatory steps can be taken here, guided by the

investigations into the rat antibrachial extensors. Broadly conceived, all mechanoreceptors can be regarded as free nerve endings with some distinguished by specialized end organs (Wal, 2009). Of primary importance is their microarchitecture. Two broad classes can be identified: ball- or bean-shaped and spray-like (Polacek, 1966; Wal, 2009). Lamellated corpuscles (e.g., Pacinian), each comprising multiple lamellae around a simple nerve fiber, are canonical exemplars of the former. Ruffini corpuscles are canonical exemplars of the spray-like class—receptive structures that are intertwined with (or ramify among) collagen fibers integrally connected with the connective tissue that embeds them. Arguably, the two classes define receptive structures tailored to the detection demands of different kinds of deformation, for example, compression and stretching in the case of bean-shaped and shearing and twisting in the case of spray-like. Their tailoring may also be in regard to kind of connective tissue, with spray-like receptive structures more suited to deformation of irregularly arranged connective tissue (see Table 1).

A generalization of this latter point is that the spectrum of receptive structures is likely to depend on the regional specifics of the architecture of force transmission—on the morphology of the transitional zones between tissues that differ in stiffness. Three zone-specific spectra have been distinguished in the deep lateral elbow area of the rat (Strasmann et al., 1990). One zone innervated by muscle spindles, Golgi tendon organs, lamellated corpuscles, and free-nerve endings lies in the middle third of the muscle-aponeurosis transition zone of the supinator, a muscle that rotates the paw to palm up. One zone innervated by small lamellated corpuscles and free-nerve endings is located between the proximal muscle fibers and the distal edge of the sesamoid bone (interposed in the supinator septum; see intermuscular septa, Table 1). And one zone limited to free-nerve endings is situated in the most

proximal part of the supinator septum, close to its insertion in the lateral epicondyle.

Long-Distance Force Propagation

By way of summary, the reviewed data and theory relating to mammalian joints identifies the functional morphological unit of MCS as an in-series organization of muscular, connective, and skeletal tissues, with the receptive structures concentrated in the tissue-transition zones. This responsive viscoelastic architecture is both active (its muscular tissue generates contraction forces) and passive (its connective tissue conveys tensile forces, and its skeletal tissue sustains compressive forces). Further, it is seemingly repeated at all articulated segments. Although made evident in the present discourse in the jointed limbs, it is equally manifest in the spinal column.

The similitude presumed to hold between MCS and CSK (communicated through Figure 6) is a source of insight into MCS. Particularly illuminating is the CSK relation between material composition and force propagation. Whereas chemical diffusion and molecule transport proceed within the cell at speeds measured in $\mu\text{m/s}$ (e.g., molecule transport occurs $\approx 1 \mu\text{m/s}$), mechanical stresses propagate (along tensed CSK filaments) at speeds measured in m/s, specifically, about 30 m/s (Wang et al., 2009). In arguments given by Wang and colleagues (Wang & Suo, 2005; Wang et al., 2009), the key to understanding the propagation of stress, its speed and distance, is the inhomogeneity of the materials composing CSK. If all stress-supporting CSK structures were of one kind, any stress imposed on a cell would be dissipated rapidly by the demand to distribute equally among the components. In contrast, if the stress-supporting CSK structures were inhomogeneous, stresses would be preferentially channeled or guided over stiffer components, for example, those subject to prestress (e.g., Okada et al., 2011).

The latter yields two conceptual understandings of potential significance to MCS: (a) stresses tend to dissipate less in stiffer components; (b) the distance over which stresses are propagated depends on the stress/strain modulus of the more-stiff components relative to the stress-strain modulus of the less stiff components (Wang & Suo, 2005; Wang et al., 2009). The assumed similitude of the adjustive-receptive architecture at the scale of the body (MCS) and the adjustive-receptive architecture at the scale of the cell (CSK) leads to the expectation of conditions under which stresses arising locally in MCS can propagate selectively over relatively long distances. It is an expectation that dovetails with evidence for long-range anatomical connectivity within MCS. Such evidence was detailed previously in developing an answer to the question: Is MCS a tensegrity system?

The similitude of MCS and CSK casts light on MCS in one further, closely related way. Via the preferential pathways for the distribution of stress, forces arising at the cell-substrate points of adhesion are transferred distally by CSK to multiple cellular parts (e.g., the microtubules and nucleus). The up-

shot is similar to tugging a strut or a cable of a classic Snelson sculpture: however minimal the tug, a rearrangement necessarily follows of all the components—of all the functional struts and cables—defining the system (Galli, Guizzardi, Passeri, Macaluso, & Scandroglio, 2005). The rearrangement is a new equilibrium. A similar phenomenon should be expected for MCS.

Upright standing of a human without intended movements (so-called quiet standing) is an equilibrium state, or so it may be claimed. A brief force equal to 0.6% g delivered to the flexor pollicis longus muscle of the thumb induces a near simultaneous muscular adjustment in the tensile state of the pectoralis major on the same side (Marsden, Merton, & Morton, 1983). This force is equal to the acceleration of a ball rolling on a smooth inclined plane at only 0.3° to the horizontal. In respect to the distal adjustment this very small disturbance of quiet standing shows up on individual examination in other muscles—those of the lower and upper limbs, and those of the trunk, either on the same side or opposite sides. In all cases the muscle adjustment proves appropriate to the direction of the perturbation when interpreted from the perspective of preserving postural equilibrium (Marsden et al., 1983). Of special relevance to the possible relation of the results to tensegrity is the experimental determination by Marsden and colleagues that the remote postural adjustments were not stretch reflexes triggered by muscle-length changes (see also McIlroy & Maki, 1995).

A sustained force of different magnitudes can be generated locally, for example, by squeezing a hand dynamometer (Kugler & Turvey, 1987; Silva, Moreno, Mancini, Fonseca, & Turvey, 2007), or by pushing down on a foot dynamometer (Bingham, Schmidt, Turvey, & Rosenblum, 1991). At issue are remote consequences, if any. In the hand case, contemporaneous oscillations in the nonsqueezing hand change either in frequency (Kugler & Turvey, 1987) or in amplitude and stiffness (Silva et al., 2007). In the foot case, contemporaneous oscillations of the two hands in antiphase change in their common frequency and their phase relation. These remote effects of local constant force on rhythmic limb movements could be mediated mechanically, in agreement with the tensegrity hypothesis, but they could also be mediated neurally (e.g., increased afference) or physiologically (e.g., increased blood and oxygen flow), fully or partially. Experimental adjudication is required (Silva et al., 2007).

The issue of whether subtle mechanical forces applied to the body might have remote effects is an aspect of a broader issue, namely, that of principles which unify connective tissue at the scale of the whole body. Langevin (2006) has offered some speculations.

Unspecialized, loose, irregular connective tissue (non-dense in Table 1) is the most generalized form. It is distributed extensively and serves primarily to bind structures together but not so severely as to prohibit their movement (Standing, 2008). In appearance, it is a mesh of thin collagen and elastin fibers (providing both tensile strength and elasticity) that interlace in all directions. For Langevin (2006), this ubiquitous

connective tissue, potentially subject to mechanical forces varying from the instantaneous to the prolonged, could behave in a unified manner by virtue of interactions among its fast time-scale electrical activity, its medium time-scale cellular motility, and its slow time-scale tissue remodeling (see Langevin et al., 2010). Functional unification of the unspecialized, loose, irregular connective tissue could be through the dynamic diffusion patterns emergent from the interactions.

Haptic Medium as Multifractal Tensegrity

At this juncture, the central thesis under development in the present article can be expressed in the following form: The medium for the haptic perceptual system is an assemblage of nested viscoelastic tensegrity systems. Two steps in this development, to which we now turn, are identifying specifics of the assemblage's composition, and developing the conception of assemblage. The development is conservative. It proceeds on the assumption of a single kind of tensegrity system composing the assemblage rather than multiple kinds (for the latter see Ingber, 2003a; Turvey & Carello, 2011).

The Icosahedron as the Base Tensegrity System

We assume that to compose a tensegrity assemblage, each individual tensegrity system must be able to fit (connect) to its neighbors, whatever their sizes and orientations. At bottom, this criterion requires flexibility of all of a tensegrity system's joints (the points of articulation of its tensioned and compressed elements). The shared symmetries of regular polygons and tensegrity systems suggest that this criterion can only be met by tensegrity systems that are fully triangulated in the manner of tetrahedra, octahedra, and icosahedra.¹² Among the latter, the icosahedron stands out in being (a) the most symmetrical, (b) omnidirectional in form and function, (c) exhibiting largest volume for surface area, and (d) most able to enclose three-dimensional space. Properties (a–d) are preferential for close packing of polyhedra and, perhaps, close packing (full connectivity) of tensegrity systems. In sum, a promising hypothesis, and the one pursued here, is that the tensegrity assemblage is constituted by icosahedral tensegrities (Levin, 2002, 2006).¹³ Figure 17 (a–c) is the concept of an icosahedral tensegrity expressed in both its geodesic (a) and prestressed forms (b and c), with the latter in both straight strut and curved strut variants. Figure 17 (d and e) is a squished icosahedral tensegrity accompanied by the so-called J-shaped stress-strain function (Levin, 2006) that expresses the tensegrity's prestressed nature and its nonlinear response to deformation.¹⁴ A prestressed icosahedron tensegrity has six struts and 24 cables (for a total of 30 edges and 20 faces). In its MCS incarnation its 24 cables would be viscoelastic. Figure 18 is an example of an assemblage of icosahedral tensegrities.

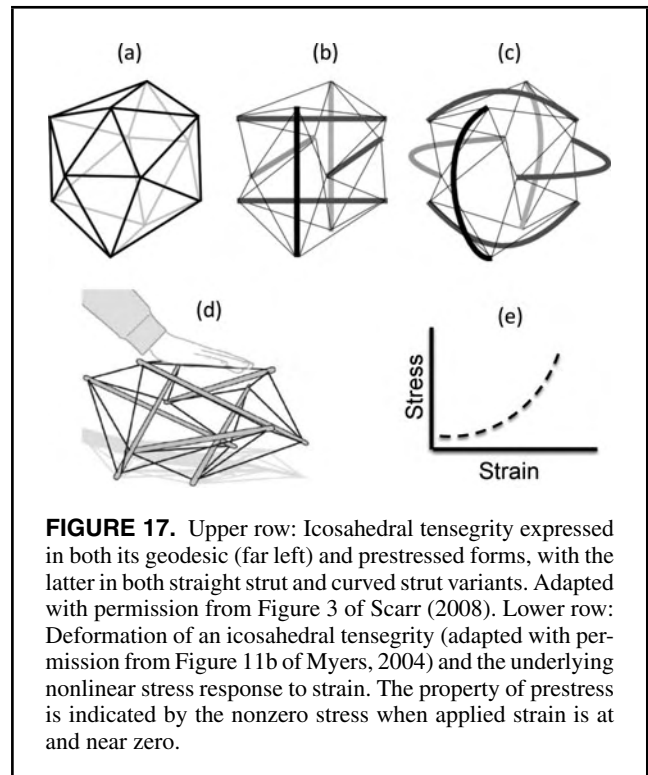


FIGURE 17. Upper row: Icosahedral tensegrity expressed in both its geodesic (far left) and prestressed forms, with the latter in both straight strut and curved strut variants. Adapted with permission from Figure 3 of Scarr (2008). Lower row: Deformation of an icosahedral tensegrity (adapted with permission from Figure 11b of Myers, 2004) and the underlying nonlinear stress response to strain. The property of prestress is indicated by the nonzero stress when applied strain is at and near zero.

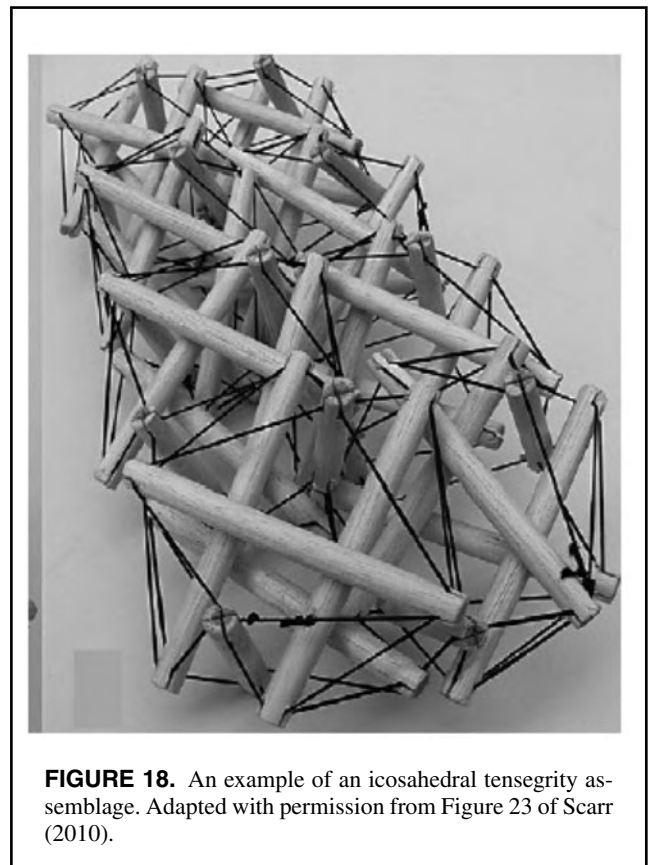


FIGURE 18. An example of an icosahedral tensegrity assemblage. Adapted with permission from Figure 23 of Scarr (2010).

Haptic Cube Redux

Our departure point for developing the concept of assemblage and its instantiation through icosahedra is the haptic cube. Kugler and Turvey (1987) suggested an idealization of the haptic system, in whole or in part, as a cubic slab of tissue with its constituent elements—the individual mechanoreceptor-served microregions of tissue—standing in an invariant spatial relation. The fact that the body is ordinarily immersed in a field of forces means that most microregions of any arbitrarily chosen haptic cube are ordinarily distorted (stressed) to a greater or lesser degree: “the ‘haptic cube’ is always warped by the presence of potentials” (Kugler & Turvey, 1987, p. 166). With warping of the cube (e.g., by the stresses of limb movement or a given posture), each microregion would exhibit a time varying change in strain expressible by a vector in a one-dimensional state (strain) space, with the individual microregion’s vector value dependent on the microregion’s location and orientation relative to the cube’s axes. Collectively, the strain velocity vectors across the microregions would define a velocity vector field instantiated in the place-to-place and moment-to-moment patterning of mechanoreceptor activity (see Roll et al., 2009).

The issues and arguments broached so far in respect to MCS motivate a refinement of Kugler and Turvey’s haptic cube: A microregion housing a receptive element is a specific location within a specific architecture, that of a prestressed and viscoelastic tensegrity icosahedron. Following Strasmann et al. (1990), the specific location is a transitional zone between tissues that differ in stiffness. For a tensegrity system the zone would span the softer tissue-harder tissue, tensioned-compressed, cable-strut join. For a tensegrity icosahedron within MCS there would be 12 such zones. The thrust of the foregoing is a repetitive theme in the present article, namely, that in understanding the biological basis of haptic perception, nerves and connective tissue have equal theoretical status. They go hand in glove. The nervous system as *cynosure* is deficient.

In the refined haptic cube, tensegrity icosahedra replace individual mechanoreceptor-served microregions of tissue. Within the cube the individual tensegrity icosahedra will change shape and stiffness as a function of the changing force environment, and will do so in a highly systematic manner, in part because of the tensegrity quality of shape memory (e.g., Defosse, 2003) alluded to previously (Galli et al., 2005). The stiffness of a tensegrity system comes from two sources: the change of force carried by members as their length is changed, and the reorientation of forces as already stressed members are rotated.

A tensegrity icosahedron subject to external shearing in the $x-z$ plane is shown in Figure 19a. The consequent emergent relation of cables and struts—the tensegrity’s adjacent order—is expressible formally in terms of a finite number of characteristic relations of cables and struts, the tensegrity’s elastic eigenmodes. Some insight into their nature is provided by the simpler planar tensegrities of Figure 19b. The

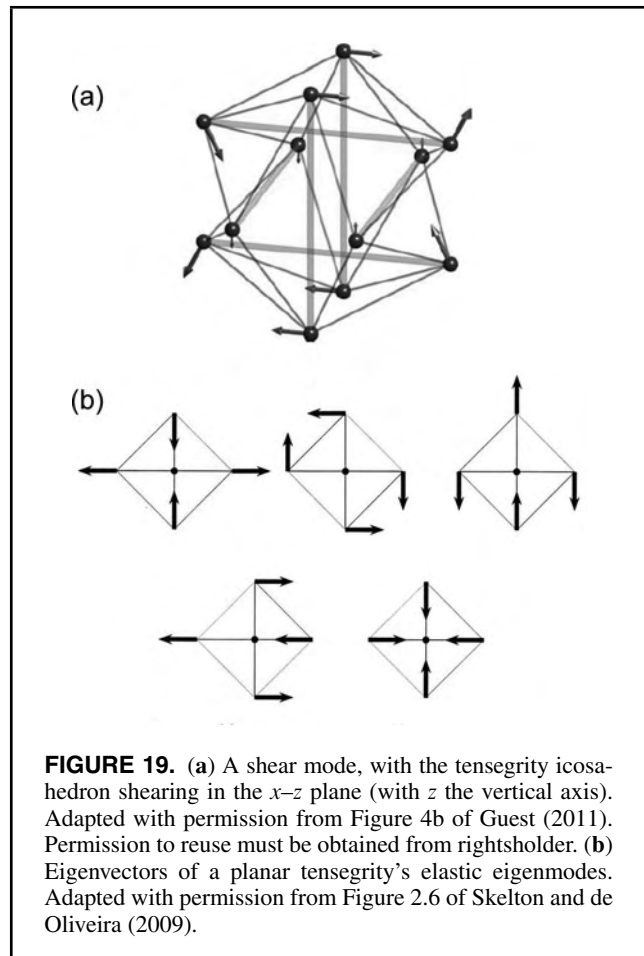
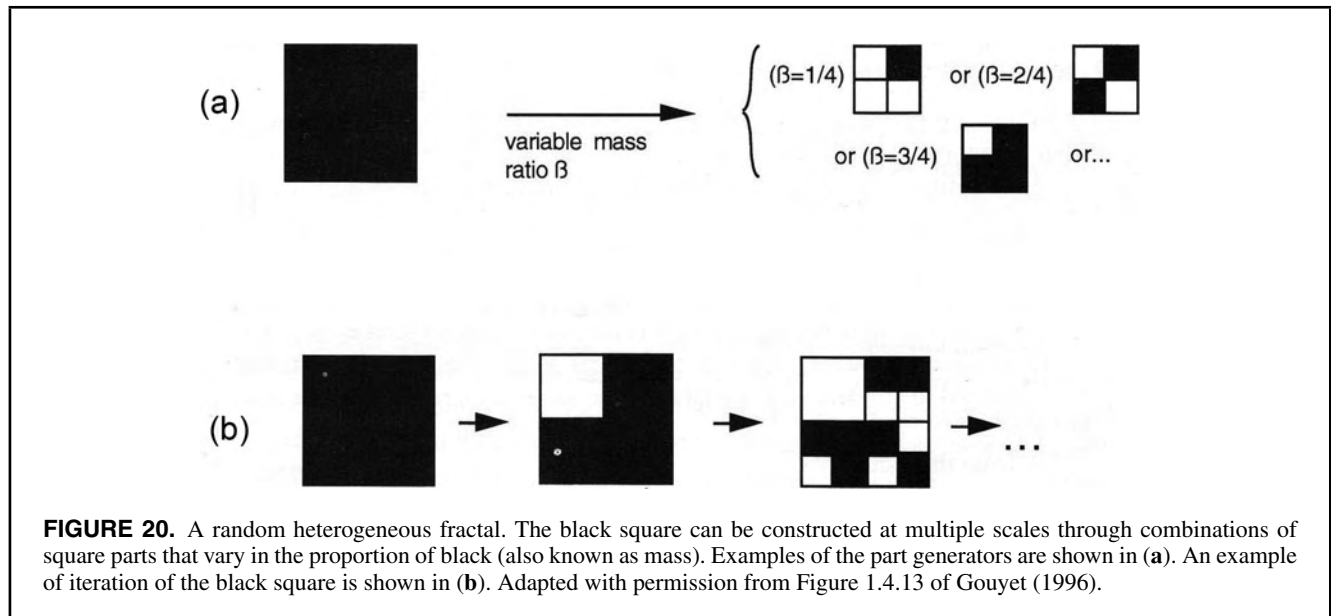


FIGURE 19. (a) A shear mode, with the tensegrity icosahedron shearing in the $x-z$ plane (with z the vertical axis). Adapted with permission from Figure 4b of Guest (2011). Permission to reuse must be obtained from rightsholder. (b) Eigenvectors of a planar tensegrity’s elastic eigenmodes. Adapted with permission from Figure 2.6 of Skelton and de Oliveira (2009).

change in the tensegrity icosahedron’s adjacent order due to shearing is itself understood as an order, namely, the tensegrity’s sequential or successive order. The important conception conveyed by these remarks in respect to Figure 19 is that the pattern of activity of an individual tensegrity icosahedron’s receptive elements will be a concerted receptive response specific to the adjacent and successive order, the nonchange and change (see Gibson, 1966), of its adjustive elements (its functional cables and struts). This concerted response imposed on the mechanoreceptors means that the variables expressing the state of any tensegrity icosahedron are defined at the level of the tensegrity icosahedron. They would differ in number and kind from the variables traditionally associated with individual mechanoreceptors (see Chapters 2 and 5 in Kugler & Turvey, 1987). The charge for a science that would identify them is that the variables express the tensegrity’s concinnity, its unitary nature, and do so in a functionally specific way. Assuming that the refined haptic cube fully bounds an interconnected arrangement of icosahedral tensegrities (that is, the haptic cube is, in fact, icosahedral rather than cubic), then the foregoing pivotal conceptions transfer readily to each haptic cube—to the concerted response of each arbitrary array of tensegrities, and



to the cube level as the level at which the variables of this concerted response are defined.

Multifractal Tensegrity

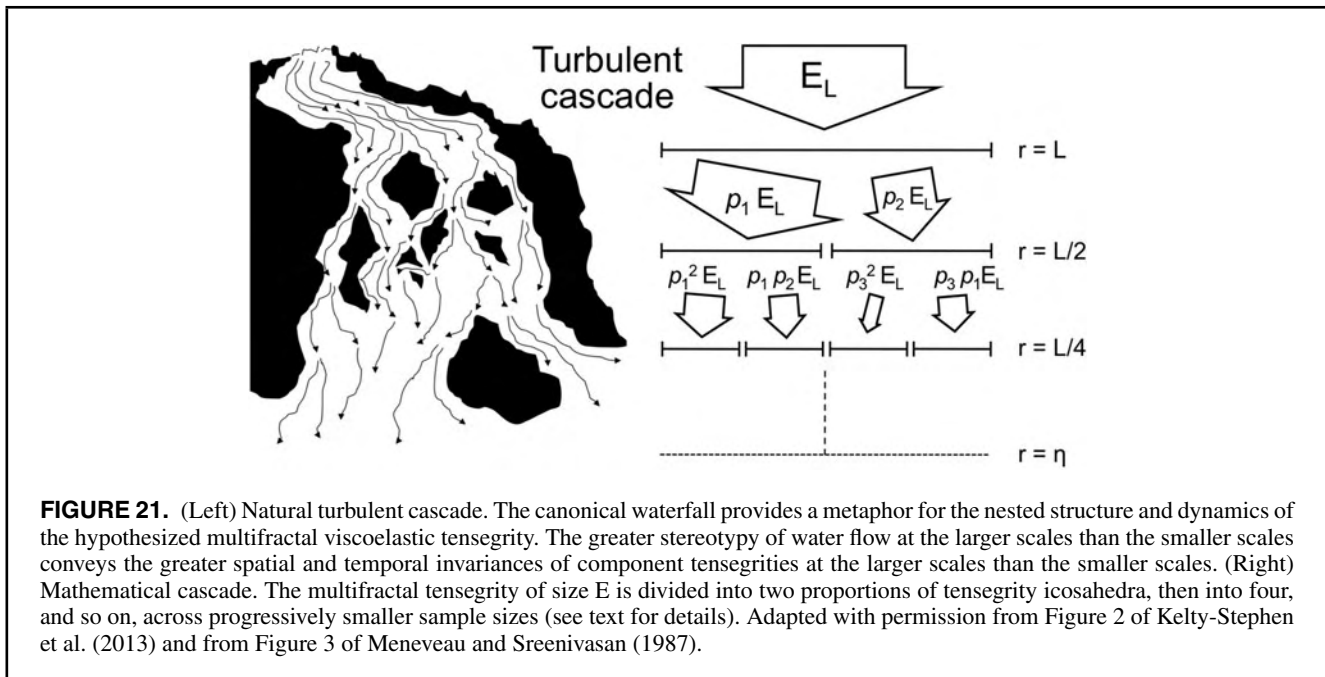
The assemblage of nested icosahedra is an assemblage of self-similar geometrical objects filling a high dimensional space. As such it is a fractal object (roughly, one with the same kinds of components at all scales of analyses). The concept of haptic medium under construction here, however, is more aptly described in mechanical rather than geometrical terms. Namely, as an assemblage of self-similar mechanical objects (tensegrity icosahedra) that fill a finite dimensional space (e.g., that bounded by an animal's skin). Skelton and de Oliveira (2009) suggest that such an assemblage be termed a tensegrity fractal. For our purposes it will be more appropriate for fractal to qualify tensegrity; that is, the assemblage is better termed a fractal tensegrity.

Appreciation of the notion of a fractal object is commonly derived from deterministic mathematical examples such as the Koch snowflake and the Sierpinski triangle. Nature's fractal objects, however, are predominantly random (Gouyet, 1996). For these objects or structures the recurrence defining the successive levels follows laws (likely thermodynamic) that fix the choice of iterative operation at each level. A random fractal object is said to be homogeneous when its volume or mass is distributed uniformly at each scale or hierarchical level and heterogeneous when its volume or mass is distributed nonuniformly (Figure 20). We will make the assumption, depicted in Figure 21, that the distribution of tensegrity icosahedra is nonuniform. Reasonable grounds for doing so are the diversity of connective tissue (building materials of the tensegrity icosahedra), expressed through

the fascia of Table 1, and the variety and scales of icosahedral tensegrity constructions that it can give rise to. On this assumption, the assemblage of tensegrity icosahedra does not possess a global scale-invariance and is, accordingly, not characterizable by a single fractal dimension (Gouyet, 1996). A spectrum of dimensions is needed for its description. The proposed assemblage of tensegrity icosahedra, the hypothesized haptic medium, is a multifractal tensegrity (or, more precisely, a viscoelastic multifractal tensegrity). Our development of the concept of multifractality cleaves closely to that of Meneveau and Sreenivasan (1987) and Kelty-Stephen, Palatinus, Saltzman, and Dixon (2013).

The arrow at the top level of Figure 21 (right) represents the full assemblage of tensegrity icosahedra, the equivalent of the black square (a volume or mass) in Figure 20. The levels below are samples that proportion the full assemblage (that is, proportion the volume or mass). They are the equivalents of the iterations of the black square shown in Figure 20b. The samples at each given level of Figure 21 (right) are split into two samples at the next level giving rise to a succession of j generations, where each parent sample splits into two child samples. The proportion average for the sets of samples defined across successive generations necessarily progresses from 1.00 to 0.50, to 0.25, and so on, while summing to 1.00 in each generation. Our example is the simplest kind of a multifractal tensegrity. If the iteration at one level leaves some samples with less than an even split of their parent samples, then the next iteration must leave their sibling samples with more than an even split of the parent samples.

The significance of the aforementioned average must be noted. It is the pattern of variability around the average proportions that determines the specific nature of any particular multifractal tensegrity. There are indefinitely many versions of a random heterogeneous fractal, indefinitely many cascade



patterns of a waterfall (a common exemplar), and indefinitely many versions of Figure 21.

It is worth underscoring that a multifractal tensegrity is unlikely to be compromised by a loss of members of the assemblage below some critical number. At the scale of the body, to sever the Achilles tendon is to lose control of the foot but not control of the body as a whole.¹⁵

Haptic Medium, Haptic Information, and Haptic Perception

Invariance Over Heterogeneity

Figure 21 and the prefacing arguments and analyses should lead us to expect that within any given animal species the pattern of variability in the assemblage of tensegrity icosahedra would differ from one individual member to the next. We should also expect that it should differ locally between two or more same-named body segments within an individual, such as a given human's two hands or a given human's two shoulders (e.g., Bergman et al., 2012; Zilber & Oberlin, 2004).

As highlighted previously, the haptic medium of each and every animal must be above such heterogeneity, consonant with Elsasser's (1998) central biological thesis. For each and every animal the medium must support information about, in the sense of specificity to, states of affairs of the animal's body, and of the body's relation to its surroundings. At this point it can be argued that the support is the deformability of the multifractal tensegrity, and the information about is state-specific deformations of the multifractal tensegrity. On the ecological thesis of specificity (Gibson, 1966, 1979;

Runeson, 1988; Shaw, Turvey, & Mace, 1982; Turvey, 2013; Turvey et al., 1981), whereas multifractal tensegrities are heterogeneous, differing from animal to animal, within and across species, a deformation pattern of a multifractal tensegrity that informs about a particular body state (an MCS state) of any one animal should prove to be a deformation pattern that informs about the functionally comparable body state for all animals. The required mathematical formulation of such specifying deformation patterns must be at a level of abstraction sufficient to express this invariance and universality. A glimpse of what is required is provided by Lee's sustained inquiry (Lee, 1998, 2009; Pepping & Grealy, 2007) into the controlled collisions with surrounding surfaces that humans, birds, bats, bees, and flies alike, achieve regularly. The time-to-contact variable τ , and its explanatory extension τ -gap, takes the same mathematical form indifferent to the neural complexity of the perceptual system and indifferent to whether the field is optical or acoustical (or electrical, as in the case of paramecia; Delafield-Butt, Pepping, McCaig, & Lee, 2012). It is a further example of invariance over heterogeneity.

The Conventional Tack and the Riddle of Abduction

Theoretical discussions of the haptic perceptual system (identified primarily with proprioception and cutaneous touch) have tended to focus upon neural components within the 19th century traditions of local sign theory and linear signaling pathways (Boring, 1942). Historically and contemporarily, two presumed primary charges of the central nervous system, most especially the brain, are to integrate

and to interpret the afferent signals from multiple independent mechanoreceptors. The need for integration is because these signals refer to states of individual mechanoreceptors, and the need for interpretation (e.g., inferring, hypothesizing, guessing) is because these signals form a small closed set confined to the variables of Newton's mechanics. The interpretation would have to be in the form of abduction: arguing from effect to cause. In approximate terms, this would be providing an answer to a question of the kind: Given *that* activity in those mechanoreceptors, what combination of states (geometric and kinematic) of the upper limbs, lower limbs, trunk, and head, and attachments to them, would have to have occurred, and under what environmental circumstances, to produce it?

Abduction poses a riddle (Fodor, 2000; Rellihan, 2009; Turvey, 2013).¹⁶ The riddle arises in the effort to answer the question, How can abduction be mechanical (*M*) and feasible (*F*) and reliable (*R*)? *M* is the assertion that abduction is computationally implementable. In the example above, the step from effect (mechanoreceptor activity) to cause (body states) is assumed to be computable. *F* is the assertion that modular computational components are informationally encapsulated (constrained to current input and proprietary database, otherwise they will be nonterminating). And *R* is the assertion that abduction is unencapsulated (no a priori basis for reliably delimiting the requisite variety and depth of domains of knowledge and attendant facts needed for a successful inference). The knowledge required for *F* is local; that for *R* is nonlocal (Fodor, 2000), as implied in the previous sentence.

Here is the riddle: Abduction can be *M* and *F* only if not *R*; *M* and *R* only if not *F*; *F* and *R* only if not *M*. Here is the resolution. If assertions *F* and *R* are deemed nonnegotiable (no possibility of computation without them), then assertion *M* is false. That is, abduction is not mechanistically viable. It would seem that whatever is the state of affairs that one chooses to label abductive inference it is not of a computational nature. It is not an inherently logical state of affairs. It may not be what it seems to be.

The integration and interpretation requirements that preface the abduction riddle are both consequent to the same implicit understanding, namely, that the classically termed somatosensory system operates with a limited set of types of states that is fixed and given a priori. The idea of a multifractal tensegrity with components that deform in specific ways according to the distribution of forces generated by and imposed upon MCS implies no limit to the number of (directly) perceptible states. Contrary to the conventional view, the types of states of the somatosensory system are most aptly understood as an open a posteriori set.

The Necessity and Implications of Specificity (Qua Lawfulness)

The notion of specificity warrants further comment. For any animal, the possibility of any coordinated movement in

any given situation and at any point in time is grounded in the fidelity of haptic perception to the body's disposition. Any lesser grounding would make haptic perception suspect, and, perforce, adaptive movement an unlikely occurrence. To construe haptic perception as a variant of inference making, hypothesis testing, and sophisticated guessing is to view its indefinitely many veridical achievements in the course of even a single act as good fortune or happenstance. The overwhelmingly self-evident precision of haptic proprioception and exproprioception manifest within life's ordinary circumstances suggests that the information available in the multifractal tensegrity is so specific to body states that an animal could be said to make only one inference, hypothesis, or educated guess—namely, the right one (Neisser, 1978). On this observation, putative mechanisms of inferring, hypothesizing, and guessing are superfluous.

Here is the tenor of the preceding argument expressed in a different form. In Gibson's (Gibson, 1950, 1966, 1979) rethinking of the optical basis for vision he focused on the nomic (systematic, lawful) consequences of light structured by multiple surfaces environing a point of observation (Runeson, 1988). Ordinarily, surfaces differ in texture, pigment, reflection, and shadowing. And, ordinarily, surfaces are variably inclined relative to each other and variably distanced from each other. Collectively, these factors nomicly constrain the optic array at any arbitrary point of observation in the environment (Gibson, 1966, 1979). To reiterate, the optical array is a nesting of optical solid angles at the observation point the bases of which correspond to the faces and facets of surfaces, and the boundaries of which arise from the fact that the faces and facets reflect different amounts and color of light. Any such nesting of optical solid angles, therefore, will always be unique and specific to the surface layout that gave rise to it.

A frequently cited counter argument to specificity is a geometrical arrangement of trapezoidal surfaces (identical in texture, pigment and reflectance) that give rise to a false experience of a normal rectangular room when viewed through a designated peephole in one of the walls (Ittelson & Kilpatrick, 1961). Back-of-the-envelope calculations show that such a surface arrangement has a chance occurrence of only one in 100 million. Relaxing the restrictions on size, furnishings, and surface structure imposed upon the construction of the room reduces the chance occurrence by orders of magnitude (Runeson, 1988). Although man can conspire against specificity, Nature is not so inclined.

Toward a Haptic Conceptual Equivalent of the Optic Array

To reiterate, the multifractal tensegrity is a medium that permits the propagation and distribution of mechanical forces generated by, and imposed on, MCS. It is companion to air and water, which permit the flux of light, the transmission of vibrations, and the diffusion of volatile substances. The force distributed within the multifractal tensegrity arises from

multiple sources originating in the multifarious changing and persisting aspects of the mechanical relation of an animal and its environment. The primary question is how information about these sources is made available in the multifractal tensegrity. Taking the visual system and optic array as guide, we should ask: What would be the corresponding array for the haptic system? We intimated previously that it would be in terms of deformation. This potential answer requires further detail on the optic array.

The conception of optic array (Gibson, 1966, 1979) starts with the rejection of discrete points or spots of light, each with a locus indexed by coordinates, and each with a determinate intensity and frequency. (As implied previously, it rejects the theory of local signs.) The nesting of optical solid angles replaces the point matrix, the relation of inclusion (cf. Figure 21) replaces coordinates, and the relation of margin or contrast (e.g., differences of intensity and frequency in different directions) replaces individual magnitudes of point intensities. The optic array is an alternative description of the light distribution. It is a description that gives emphasis to relations (within an energy distribution) rather than energy. It is a description that expresses the structure in ambient light and, in consequence, provides a basis for identifying information about the conditions that give rise to it (see Gibson, 1966, 1979; Lee, 1980). Individual tensegrity icosahedra would be the functional equivalents of optic solid angles defined independently of a point of observation. In the same manner that optical solid angles assume their forms in respect to the layout of surfaces, tensegrity icosahedra will assume their forms in respect to the layout of forces. Insofar as they have a form in isolation, their concerted responses to a layout of forces would be a change of form, a deformation (see Figure 17d and Figure 19). Understanding this deformed state provides a deeper understanding of the hypothesized basis for information about.

For purposes of exposition, we focus on the strictly elastic tensegrity system (for deformation of the viscoelastic version, see Canadas et al., 2006). In the absence of external forces, the geometrical symmetry of an elastic tensegrity icosahedron (the six struts or bars aligned in pairs in three perpendicular spatial planes) fixes the ratio of cable length to bar, namely, cable length/bar length = $\sqrt{3/8}$ (Wendling, Canadas, Oddou, & Meunier, 2002). Without external forces, the 24 cables are tensioned equally and the stability of the tensegrity icosahedron's shape derives from the equilibrium of the internal forces and the constant ratio between the compression of the rigid bars and the tension of the elastic cables. With external forces, that is, with loading, tension equality across cables and, therefore, in all directions, transforms to different tensions in different directions (or differences in tension in different directions). In Gibson's ecological optics, it is these directional differences in respect to light intensity that endow the reflected light ambient to a point of observation with structure and, perforce, the potential for being information about environmental layout.

Of special relevance to the intimated parallel between light intensity differences and cable tension differences is the (perhaps unsurprising) observation that the tension structure of a tensegrity icosahedron is specific to the type of deformation. Externally imposed forces that extend, compress, shear, and torque the tensegrity icosahedron have a differential effect on (a) the number of slack and stretched cables, and the directions and amplitudes of the stretching, and (b) the directions and amplitudes of bar displacements (Wendling et al., 2002). Effects (a) and (b) induce two nonlinearities in the tensegrity icosahedron, geometrical and material. The geometrical is due to the spatial reorganization and mobility of the compression bearing bars, exerting a dominant influence on the linear deformation of the tension bearing cables. The material is due to the extension of some cables and not others during the overall deformation of the tensegrity icosahedron.

In sum, tension array (or, equivalently, deformation array) has emerged as the alternative description requested previously of the mechanical energy distributed in the multifractal tensegrity. Defining and elaborating the properties of the tension array will require an emphasis on relations analogous to that defining the optic array. They would be relations definable over the concerted responses of the individual tensegrity icosahedra and they would specify the states of MCS. Pursuant to Kugler and Turvey (1987, Table 4.1), whereas the multifractal tensegrity requires a force description (one in terms of all three fundamental dimensions of mass, length and time [M, L, and T, respectively]), the descriptors of the tension array are kinematic (L, T), geometric (L), and temporal (T). In picturesque terms, the nonkinetic tension array is expressed as flows, spatial patterns, and spectra, respectively.

Construing Haptic Perception

Given the hypothesized haptic medium, and the hypothesized specificity of haptic information, how should haptic perception be construed? What manner of functioning is to be attributed to the nervous system in this regard? Answers can be crafted from (a) basic premises of the ecological perspective on visual perception (e.g., Gibson, 1966, 1979) and (b) a slowly evolving reconceptualization of the somatic nervous system. We begin with (b).

Purves et al. (2008) ended their summary of the somatic nervous system as in following way:

Finally, a fundamental but often neglected feature of the somatic sensory system is the presence of massive descending projections. These pathways originate in sensory cortical fields and run to the thalamus, brainstem, and spinal cord. Indeed, descending projections from the somatic sensory cortex outnumber ascending somatic sensory pathways! (p. 206)

In brief, the somatosensory nervous system, classified historically as afferent, is largely efferent (Nunez & Malmierca, 2007). The same can be said of the visual nervous system. The

majority of synapses on thalamic relay neurons are cortical in origin, not retinal (Montero, 1991; Nunez & Malmierca, 2007; Sherman & Koch, 1986). What role might the descending somatosensory projections serve? Do they exert detailed control on the afferent flow from spine to thalamus to cortex (Atkinson, Seguin, & Wiesendanger, 1974; Malmierca & Nunez, 2004)? Do they filter irrelevant afference (Brodal, 1992)? Or do they play (as often implied) the lofty role necessitated by abductive inference, that of modulating afference to evaluate whether it is explainable by one or more postural models complemented by one or more environmental models? Although the specific functional significance of the descending projections is enigmatic, the general functional significance is not. The fast conducting descending projections provide a flexible and dynamic way of changing the effectiveness of subcortical somatic nervous activity as conditions of stimulation change (see King, 1997).

We now consider (a)—the basic premises of the ecological perspective identified in respect to vision. The structure of the optic array in air or water is information about, in the sense of specificity to, the layout of surfaces (of the environment, of one's nonoccluded body) and its transformations.

The information about manifest in the optic array is not transmitted (conveyed) to the brain but, rather, is detected by the visual perceptual system of which the brain is the central component. Given the ecological fact of specificity, this act of information detection is visual perception (Turvey & Shaw, 1995; Turvey et al., 1981)

The preceding can be readily adapted to the haptic case. Doing so answers the question of the construal of haptic perception.

The tension array is information about, in the sense of specificity to, the layout of the body, its transformations, and its attachments. This information about manifest by the tension array is not transmitted to the brain but, rather, is detected by the haptic perceptual system of which the brain is the central component. Given the ecological fact of specificity, this act of information detection is haptic perception.

The question of the manner of functioning to be attributed to the nervous system in haptic perceiving can now be answered. The ascending (receptive) and the descending (adjustive) somatosensory activities constitute a unitary architecture for detecting. It is a strictly neural variant of a responsive architecture, an organ of sensitivity (Gibson, 1966), exemplified previously by the cochlea.

Synchrony and Resonance

The contrast drawn previously between an inference-based (abduction) perspective on haptic perceiving and the ecological perspective can be drawn more crisply in a way that promotes further speculation on haptic perceiving's neural support.

The abduction perspective: Haptic perceiving identified with an inferential conclusion (about the dispositions of the

body, its parts, and the adjacent environment). True by force of argument. Entails computation.

The ecological perspective: Haptic perceiving identified with an existential fact (about the dispositions of the body, its parts, and the adjacent environment). True by force of existence. Entails resonance.

The concept of resonance is allied with the concept of synchrony. Neither plays a truly major role in theorizing about the nervous system but both are recognized as being of potential significance to understanding its function (e.g., Brette, 2012; Hutcheon & Yarom, 2000; Roy & Alloway, 1999; Singer & Gray, 1995). To date, efforts to inject them into theory consist of suggestions as to how they might facilitate computation. They are not recognized as stand-alone conceptions of a diametrically opposite theory.

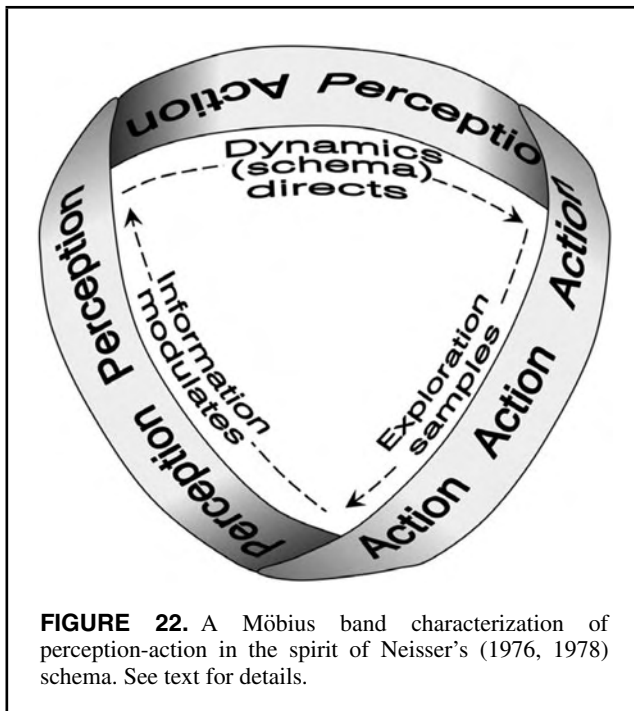
In regard to the somatosensory system, there is considerable evidence of synchronization within the responsive (adjustive-receptive) architecture (see summary in Nunez & Malmierca, 2007). Neurons that are spatially distributed but share common receptive fields may be synchronized by both the conditions of receptor stimulation and the adjustive activity of the descending projections (Temereanca & Simons, 2004). Rhythmic whiskering behavior in the rat is prefaced in the trigeminal system (the somatosensory system for the face) by synchronicity at brain stem, thalamus, and cortical levels. The role of the synchronicity is arguably twofold: it hones the registering of receptor stimulation and optimizes the integration of neural activity within the trigeminal system (Nicolelis, Baccala, Lin, & Chapin, 1995). When sought more broadly, at the scale of the cerebrum, synchronicity's role seems to be rapid (zero time-lag) coordination of cortical functions. In cat brain, a sudden change in a viewed pattern engenders instant visual-parietal-motor coherence (Roelfsema, Engel, Konig, & Singer, 1997).

For Gibson (1966), the preferred technical language for the neural support of perceiving was colloquial physics: perceptual systems attune to, resonate to, or with, and hunt, seek, or explore for. Although it was not spoken of in these terms, Neisser's (1976) perceptual cycle can be cast as the means of coming into resonance with. It is expressed in Figure 22 in terms of a perception-action Möbius band (paralleling Figure 7). The band's schema component identifies dynamics that modulates the activity of making information available and is modulated, in turn, by the information made available thus far, and so on, concurrently, up to resonance.

Does the Multifractal Tensegrity Include Brain?

Dictionaries (e.g., Merriam-Webster) are likely to begin the definition of brain with the portion of the vertebrate CNS enclosed in the skull and continuous with the spinal cord through the foramen magnum that is composed of neurons and supporting and nutritive structures (as glia). The question of brain raised here is in respect to supporting structures.

In forming the body's ECMs, fibroblasts secrete into every nook and cranny. There are no empty spaces.



Consider the onion-like Pacinian corpuscle, a mechanoreceptive element in connective tissue. The concentric lamellae surrounding the unmyelinated fiber at the corpuscle's core are thinly separated. ECM fills these spaces (see summary by Vega, Garcia-Suarez, Montano, Pardo, & Cobo, 2009). The action potential of the corpuscle may arise not only from deformation of the lamellae but also from changes in C and T within the interlamellae ECMs.

Similar to the narrow spaces of the Pacinian corpuscle's lamellae, the narrow spaces in the brain prove to be filled with ECM—not that secreted by fibroblasts but that secreted by neurons and glial cells (e.g., Faissner et al., 2010). The view until very recent times was that the close packing of neurons and glia left no room for any other material. Newer technologies proved otherwise, identifying empty spaces (e.g., Feigin, 1980) and a variety of ECM molecules that fill them (e.g., Rutka et al., 1988). It is now known that ECM accounts for 10–20% of the mature brain (Ruoslahti, 1996).

The ECM of the brain and its neurons is not the same as the ECM associated with joints, muscles and organs (Ruoslahti, 1996; Zimmermann & Dours-Zimmermann, 2008). As noted, it is created by, and embeds, glial cells, not cells of the fibroblast family. Further, in respect to ECM depicted in Figure 2, brain ECM is primarily extracellular macromolecules of the first main class, the glycosaminoglycans, with extracellular macromolecules of the second main class, the fibrous proteins (e.g., collagen), largely absent.

Hyaluronan-Based ECM

The formative glycosaminoglycan of brain ECM is hyaluronan. Similar to glycosaminoglycans in general,

hyaluronan (a) occupies a very large volume of ECM relative to its mass, (b) forms gels even at low concentrations, and (c) binds a large quantity of water that is extruded when the ECM is compressed and replenished when the compression is released. As emphasized in regards to Figure 2, and the ECM of connective tissue discussed thus far, the inward drawing of water creates a swelling pressure (a turgor) allowing the ECM to withstand compressive forces. The same can be expected of brain ECM (Ruoslahti, 1996): hyaluronan provides an ECM state that bears compression. It provides the C of tensegrity. What remains to be discerned—absent fibrous matrix proteins such as collagen—is what in brain ECM could bear the counterbalancing tension? What provides the T of tensegrity?

Experimentally, hyaluronan can be shown to exhibit multiple conformations including extended chains or cables, helical coils, and toroids (Cowman et al., 2005). It could, therefore, in principle, do more than bear compression. The ability of hyaluronan to form cables suggests that hyaluronan-dependent ECM can be tensioned as well as compressed (Evanko, Tammi, Tammi, & Wight, 2007). Structured hyaluronan-based ECM has the potential for tensegrity.

Astrocytes

Similar to collagen-based ECM, hyaluronan-based ECM embeds nonneuronal (nonconducting) cells. Collectively these cells and hyaluronan-based ECM define the brain's connective tissue enveloped by the collagen-based meningeal connective tissue (see subsequent discussion). Of particular significance are the mechanosensitive astrocytes. As shown in Figure 23, numerous long processes emanate from such cells (analogous to the caricature of a star from which they take their name) to make multiple connections with neurites (the axons and dendrites of neurons), blood vessels, other astrocytes, and, most importantly for present purposes, the pia mater. As emphasized by Ostrow and Sachs (2005), the ubiquitous and rich three-dimensional interconnectedness of astrocytes yields a morphology ideal for a broad registration of, and response to, mechanical disturbances. Included in these mechanical disturbances are those disturbances associated with the neurites as they systematically adjust in length to maintain a steady tension (see summary of neural mechanics in Van Essen, 1987). Also included in these mechanical disturbances are those disturbances associated with the meninges. As the following paragraphs make evident, this latter fact is the basis for including brain and spinal cord in the proposed haptic medium, the multifractal tensegrity of the MCS system.

The Meninges

The dura, arachnoid, and pia maters comprising the meninges are collagen-based fibrous sheets that cover the brain and the spinal cord and penetrate both. The dura is the outermost layer; the pia is the innermost layer. Both are dense irregular fibrous tissue (see Table 1). The intermediate

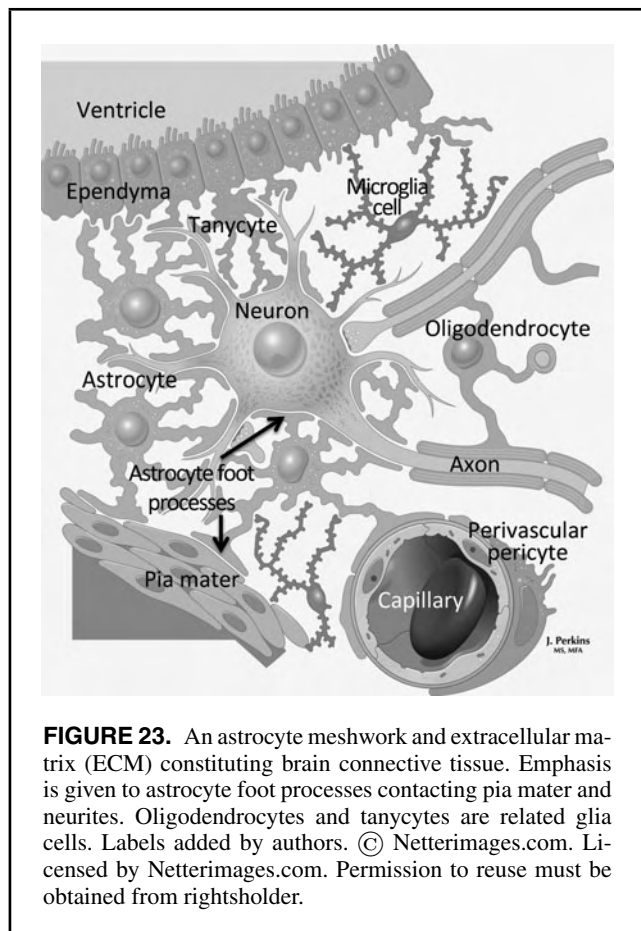


FIGURE 23. An astrocyte meshwork and extracellular matrix (ECM) constituting brain connective tissue. Emphasis is given to astrocyte foot processes contacting pia mater and neurites. Oligodendrocytes and tanycytes are related glia cells. Labels added by authors. © Netterimages.com. Licensed by Netterimages.com. Permission to reuse must be obtained from rightsholder.

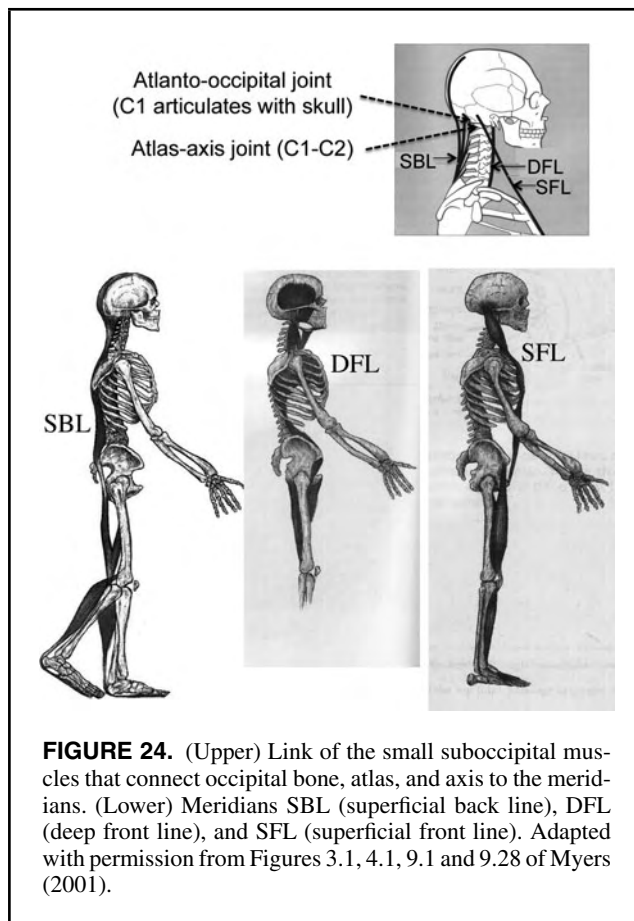


FIGURE 24. (Upper) Link of the small suboccipital muscles that connect occipital bone, atlas, and axis to the meridians. (Lower) Meridians SBL (superficial back line), DFL (deep front line), and SFL (superficial front line). Adapted with permission from Figures 3.1, 4.1, 9.1 and 9.28 of Myers (2001).

arachnoid layer is loose fibrous tissue (see Table 1). Traditionally conceived as merely protective covering for the CNS, the meninges are currently touted as modulatory of many, if not most, of the physiological and pathological events of the CNS (Decimo, Fumagalli, Berton, Krampera, & Bifari, 2012).

Focusing on the pia mater, the cranial variant envelops the cerebrum and cerebellum, extends into the sulci and fissures, and forms the nonneural roof of several ventricles. Its attachment to the brain is through the mechanically responsive meshwork of astrocytes—specifically, through their foot processes (see Figure 23). Accordingly, forces generated within the cranial pia mater, and forces impressed on it from any source, will modulate the astrocyte meshwork through the meshwork’s foot-processes and, in turn, the neurites to which the meshwork connects.

Myodural Bridges

One likely source of forces exerted on the cranial pia mater is the cranial dura mater. Assuming such dura mater forces, the joining fibrous linkages would transfer them to the arachnoid mater. In turn, the fine fibrous strands tethering the arachnoid and pia meninges would transfer the forces of the former to the latter. The question begged by the foregoing

is that of the variety and origins of the hypothesized forces on the brain’s dura mater. Some insights are provided by almost brain dura mater (that between the first and second cervical vertebrae) in the raising, lowering, and turning of the head.

The cervical intervertebral spaces at the back of the head contain intricate connections between suboccipital musculature and cervical dura mater (e.g., Hack, Koritzer, Robinson, Hallgren, & Greenman, 1995). Four small suboccipital muscles connect occipital bone, atlas, and axis (Standring, 2008). They are involved in (a) flexion–extension of the head at the atlanto-occipital joints, and (b) rotation of head and atlas on the axis (see Figure 24, upper panel). Studies of this region reveal myodural bridges—fibrous linkages between the suboccipital muscles and the cervical dura mater (e.g., Pontell, Scali, Marshall, & Enix, 2013; Scali, Marsili, & Pontell, 2011; Scali et al., 2013). One suggested role of these bridges is to coordinate motion of the upper cervical spine and the craniovertebral joint with that of the cervical dura mater. The present thesis would suggest a further role for the myodural bridges. Namely, contributing to the whole-body continuity of myofascial force transmission as constituents of the hypothesized multifractal tensegrity of the MCS system.

Myofascial Meridians

Figure 24 (lower panel) depicts three functionally connected meridians of myofascia—three precise lines of pull through the body—advanced by Myers (2001). They are derived by rules, for example, “Follow the grain of the connective tissue, maintaining a fairly steady direction without jumping joints or crossing levels through intervening planes of fascia” (Myers, 2001, p. 57). The meridian termed the superficial back line (SBL) connects the entire posterior surface of the body from the bottom of the feet to the top of the cranium. (It does so in two sections, from toes to knees and from knees to brow.) The meridian termed the superficial front line (SFL) connects the entire anterior surface of the body from the top of the feet to the side of the cranium. It also does so in two sections, from toes to pelvis and from pelvis to cranium. Sandwiched between these two meridians (in reality and in Figure 24 lower panel) is the “body’s myofascial ‘core’” (Myers, 2001, p. 191), the meridian termed the deep front line (DFL), running from deep inside the foot to the neurocranium (dorsal skull enclosing the brain) and the viscerocranium (facial skeleton). Minimally, the meridians provide a myofascial context for the myodural bridges (as shown in Figure 24 top panel); maximally, they are inclusive of them.

To an important degree, a positive answer to the question of “Does the multifractal tensegrity include brain?” rests on showing that myofascial lines inclusive of myodural bridges are also inclusive of the meninges. That such could be the case is an open possibility given that brain dura and spine dura, though different in composition, are continuous through the foramen magnum. If the possibility proved to be actuality, then a reasonable expectation would be that the interplay of tension and compression from near and distal parts of the MCS system are communicated to cranial dura mater and thence to cranial pia mater and the brain’s connective tissue—the hyaluronon-based ECM and the various cells, neurons and glia, embedded within it. By the same token, there should be a reciprocal consequence, however minimal, for tension and compression arising within the brain’s connective tissue. Astrocyte stress-fibers *in vitro* organize into parallel bundles that can span many cells. Ostrow and Sachs (2005) suggest that such an arrangement *in vivo* would allow the astrocyte network to exert (long-range) forces on the ECM. If the impedance matching was of the right order, then such forces could, in principle, modulate the tensile state of the pia mater, and communicate subtle mechanical states of brain tissue to the multifractal tensegrity in the large.

Phantom Limbs and Impossible Limbs

Can the experiencing of an amputated limb, or a limb absent from birth, be accommodated by the MCS concepts of multifractal tensegrity and tension array? The leading perspectives on the phantom experience situate its basis in the brain as opposed to (a) the peripheral nervous system, or (b) the intact (albeit incomplete) body. Opposition (a) is the immediate focus.

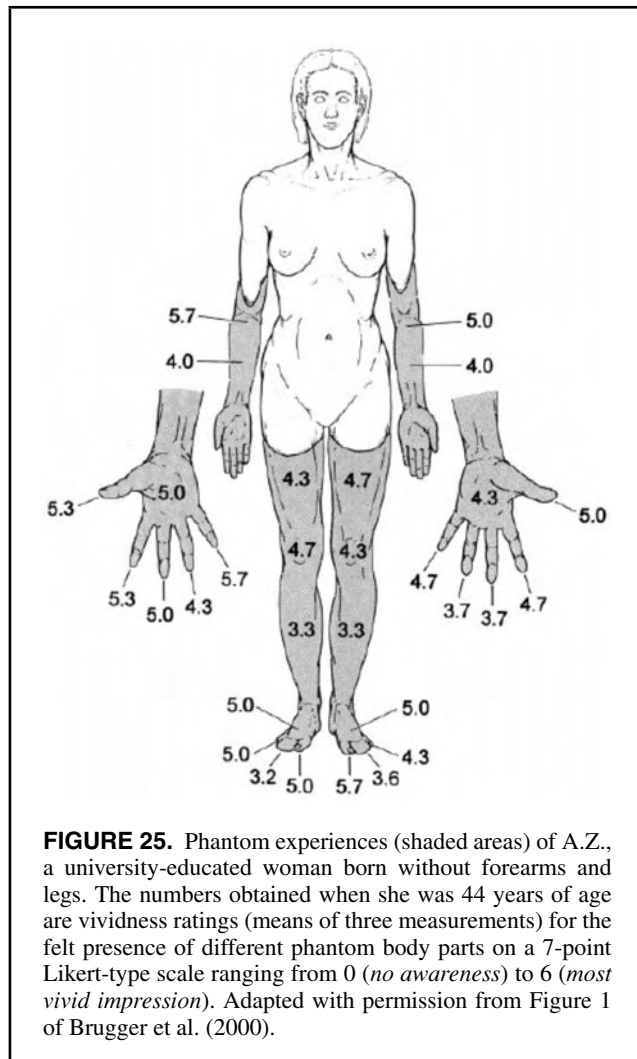
Neuromatrix Theory

The motivation for central neural processes as opposed to peripheral is threefold: (a) the observation that phantoms (e.g., of an amputated hand) persist when the affected body part (the arm) is disconnected from the central nervous system by a high-level spinal transection (e.g., Melzack & Loeser, 1978), (b) the evidence of aplasic phantoms, those that occur for limbs that never were, that is, limbs absent from birth for congenital reasons, not surgical (see Figure 25; Brugger et al., 2000), and (c) the well-documented topographical organization of the primary sensory cortex and its reorganization following amputation. Parts (a) and (b) of the threefold motivation suggest that the design of the human brain must be such that body part x is neither a necessary nor sufficient cause of awareness of body part x . What would seem to be necessary and sufficient is a distributed aspect of human brain, genetically endowed with an enduring and relatively intransigent functional map of the human body. The foregoing is Melzack’s (1990) neuromatrix theory. Its implication is that “the anatomical substratum of the physical self is a network of neurons that extends throughout widespread areas of the brain” (p. 91).

Some caution is warranted with respect to the degree of significance attributable to (b). Aplasic phantoms occur infrequently, in less than 20% of the cases; the number is 50% for people subject to amputation prior to 6 years of age (Melzack, Israel, Lacroix, & Schultz, 1997). The comparative rarity of aplasic phantoms in conjunction with a systematic increase in amputee phantoms from two years or less since surgery to 10 years since surgery suggests the involvement of experiential factors (Price, 2006).

Hypothesized Invariance of Motor Command Map

An alternative account of the threefold motivation takes as its focus the neurobiological support for action rather than the neurobiological support for perception. Reilly and Sirigu (2008) hypothesize that in the primary motor cortex movements of body parts are specified at two levels: (a) that of the part’s motor commands (the command map) and (b) that of the specific muscles expressing the part’s movements (the muscle map). Reorganization following amputation is in terms of the muscle map, not the command map. The persistent integrity of the command map underlies the existence of phantoms. Spelled out: reorganization of cortical topography consequent to loss of a body part is such as to leave the motor command map unchanged over changes in the muscular map. With respect to phantom limbs, representations of movement commands survive amputation and are manifest under certain circumstances. The manifestations are possible because spinal, subcortical, or cortical reorganization permit the preserved representations of movement commands to express themselves within new sensorimotor organizations (Reilly & Sirigu, 2008). The primary counterpoint to the command map conjecture is that



phantoms occur for body parts, such as the breast, where movement is not an issue (e.g., Kinsbourne, 1995).

The role of topographical maps in respect to phantoms—motivation (c) of the threefold motivation—is pivotal to the contrast with neuromatrix theory. For both perspectives, the sensory and motor cortical maps as conventionally described must be excluded from the proposed explanation. The two perspectives differ in how they effect that exclusion—by either entrusting most of the brain with responsibility or by assigning it to motor commands—but they are alike in their reason for doing so.

Following amputation of x (e.g., right hand), the common understanding is that regions of sensory and motor cortex that represent x are annexed by neighboring regions (e.g., the right forearm, the right side of the face), to the extent that x 's representation is deleted (for deletion in motor topography, see Irlbacher, Meyer, Voss, Brandt, & Roricht, 2002). This understanding is at odds, however, with an amputee's detailed awareness of the current disposition of a phantom arm—its position, its movement, its temperature (Reilly & Sirigu, 2008)—and an apraxia's detailed awareness of the

dimensions of a phantom hand (Longo & Haggard, 2012). It is also at odds with the observation that phantom finger movements are accompanied by electromyographic activity in the arm's biceps, triceps and deltoid muscles, activity that would have been notably absent when the limb was intact (Reilly, Mercier, Schieber, & Sirigu, 2006).

That phantom experience might be indifferent to changed topography is strengthened by the mixed results on so-called referred sensation: the site at which a touch is felt (e.g., arm) is not the site that was touched (e.g., face). In the presumed topographic reorganization following upper limb amputation, the somatosensory homunculus commonly portrayed in textbooks would have the head's representation encroach upon the neighboring space of the arm's representation. There should be occasions, therefore, on which a touch on the face should be felt as a touch on the arm (Ramachandran & Hirstein, 1998; Ramachandran, Stewart, & Rogers-Ramachandran, 1992). While such is sometimes the case, unpredictable referrals and no referrals are common (e.g., Grusser et al., 2004; Grusser et al., 2001; Knecht et al., 1996). Hunter, Katz, and Davis (2003) concluded that "functional sensory mapping is a relatively rare phenomenon" (p. 587).

Reorganization and the Unitary Adjustive-Receptive Architecture

A rapidly evolving conception of fundamental importance, foreshadowed previously, is that the large-scale reorganization of the somatosensory cortex subsequent to deafferentation from loss of a body part may not arise cortically (at least not in full). It may arise from the spinal cord, brainstem, and thalamus, via afferents that sprout into the now afferent-deprived territories of neighboring body parts (e.g., forearm in the case of an amputated hand; Faggin, Nguyen, & Nicoletis, 1997; Florence & Kaas, 1995).

Of special note are experiments in which peripheral deafferentation is induced temporarily by chemical means (e.g., Jung & Shin, 2002; Krupa, Ghazanfar, & Nicoletis, 1999). Cortical sensory reorganization follows immediately, paralleled by simultaneous reorganization at thalamic and other subcortical levels—observations consonant with evidence for continuous ECM dynamics (Sivakumar et al., 2006). The close similarity of the novel cortical and subcortical spatiotemporal activity is suggestive of a dynamic equilibrium (Krupa et al., 1999) within the unitary ascending (receptive) and descending (adjustive) architecture of the somatosensory system. The immediacy of this new equilibrium has obvious bearing on the observation of instant phantom limbs created experimentally through anesthesia (e.g., Bromage & Melzack, 1974; Melzack & Bromage, 1973; see subsequent discussion).

Implied Group Symmetry and the Symmetry Principle

Overshadowing the differences between the neuromatrix theory and the motor command-map perspective is the profound aspect of limb perception that grounds them both—its

symmetry in the group theoretic sense. The latter, colloquially speaking, is the number and kinds of transformations that can be done to a thing so that having done them the thing remains the same as before. Experiencing a limb—or, better, for present purposes, limb perception—persists in the face of (a) loss of limb, (b) nondevelopment of limb (best indexed to date by Brugger et al., 2000; see Price, 2006), (c) upper level transection of the spinal cord, and (d) reorganization of the topographic maps of the sensory and motor cortices.

The ideal strategy for developing a theory that accommodates the phantoms-based characterization of limb perception is via the symmetry principle, namely, the symmetry group of the cause is a subgroup of the symmetry group of the effect (Rosen, 1995). The inventory (a–d) is an inventory of phenomena defining the effect. One would like to identify the cause of this effect and its lawful basis. The symmetry principle sets an upper bound on the symmetry of the cause: it can be no more symmetric than the effect. The ideal strategy therefore would be to identify the symmetry of phenomena (a–d) and then proceed to construct a theory in which the cause has the same symmetry (Rosen, 1995). Working against this ideal is that the symmetry of the effect is usually only approximated by the phenomena. The present case is very much a case in point.

Although discerning the desired symmetry principle is beset with difficulties, the starting point from the present perspective is self-evident. The symmetry group of the cause is that of the MCS system's multifractal tensegrity and its tension arrays. The arguments made in the preceding section for the brain's inclusion within the multifractal tensegrity introduced concepts essential for addressing how this cause applies to phenomenon (c). Our earlier comments with respect to the thermodynamics of nested biological tensegrity systems and the reciprocity of architecture and process may have bearing on phenomenon (d). That bearing would be especially so if the organization and reorganization of brain topography have less to do with the neural support for perception and more to do with "housekeeping" (Weinberg, 1997, p. 115), for example, facilitating the microcirculation within primary cortex of oxygen and glucose, or minimizing wiring costs for a given intracortical connectivity (see Chklovskii & Koulakov, 2004; Van Essen & Dierker, 2007).

It is in the context of these remarks on the symmetry principle that we turn to the second of the two oppositions introduced at the outset of the present section. We phrase the opposition as the possibility that the basis of phantoms is not the brain (as commonly assumed, e.g., Melzack, 1990; Ramachandran & Hirstein, 1998) but the intact (albeit incomplete) multifractal viscoelastic tensegrity. We ask how the proposed cause—MCS's multifractal tensegrity and tension arrays—includes phenomena (a) and (b) in its effect.

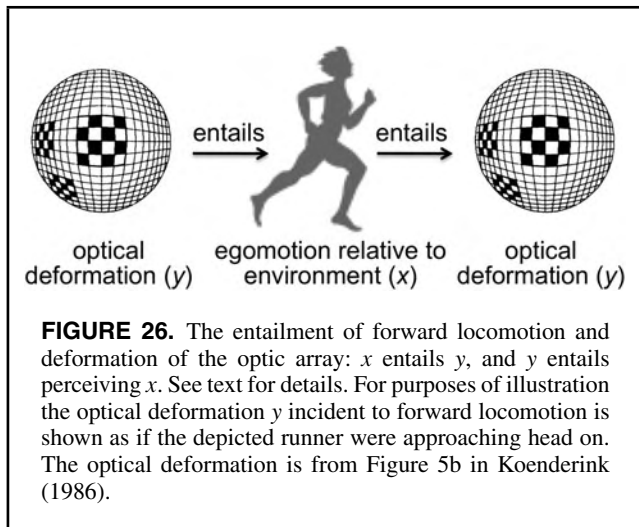
Multifractal Tensegrity and Neuromatrix

Loss of a limb is a selective ablation of the multifractal tensegrity (abbreviated henceforth as MFT). Nondevelop-

ment of a limb is an incomplete epigenesis of MFT. In either case, we could hypothesize that MFT architecture and dynamics are such that the full MFT is implicit in a partial MFT of some minimal magnitude and form. The symmetry relation or law identified for some multifractal phenomena (Mirlin, Fyodorov, Mildenerger, & Evers, 2006; Monthus, Berche, & Chatelain, 2009; Rodriguez, Vasquez, & Römer, 2008) gives encouragement for the conjectured MFT part-to-whole implication: It suggests that distributions of events or structures at larger and smaller scales are co-implicative. A less demanding hypothesis is that the residual MFT is sufficient to support tension arrays specific to a large variety of limb states.

The neuromatrix hypothesis (Melzack, 1990) requires the body in all its details, a neural representation of the body in all its details, and a mechanism that coordinates the two (requirements that, in combination, are deemed genetically anomalous by Price, 2006). The MFT hypothesis shares with the neuromatrix hypothesis the notion of a basis for limb perception that is persistent and common to intact persons, persons with amputations, and persons with amelia (Figure 25). The MFT hypothesis differs from the neuromatrix hypothesis in that this basis is singular. Any body part x , in any particular configuration, on any particular trajectory, is specified by a tension array of MFT. The specification is presumed to hold whether MFT is complete or incomplete, whether the body part x is extant or nonextant. The MFT hypothesis can, therefore, be expressed in language that parallels the language of Melzack's (1989, 1990) starting point for the neuromatrix hypothesis: The experience of a phantom limb has the quality of reality because it is governed by the same principles of ecological realism (for Melzack, "produced by the same brain processes") that underlie the experience of the body when it is intact.

As argued previously, what is fundamental to the tension array is not (a) the tension magnitudes of MFT's component tensegrities, but (b) the differences of the tension magnitudes of MFT's component tensegrities in different directions. The significance of (b) is twofold. First, the emphasis on differences or contrasts—broadly speaking, an emphasis on relations—is a stepping-stone to first appreciating, and then identifying, the specifying richness of tension arrays. Second, it provides a primary entry point into understanding phantom limbs as body-based not brain-based: Contrasts of tensions (e.g., tension $p = 3 \times$ tension q) are invariant over magnitudes of tensions. A tension array specifying body part x is scale invariant. In principle, therefore, the same tension array, specifying the same MSC state of affairs, can occur at indefinitely many tension magnitude levels. On this understanding, there are two scientific issues in respect to the occurrence of phantoms. First, what are the circumstances that give rise to the minimally detectable tension array y that specifies x ? Second, what are the circumstances that dispose a person lacking body part x to attend to that minimally detectable tension array? Answers to these questions would explain, in the current perspective, why a person without body part x nonetheless perceives body part x .



Information About x Is Not x

The concept implicit in the preceding exposition of phantoms is that information about something is not that something. To recapitulate, a tension array specific to x can arise in circumstances in which x is absent.

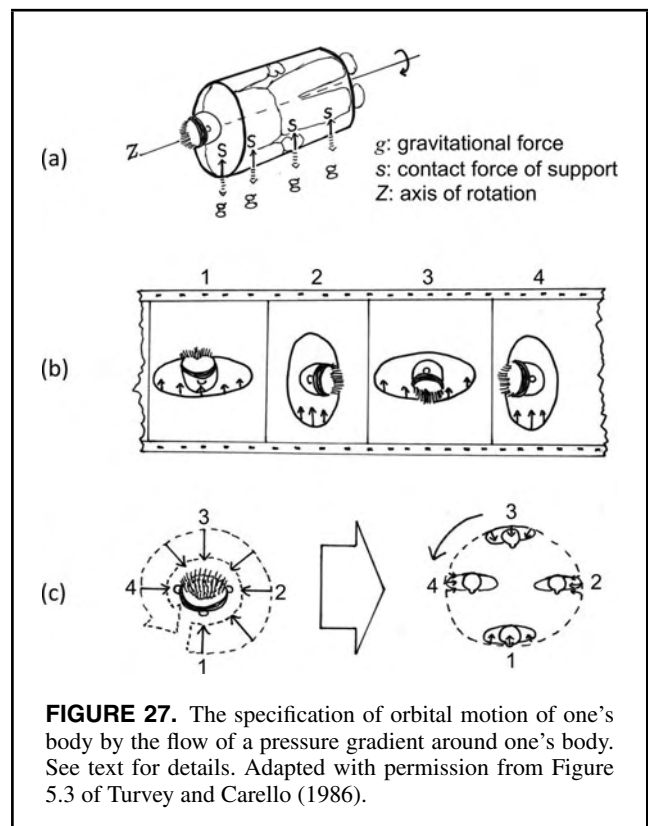
Tension arrays such as optic arrays are not identical to that which they specify. Within the ecological perspective, specificity implies a nomic relation between a property of an array (optical, tensional, etc.) and a property of the environment (broadly speaking, the layout of surrounding surfaces and accompanying events in the optical case, and the layout of the body and accompanying events in the tensional case). Consider Figure 26. From center to right the figure schematizes the optical deformation y entailed by egomotion x in a structured environment. From left to center the figure schematizes egomotion x entailed by the optical deformation y . The latter is confirmed experimentally by conditions that simulate or produce y in the absence of x . In such conditions a person perceives x —that is, perceives he or she is in forward motion relative to the environment (e.g., Lishman & Lee, 1973). Information about x is not x .

A further example, in the haptic domain, is valuable. It is a contrived setting, not a natural one (for details, see Lackner, 1981). It is depicted in Figure 27. In this example, an implied orbiting of the body with the body facing in a constant direction is x . The information y about this orbiting arises from a barbecue spit rotation of a blindfolded participant (Figure 27a). A consequence of the rotation is a gradient of the supporting contact forces countering gravity that peaks on the underside of the drum (see arrows). Figure 27b shows how this gradient moves around the body in a direction opposite to that of the rotation. It shows y . As expressed by Figure 27c, this global deformation y of the body’s tissue specifies x . Again, information about x (here, x is orbiting) is not x .

Vibrating MCS

Close cousins of phantom limbs are phenomena observed with intact persons that are similarly addressable from the perspective of information about x is not x . These phenomena are incident to experimental vibration of muscle and its connective tissue (including its aponeuroses: see Table 1). They include the experiencing of limb orientations that are anatomically unattainable, such as hyperextension in which the hand seemingly bends backwards into the dorsal surface of the forearm (Craske, 1977; Gandevia, 1985; Lackner & Taublieb, 1983). They also include (on anecdotal reports) the experiencing of more than one limb and the separation of adjacent limb segments (e.g., finger from hand, hand from forearm; Craske, 1977; Lackner & Taublieb, 1984). The most common and most thoroughly investigated phenomenon arising from vibration of MCS is the experiencing of limbs at inclinations greater than or less than actual inclinations, and moving to these positions at speeds greater than or less than actual speeds (see summary by Jones, 1988). It should be underscored that a vibration-induced limb movement constrains visual behavior similarly to an actual movement (Lackner & Levine, 1979). Subject to vibration of the arm’s biceps muscle, a person will lower the direction of gaze when tracking the position of the index finger hidden from view (Lackner & Taublieb, 1984).

According to the present argument, the muscle spindle activity induced by vibration is an aspect of the detecting



(or pickup) of information by the responsive architecture of the haptic perceptual system. Muscle spindle activity is not information about the state of the limb (likewise for the muscle spindle population-coding vector; e.g., Ribot-Ciscar, Bergenheim, Albert, & Roll, 2003). Vibration can be expected to perturb and deform MFT in ways dependent on the vibration parameters (see Ettema & Huijing, 1994). The tension array, specific to the vibration-dependent deformation, is information about the state of MFT. Muscle spindles and other mechanoreceptors embedded in MFT are responsive, at the scale of muscle fibers, to changes in the tension magnitudes of MFT's component tensegrities. Detection of the tension array, the information about MFT, is the charge of the full adjustive-receptive architecture of the somatosensory nervous system (embedded in a movable, and typically exploring body).

A Common Principle

Phenomena of phantom limbs and of limbs driven by vibrations of muscles and their connective tissue are potentially understandable through a common principle. We regard this principle, a principle of information specificity, as foundational to the ecological approach to perception and action. If y specifies x , then to detect y is to perceive x . This is so even if x is absent, and even if x is improbable. The sole desideratum of the MFT hypothesis is that MFT either intact (vibratory phenomena) or partial (phantom phenomena) can support y . It should be strongly noted how the logic of abduction (the logic implicit in brain centered theoretical accounts of phantom limb perception) fares in this regard. If x is absent or improbable, then x is an unlikely candidate for the most likely cause of y and, in consequence, x is most unlikely to be perceived.

By Way of Conclusion: Archetypal Phantoms and Neuropathy in Microgravity

Anesthetic Phantoms

Phantom arms and phantom legs occur under deafferentation by anesthesia. Bromage and Melzak (1974) investigated these occurrences in 169 participants (6 volunteers, 104 patients undergoing upper limb surgery, 59 patients undergoing lower limb or abdominal surgery). While supine, and with eyes closed, participants mimicked the arm phantom with the other (nonanesthetized) arm. They did so in two circumstances: anesthetized arm by the side, and experimenter manipulation of the anesthetized arm. For lower limb phantoms, the participants' provided verbal descriptions and an estimate of felt distance between the two knees. Phantom arm and phantom leg positions were coded as the coordinates (in degrees of arc) of the individual joint positions.

Bromage and Melzak (1974) found that that arm phantoms were similar from participant to participant (regardless of circumstance), and leg phantoms, though much less frequent, were likewise similar from participant to participant.

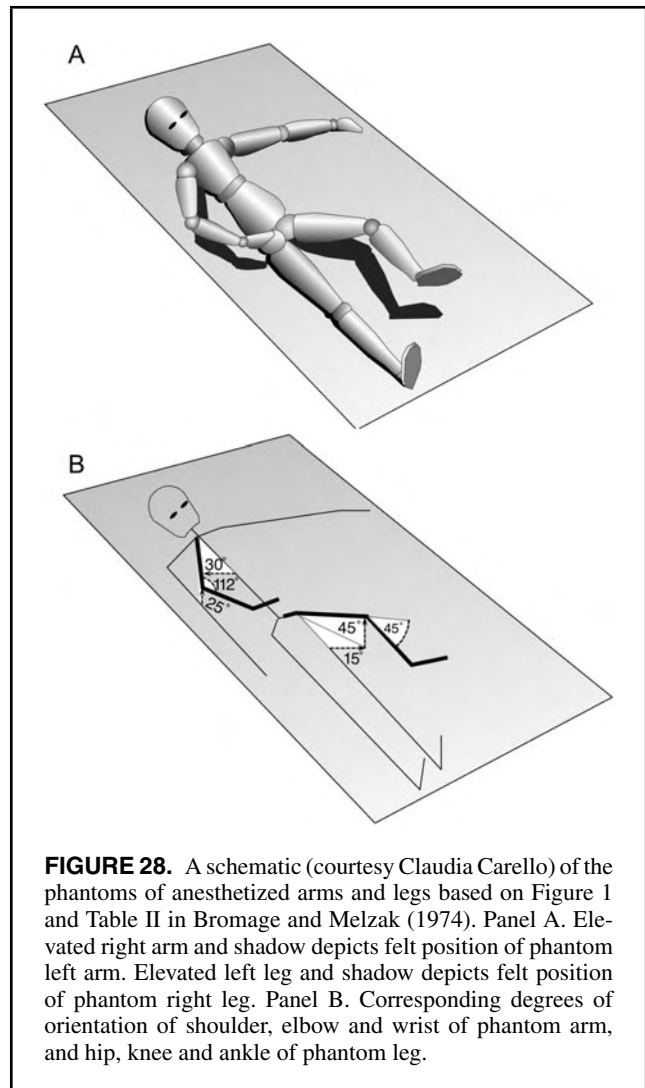


FIGURE 28. A schematic (courtesy Claudia Carello) of the phantoms of anesthetized arms and legs based on Figure 1 and Table II in Bromage and Melzak (1974). Panel A. Elevated right arm and shadow depicts felt position of phantom left arm. Elevated left leg and shadow depicts felt position of phantom right leg. Panel B. Corresponding degrees of orientation of shoulder, elbow and wrist of phantom arm, and hip, knee and ankle of phantom leg.

The discovered archetypal phantoms are summarized in Figure 28. They described the phantom limb positions as those of orthopedic rest. The phantom joints were clustered around the null position in the mid-range of joint movement. None fell at the extremes of flexion or extension. They explained the phantom limb positions of Figure 28 in these terms:

The mid-point of joint range is the position at which periarticular structures are least stressed, and at which both agonist and antagonist muscle groups are evenly balanced. In terms of neural information to the central nervous system this is therefore the point at which net background afferent input from mechanoreceptors is minimal. (Bromage and Melzak, 1974, p. 272)

A contemporary label for the phantom limb position of Figure 28 would be the previously defined loose packed position (Magee, 2007).

The circumstance of a phantom arm or leg of Figure 28 is that of (a) complete MFT, (b) the tension array of the complete MFT, and (c) detection of the tension array of the

complete MFT with the exception of the anesthetized limb's tension array. Thus, the detectable information about, say, the anesthetized right arm is the tension array of the supine body minus the tension array of the supine right arm. For the MFT hypothesis the question that would have to be answered is this: Why should the detectable information specify the arm posture of Figure 28? Whatever the outcome, a question of the preceding kind, and the theory development on which it is based, have merit. They avoid the circularity, the fallacy of *petitio principii*, or question begging, that is currently dominant in the scientific literature on phantom limbs.

The phantom experience of Bromage and Melzak's (1974) anesthetized patients is that referred to by Hunter et al. (2003) as phantom limb awareness (PLA), to be distinguished from phantom limb sensation (PLS). PLA is general awareness of the limb's presence. PLS is a specific sensory experience of the limb such as warm, cold, or painful. Hunter et al. (2003) underscore that PLS is not a necessary accompaniment of PLA. Two shoulder-level amputees were included in their sample of 13 amputees. One of the two, on the occasions of PLA, described the phantom limb's posture as elbow and wrist loosely flexed, shoulder rotated internally (cf. Figure 28).

Viral-Induced Neuropathy and Microgravity-Induced Pseudoneuropathy

The obvious counterpoint to the perception of inexistent limbs is the nonperception of existent limbs. The most documented case of the latter is I.W. A common illness resulted in sensory neuropathy from the neck down. In consequence he cannot perceive his limbs and trunk, or his adjacent environment, by means of the haptic system and must resort to other, explicitly inferential, means (Cole, 1995). In darkness, or with eyes closed, he is unaware of his limbs. In darkness, or with eyes closed, he cannot stand upright. If the lights are turned off in a room in which he is standing, he collapses to the floor with no awareness of his prone posture. In order to control and coordinate his limbs (albeit explicitly and tortuously) he must be able to see them (Cole, 1995). Appreciating the sensory neuropathy that affects I.W. is enhanced by its comparison with peripheral motor neuropathy. This much less frequent neuropathy is a matter of muscle weakness, cramping, and twitching, mostly confined to the upper limbs (for a full definition, see website of National Institute of Neurological Disorders and Stroke). It is a matter of motor comfort more than motor behavior. Whereas the detailed control and coordination of movement is seriously compromised by sensory neuropathy, it is largely unaffected by motor neuropathy.

Astronauts in the microgravity of space flight report perceptual problems similar to those of I.W. There are occasions in darkness when they can be unaware of their limbs (Clement & Reschke, 2008). Beyond a general degraded awareness of limb position, Spacelab astronauts experienced a complete loss of limb perception under relaxed conditions in weight-

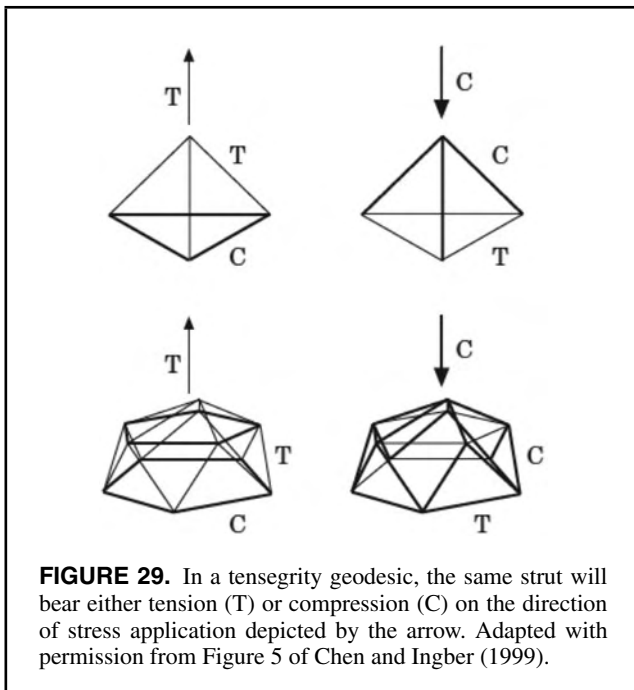
lessness with eyes closed and a restoration of limb perception when the muscles were contracted (Money & Cheung, 1991; Schmitt & Reid, 1985). An Apollo astronaut recalled (Clement & Reschke, 2008, p. 109):

The first night in space when I was drifting off to sleep I suddenly realized that I had lost track of . . . my arms and legs. For all my mind could tell, my limbs were not there. However, with a conscious command for an arm or leg to move, it instantly reappeared—only to disappear again when I relaxed.

A Gemini astronaut recalled waking in the dark during a mission and seeing a disembodied glow-in-the-dark watch floating before him. He asked himself where the watch had come from only to realize moments later that it was the watch on his wrist. The two recollections are cases of nonperception of a limb in its presence. The recollected phenomena (Clement & Reschke, 2008) stand in sharp contrast to the phantom phenomenon of perception of a limb in its absence. They also stand in contrast to the nonperception of a present limb by I.W. but on different grounds. In I.W.'s case, the nonperception is the consequence of extreme peripheral neuropathy.

Why might the nonperception of existent limbs arise in microgravity? Argument was given previously that the ECMs comprising connective tissue are compressed by the turgor of the ground substance. At the more molar level of the connective tissues of Table 1, however, concerns can be raised that fascia may be too flexible to function compressively (Scarr, 2012). Taking the concern seriously invites hypotheses about candidate sources of compression. Guidance comes from the understanding that a tensegrity system does not have to consist of isolated struts and cables (e.g., Rutka et al., 1988). The triangulated geodesic dome described earlier is only struts, as is the geodesic icosahedron of Figure 17A. Although each strut is stiff, it can resist tension or compression at a particular location depending on how it is loaded, as shown in Figure 29. The lesson of the geodesic dome and geodesic tensegrities in general is that what matters is how stresses are so distributed as to establish a force balance and stability in the face of shape distortion. In respect to fascia as the MCS system's primary component of tension, compression could be in the form of amplification of muscle diameter during contraction (Scarr, 2012) and it could be in the form of gravity. The combination seems to speak to the phenomenon experienced by the Apollo and Spacelab astronauts. In the absence of gravity and muscle contractions, there may be circumstances in which one cannot perceive one's limbs. With muscle activity, however, limb perception is restored, but only temporarily, with the perception ending when the muscle activity ceases (Clement & Reschke, 2008).

In the context of the present collection of arguments, the implication of microgravity-associated peripheral pseudoneuropathy is that reduced gravity affects MFT and, perforce, the tension array. Virus-associated peripheral neuropathy (that ascribed to I.W.) may be understood in



similar terms. Returning to the fibroblasts of Figure 1, we recall their necessary mechanical contribution to the assembly and function of connective tissue. Contemporary modeling (Lam, Bigley, Terhune, & Wakatsuki, 2012) suggests that infection disrupts the force-generating ability of fibroblasts and reduces, in consequence, connective tissue's cumulative contractile state. Given the embedding of mechanoreceptors in connective tissue, it is inevitably the case that, whatever the cause, the progressive degrading of connective tissue by chronic inflammation will negatively affect nerve fibers. Explanation of I.W.'s condition strictly in terms of loss of large myelinated sensory nerves (e.g., Cole & Paillard, 1995) may be in need of moderation. The condition might be appreciated more aptly as a compromised haptic medium, with all that that entails.

NOTES

1. The book was completed in the early 1940s. Internal politics in the USSR conspired against its publication.
2. To anticipate, we identify a particular mechanical characterization of the body (a multifractal tensegrity) as medium, and identify a multiscaled adjustive-receptive architecture as organ.
3. This further comment should be considered in light of a commonality between human and fibroblast locomotion. Human runners adjust the stiffness of their stance leg to accommodate surface stiffness during steady state running (Ferris, Louie, & Farley, 1998). This adjustment allows runners to maintain similar center of mass movement (e.g., ground contact time and stride frequency) regardless of surface stiffness. There are indications that given abrupt transitions in surface stiffness, leg stiffness adjustments occur rapidly enough to minimize disruption of the running mechanics.
4. Although our emphasis is on perception, we should note similarities between the dynamical principles of tensegrity and the Equilibrium Point Hypothesis of motor control (e.g., Feldman &

Levin, 1995). Among the similarities identified by Silva, Fonseca, and Turvey (2010) is the "very unusual property" (Skelton & de Oliveira, 2009, p. 23) that tensegrity stiffness can be changed without changing external tensegrity shape, and conversely, tensegrity shape can be changed without changing tensegrity stiffness. Central to the Equilibrium Point Hypothesis are the c and r commands: the former changes joint stiffness but not joint equilibrium; the latter changes joint equilibrium but not joint stiffness.

5. It should be noted that the literature recognizes two broadly distinguished types of tensegrity systems, one structural and one energetic. Defined structurally, a tensegrity system is a system in which prestress (in the form of tensioned components) is balanced predominantly by internal struts (compressed components). Defined energetically, a tensegrity system is a system in which equilibrium of the tensioned and compressed elements arises from minimizing the stored elastic energy (Connelly & Back, 1998). The two definitions differ in how prestress is balanced (Wang et al., 2001)—strictly by internal components in the structural case, and by external as well as internal components in the energetic case. Although structural tensegrity is the most studied, current modeling of the cell emphasizes energetic tensegrity. The contributions of microtubules to the cell's compression are aided and abetted by the external attachments of the cytoskeleton to ECM and neighboring cells (Stamenovic, Mijailovich, Tolic-Norrelykke, Chen, & Wang, 2002; Wang & Suo, 2005). The tent metaphor (Figure 4) applies to the energetic variant of tensegrity system, not the structural.

6. There is evidence of circumstances in which perception of limb position is conditional on efference as well as afference (e.g., Proske & Gandevia, 2009). It could be asked whether it is consistent with an underlying adjustive-receptive architecture at all scales.

7. As an important aside, this myofascial force transmission is evident in organisms with very different body architecture, such as insects. Active and passive forces at the ventral origin and the dorsal insertion of the flight muscle of the migrating locust prove to be significantly different (Meijer, 2007).

8. A mechanism of the flow of forces is provided by Gao, Wineman, and Waas (2009).

9. It should be underscored that for Snelson and Levin there is only one class, only one tensegrity kind (Stephen Levin, personal communication).

10. Bernstein (1996) suggested that the rare occasions in which the level of tonus assumes leadership is in situations when a human is similar to a fish in water, that is, in equilibrium with the environment, without the apparent action of gravity.

11. Windhorst (2008) suggests that Kokkorigiannis's concerns are too insular. Muscle spindles' function and contribution to haptic perception pose explanatory challenges beyond their number and distribution. For Windhorst, these challenges arise from the multifunctional nature of spindles.

12. In order for a truss with pin-connected members to be stable, it must be composed entirely of triangles. This principle generalizes to tensegrity systems as follows: given flexible joints, the only stable polygons are those that are fully triangulated (namely, the four-sided tetrahedron, the eight-sided octahedron, and the 20-sided icosahedron; see Levin, 2002, 2006).

13. See <http://tensegrity.wikispaces.com/Icosahedron> for contrasting views of the icosahedron as the basis of biological tensegrity.

14. Figure 5 complements Figure 18 through examples of nested and deforming prestressed icosahedra.

15. In terms of the physical principles that would give rise to MFT, look to constructal theory (Bejan, 2000, 2005), a theory dismissive of fractal theory but seemingly well suited to multifractality. In terms of constructal theory, the hypothesized MFT is a geometric structure that, for any point source of force, is optimal for conducting that force across all of its scales at the maximal possible speed.

16. The currently popular instantiation of abduction is Bayesian inference.

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