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STRUCTURAL HIERARCHIES

Simple geometry in complex organisms

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Summary Many cultures throughout history have used the regularities of numbers and patterns as a means of describing their environment. The ancient Greeks believed that just five archetypal forms — the 'platonic solids' — were part of natural law, and could describe everything in the universe because they were pure and perfect. The formation of simple geometric shapes through the interactions of physical forces, and their development into more complex biological structures, supports a re-appreciation of these pre-Darwinian laws. The self-assembly of molecular components at the nano-scale, and their organization into the tensegrities of complex organisms is explored here. Hierarchies of structure link the nano and micro realms with the whole organism, and have implications for manual therapies.

Introduction

Many cultures throughout history have used the regularities of numbers and patterns as a means of describing their environment. The ancient Greeks believed that just five archetypal forms — the 'platonic solids' — were part of natural law and could describe everything in the universe because they were pure and perfect (Figure 1) (Fuller, 1975, sec.820.00).

This platonic conception of nature persisted up until the mid nineteenth century when Charles Darwin published his revolutionary 'Origin of Species', ''After Darwin the whole lawful scheme was overthrown and organic forms came to be seen as contingent mutable assemblages of matter — 'clever artefact like contrivances' — put together gradually during the course of evolution primarily by natural selection for biological function'' (Denton et al., 2003). A recognition of natural patterns and shapes derived from physical laws seemed to reassert itself in 1917 when d'Arcy Thompson published his classic 'On Growth and Form' (Thompson, 1961), but in the scientific mainstream this remained little more than interesting. Using simple geometry to describe a complex organism is likely to generate a certain amount of skepticism, as esoteric and occult descriptions seem rather simplistic compared to modern scientific thinking. However, in 1928 Frank Ramsey proved that every complex or random structure *necessarily* contains an orderly substructure. His proof established the fundamentals of a branch of mathematics known as Ramsey theory, which is used to study the conditions under which order must appear, such as in large communication networks and the recognition of patterns in physical systems. The theory suggests that much of the essential structure of mathematics consists of extremely large

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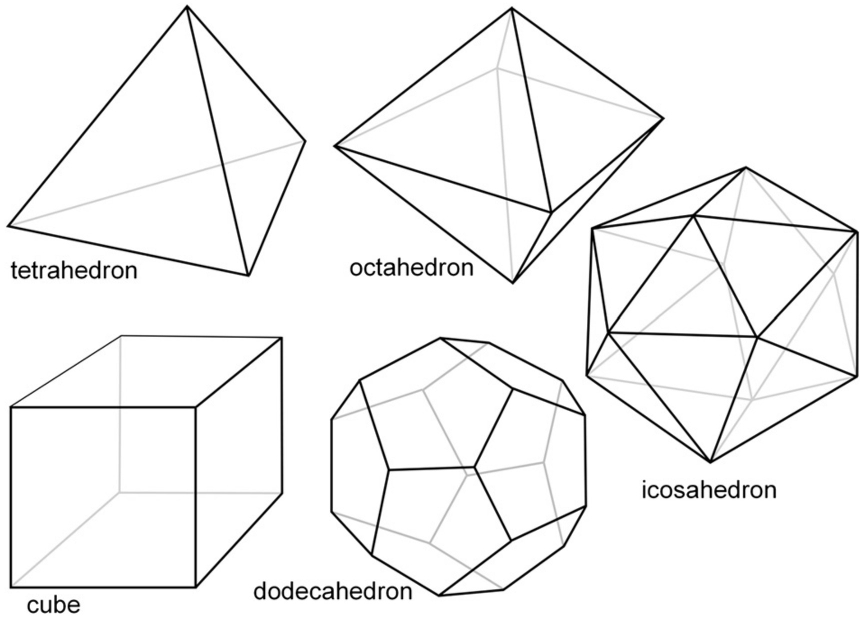

Figure 1 The five platonic solids.

numbers (with very complicated calculations) derived from problems which are deceptively simple (Graham and Spencer, 1990; Fuller, 1975, sec.227.00). From the perspective of the human body, Ramsey theory implies that simple shapes *might* form part of that underlying substructure, and an examination of how these could arise through the interactions of physical forces is presented. This supports recent research which reinstates physical law, and not natural selection, as the major determinant of biological complexity in the subcellular realm (Denton et al., 2003). The development of these shapes into more complex structures, and how they model biology, with implications for manual therapy then follows.

Simple geometry

One of the problems that nature seems to solve repeatedly is that of the most efficient ways of packing objects close together. A circle drawn on a piece of paper, i.e. in two dimensions (2D), demonstrates this. The circle encloses the largest area within the minimum boundary, which makes it a 'minimal-energy' shape (requiring the least amount of energy to maintain). Circles enclose space, as well as radiate out into it, as can be seen in a drop of oil floating on water, the growth of fruit mould, and the ripples in a pond. However, this efficiency is severely compromised when several circles are put next to each other as gaps are left in between (Figure 2). Other shapes, such as squares and triangles will both fill the space completely, but the proportion of area to boundary is not as good as with the circle. A square is inherently unstable; while triangles are very stable, even with flexible joints (Figure 3). Structures that are not triangulated can generate torque and bending moments at their joints, and must be rigidly fixed to prevent them from collapsing.

The best compromise between efficient space filling of the circle and stability of the triangle is the hexagon (Figure 2). Isolated hexagons are also liable to collapsing, but when several hexagons are packed together, they support each other as stresses balance at their 3-way

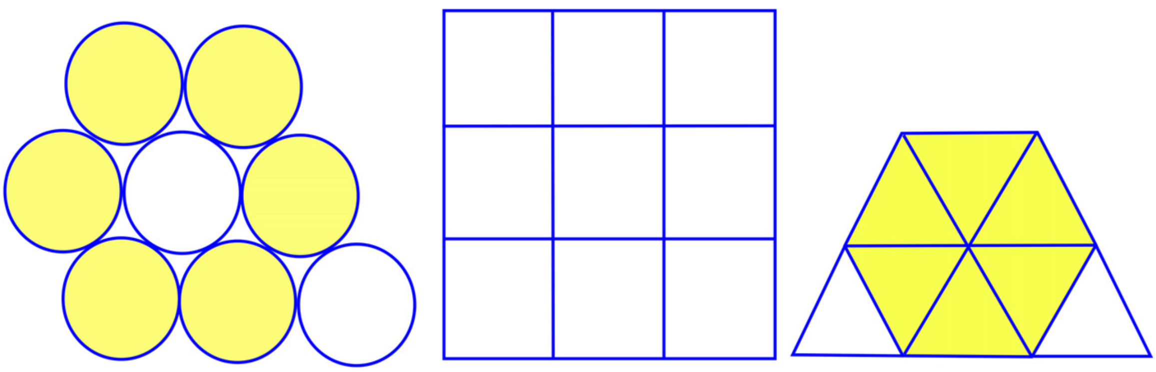

Figure 2 The tessellation of different shapes on a flat plane showing the appearance of the hexagon (shaded).

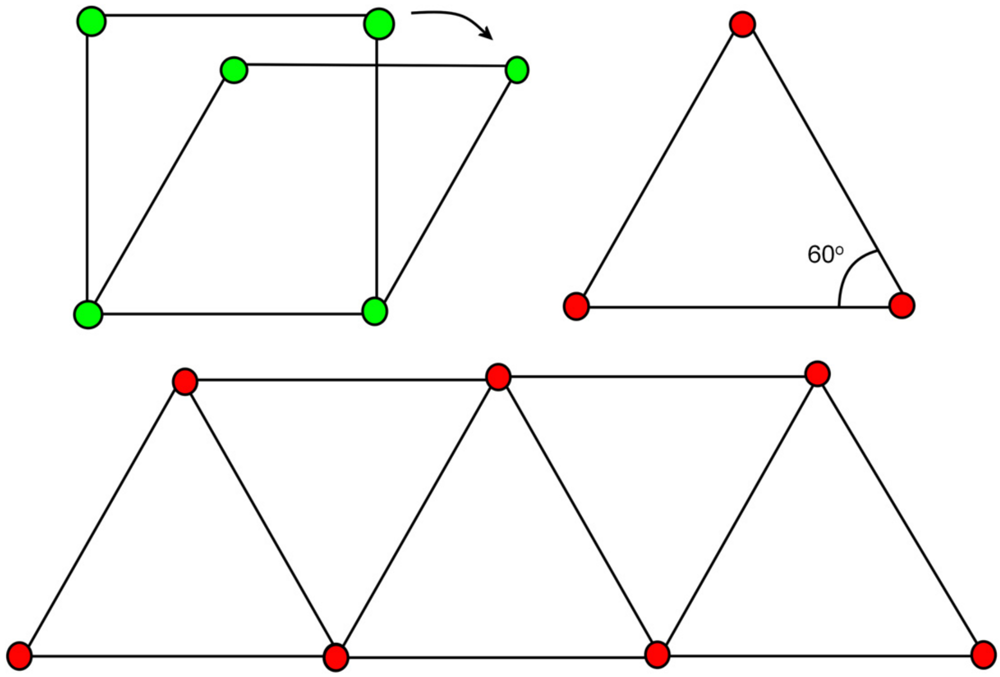

Figure 3 Diagram to show that square trusses are inherently unstable at their joints, whereas triangular trusses are rigid.

junctions (Figure 4). However, they are only fully stable when triangulated, with sides that form chords of a circle equal to the radius (Figure 4). Hexagons close-pack in an array that can self-generate to produce the same shapes at different size scales (Figure 5), and even non-uniform shapes approximate to hexagons as they pack together in sheets (Figure 7).

Soap bubbles spontaneously join together with outside surfaces that always meet at 120°, just like hexagons, whether the bubbles are equal in size or not (Figure 6). This is because soap molecules hold together through their surface tension, which tries to minimize itself and reduce the surface area (Fuller, 1975, sec.825.20; Stewart, 1998, p. 16). Some examples of naturally occurring hexagons are shown in Figure 7 (Bassnett et al., 1999; Weinbaum et al., 2003; Sanner et al., 2005).

All this would seem to make the hexagon the obvious choice for close-packing in two dimensions. In 3D, however, a structure which fulfills the same purpose may not be so readily apparent. The ancient Greeks recognized the importance of the five regular polyhedra because of their

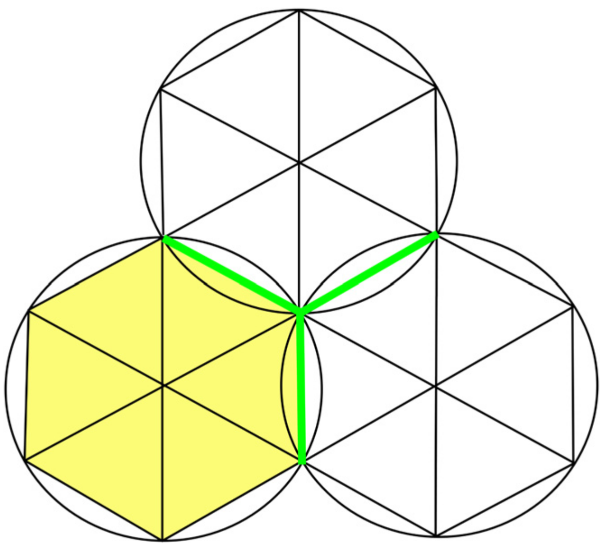

Figure 4 The relationship between hexagons, circles and triangles.

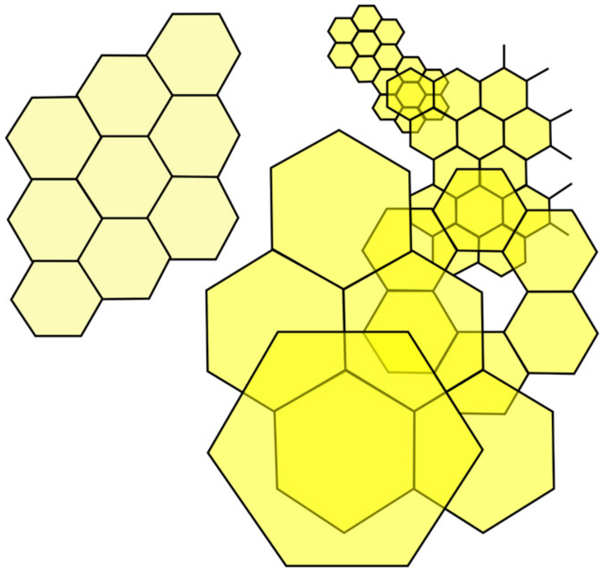

Figure 5 Hexagonal close-packing and a hierarchy of hexagons.

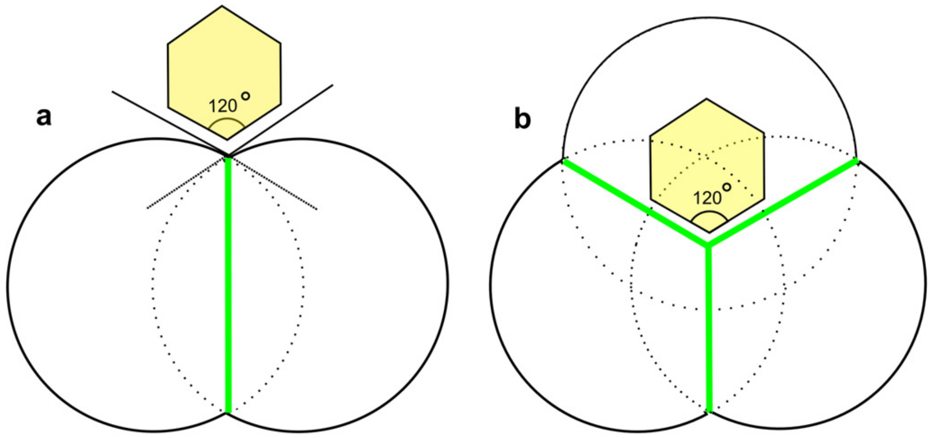

Figure 6 (a) Diagram of bubbles joining with an external surface angle of 120°, the same as a hexagon; (b) three bubbles form an internal septum (bold lines), also with an angle of 120°.

intriguing properties (Figure 1) (Fuller, 1975, sec.820.00). Their outer faces are made from shapes which are all the same; a sphere circumscribed around each one will touch all the corners, while one inscribed within will touch the centre of all the faces; and they all have 3, 4 or 5 sides. Joining up the face centres creates the 'dual' of that shape, i.e. the octahedron and cube are duals of each other; and the dodecahedron and icosahedron similarly; the tetrahedron is unique in that it is a dual of itself. Not a hexagon in sight... yet!

Just as the circle is the most efficient shape for enclosing space in 2D, so its equivalent in 3D is the sphere. Atoms, bubbles, oranges, and planets all approximate to spheres. Putting lots of spheres next to each other still leaves all those wasteful spaces in between, just like the circles did; but there is a more efficient solution. In order to tease out some of the consequences of packing spheres closely together, plastic balls have been glued together (Figure 8). The same arrangements are also shown as lattices of steel balls, with coloured magnetic sticks representing the inherent 'minimal-energy' characteristic of close-packing (i.e. their centres of mass are at the minimum possible distance apart) (Connelly and Back, 1998). Adding more spheres to a particular shape creates higher-order structures of the same shape, numbered according to the [magnetic] connections on their outer edge (Figure 8) (Fuller, 1975, sec.415.55).

The tetrahedron (Figure 8)

The simplest and most stable arrangement of spheres in 3D is a tetrahedron, because of its triangles (Fuller, 1975, sec.223.87). Methane and ice molecules configure as tetrahedrons; a pile of oranges and grains of sand are rough

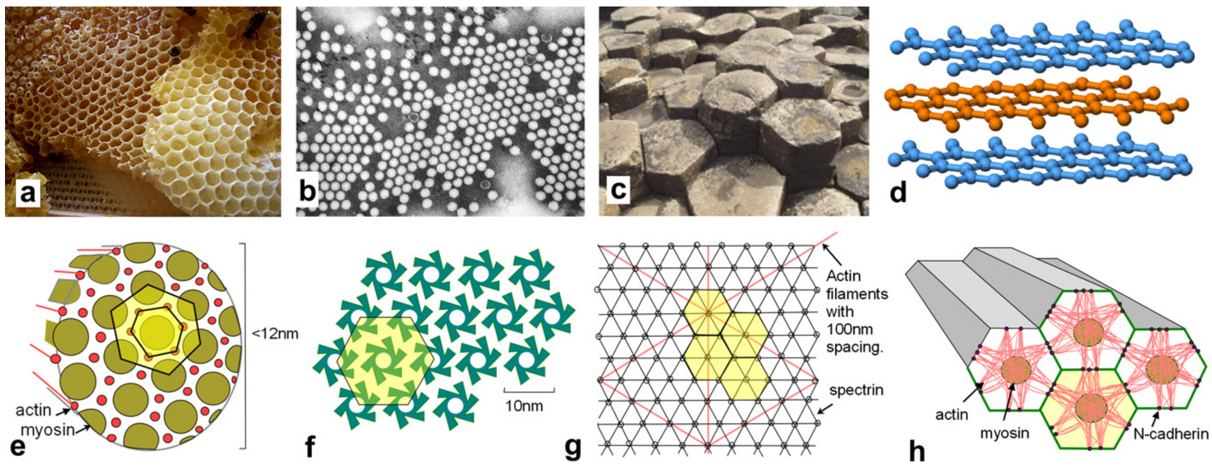

Figure 7 Some examples of hexagons in natural structures: (a) honeycomb (Wikipedia); (b) close-packing of Polio virus (Fred Murphy & Sylvia Whitfield, Wikipedia); (c) Basalt blocks on the Giants Causeway in Ireland, formed from cooling lava (Matthew Mayer, Wikipedia); (d) stacked layers of carbon atoms in graphite (Benjah-bmm27, Wikipedia); (e) hexagonal close-packing of actin and myosin in a muscle fibril; (f) hexameric complexes of uroplakin covering the epithelial lining of the urinary bladder (redrawn after Sanner et al., 2005); (g) idealized diagram of the sub-cortical cytoskeleton (redrawn after Weinbaum et al., 2003); and (h) cells in the optic lens arranged as hexagons (redrawn after Bassnett et al., 1999).

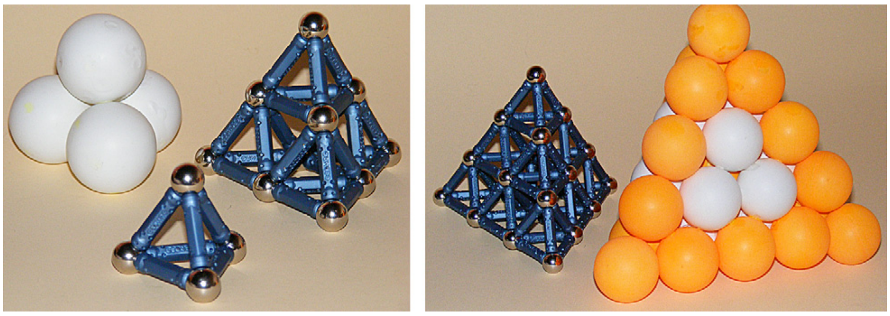

Figure 8 Closest-packing of spheres forms a tetrahedron (1st, 2nd, 3rd and 4th orders).

tetrahedrons; and in the early embryo, four cells arrange as a tetrahedron. Adding more spheres to the tetrahedron produces higher-order structures and the emergence of another shape — the octahedron.

The octahedron (Figure 9)

The octahedron appears as an inevitable consequence of close-packing. It is naturally found in radiolarian structures (Fuller, 1975, sec.203.09), and is the basis of the octet truss used by structural engineers because of its stability. It does have 3 equatorial squares at 90° to each other, but their stability is maintained because of the triangles at each vertex (Fuller, 1975, sec.420.01). A good approximation of this truss appears in the bones of birds, probably due its strength and lightness (Thompson, 1961, p. 236).

The cuboctahedron (Figures 10—12)

Increasing the tetrahedron to its 4th order (Figures 8 and 10) produces the first close-packing of spheres around a central nucleus, and the emergence of another shape — the cuboctahedron (which is not a platonic solid) (Fuller, 1975, sec.414.00). This shape is also contained within a 2nd order octahedron (Figure 11).

The cube (Figure 13)

The addition of a tetrahedron to each of the 8 triangular faces of the 2nd order cuboctahedron turns it into a cube, or looking at it another way, the cuboctahedron is a cube with the corners cut off. If these were cut away further, it would end up as an octahedron. When four corners of a cube are connected diagonally, they enclose a 4th order tetrahedron (Figure 13b).

The cuboctahedron and cube are not shapes which generally appear in biological structures, but they are still relevant to the discussion. Table 1 shows a comparison of the relative volumes of these shapes when taking each one as unity. It can be seen that the volume of the tetrahedron is the only standard where all the others can be expressed as integers; the other comparisons leave awkward fractions or irrational numbers which disguises their simple relationships. Man-made structures commonly use cubes with their 90° angles, but these shapes are relatively rare in the natural world where they are constructed from discrete components, and 60° geometry is more prevalent — an observation noted by Fuller (1975, sec.410.10). An architect of some renown, he formulated a complete system of geometry based on 60°, which applied to a wide diversity of the laws formulated in physics and chemistry.

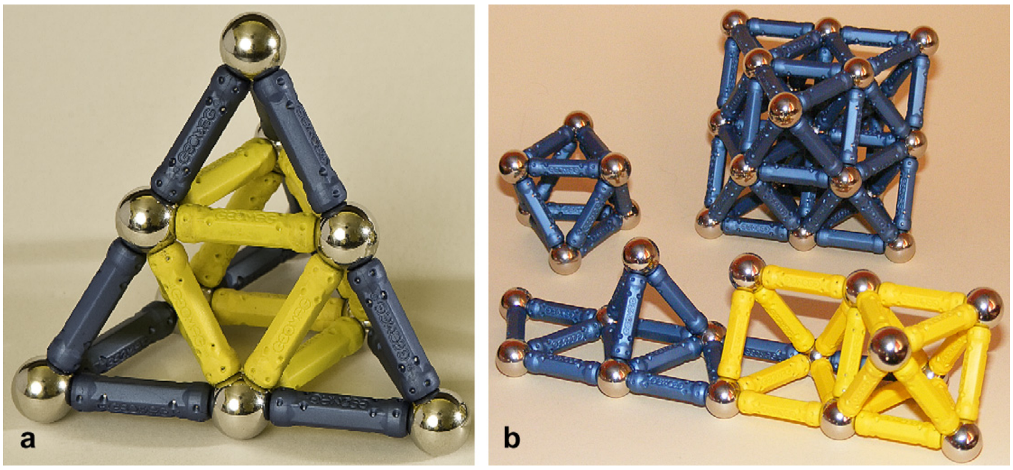

Figure 9 (a) Emergence of octahedron (light) within 2nd order tetrahedron (dark). (b) 1st and 2nd order octahedra with construction of octet truss.

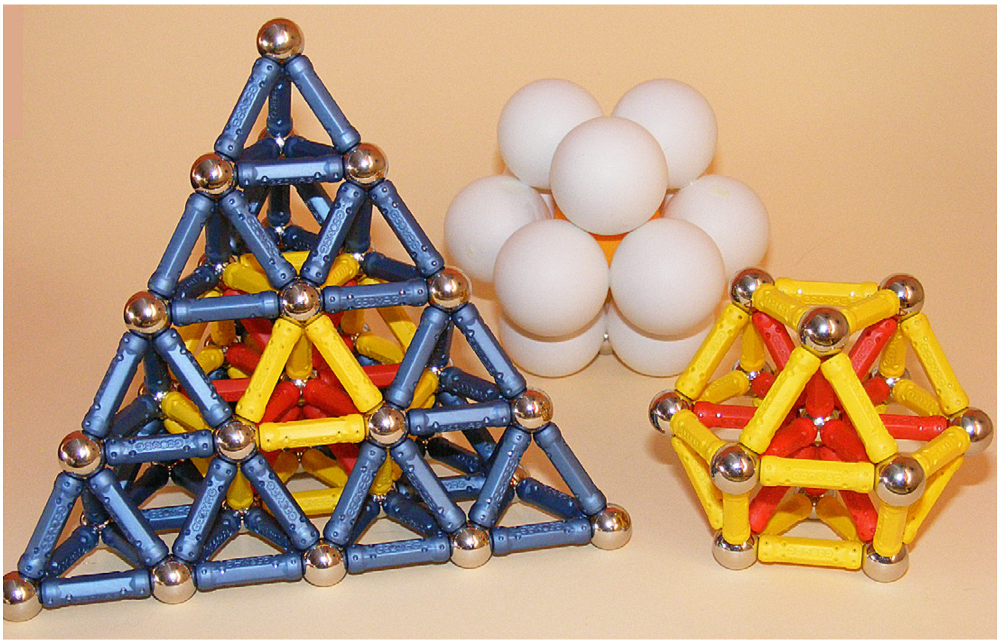

Figure 10 Nuclear close-packing starts in the centre of a 4th order tetrahedron to form a cuboctahedron.

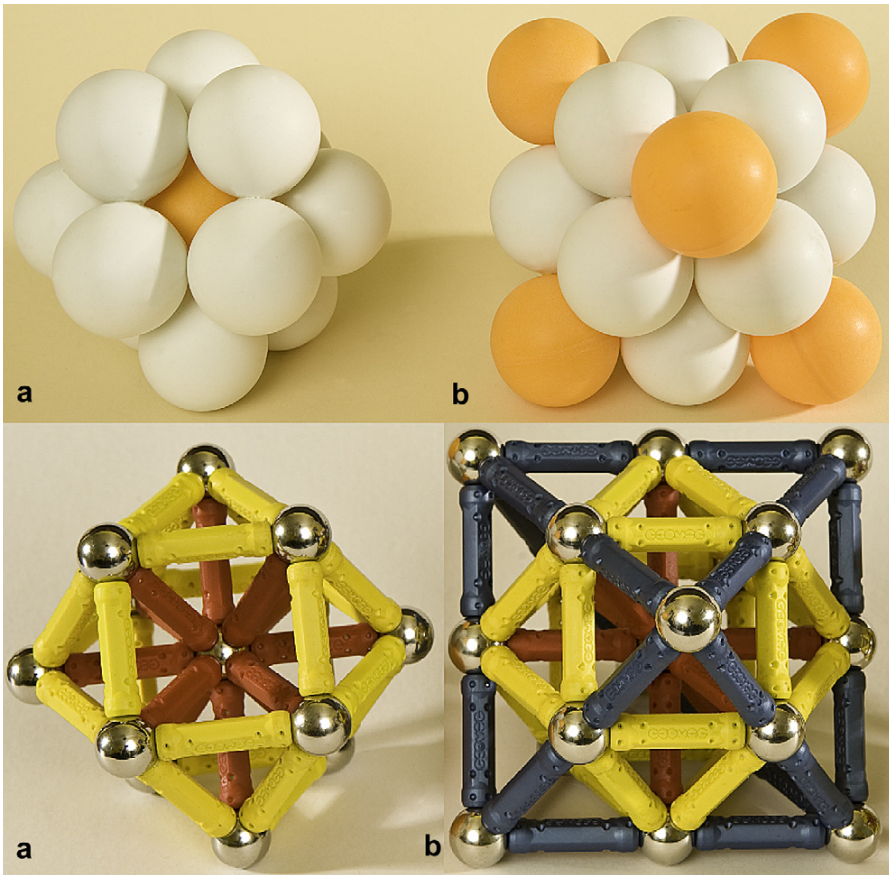

Figure 11 Nuclear close-packing forms cuboctahedron (a) and octahedron (b).

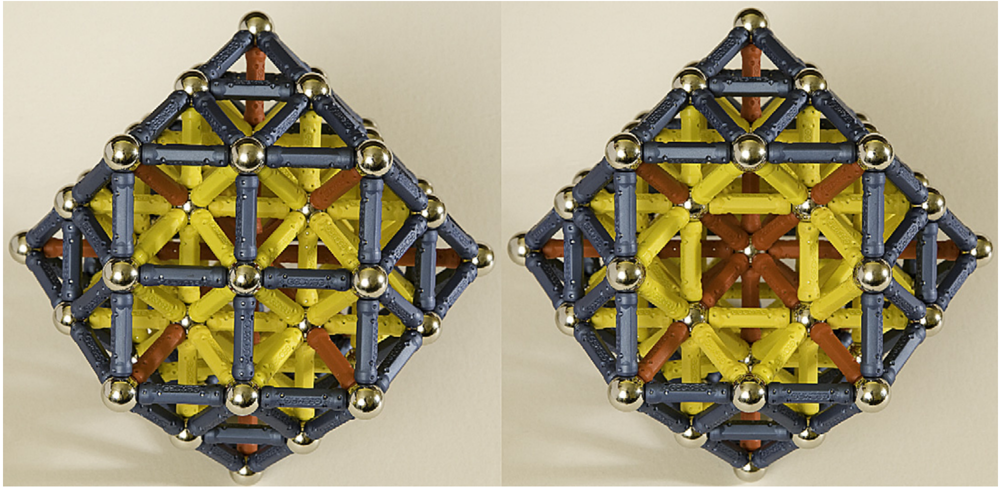

Figure 12 Cuboctahedron (2nd order) and the same with front removed to show nuclear rays.

In crystallography, for example, two basic types of close-packing are described — cubic (Figure 14a) and hexagonal (Figure 14b) (Read, 1974, p. 21). The different 'layers' are described as parallel to the surface of a cube, but as already shown, the value of this shape as a standard in nature is dubious. In 'cubic' close-packing, the *true* layers are at 60° to the surface of the cube, and all the energy bonds in these layers are oriented in the same directions (Figure 13). (This can be observed in the external angles of the hexagon in Figure 13c, which are 60°.) In 'hexagonal' close-packing, however, every third layer is rotated by 60° around an axis perpendicular to the layer plane, and it doesn't then produce simple shapes like those already described. In any case, there are plenty of hexagons in 'cubic' close-packing (Figures 13c and 15), and the tetrahedron, octahedron, cuboctahedron and cube are all examples of this (Read, 1974, p. 96). To illustrate this, diamond (the hardest natural substance) is constructed from carbon atoms arranged in a 3D *hexagonal* lattice; with complete hexagonal rings that form *tetrahedral* units; which crystallizes as an *octahedron*; and uniquely has *maximal cubic* symmetry (Figure 16) (all these polyhedra have cubic symmetry) (Read, 1974, p. 83; Sunada, 2008).

All these shapes naturally occur as inorganic crystals, and there is no suggestion that they can literally be observed in the human body. This new description, however, includes them in a unified and comprehensive approach to understanding natural forms, which are *all* influenced by the same energy-efficient ways of packing objects of similar size through the interactions of molecular forces.

Before getting to more complex structural mechanisms, it is necessary to make a brief return to the cuboctahedron, where it will be noticed that it is constructed from 12 spheres that create four interlocking *hexagons* around a central nucleus (Figures 10, 11 and 17a). Pauling (1964) described it as a 'coordination polyhedron' because its minimal-energy configuration is the common denominator of the tetrahedron, octahedron and cube. Fuller (1975, sec.430.00) considered the links between spheres as energy vectors, and called it the 'vector equilibrium'. This shape has radial and circumferential vectors which are all the

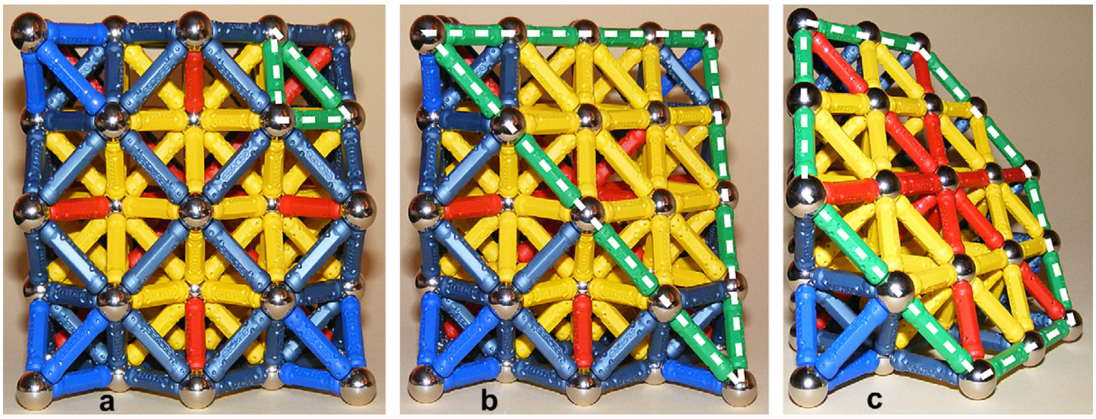

Figure 13 The layers in a cube. (a) 1st corner layer removed (white dotted). (b) 2nd layer removed to show one side of a tetrahedron (white dotted). (c) 3rd layer removed to show a hexagon (white dotted).

Table 1 A comparison of the relative volumes of different shapes with the same edge length, when taking each one as unity.

Tetrahedron	Octahedron	Cube	Cuboctahedron
1	4	6	20
0.25	**1**	1.5	5
0.1666666...	0.666666...	**1**	3.33333333...
0.05	0.20	0.30	**1**

same size. In terms of vectorial dynamics, the outward radial thrust from the nucleus is exactly balanced by the circumferentially restraining chordal forces (Figures 10 and 11). So, as well as the highest degree of symmetry (cubic), we have a coordinating shape (cuboctahedron) and a balance of forces (vector equilibrium), the significance of which will be explained later.

It is even possible to pack spheres tighter and at a lower energy level by removing the nucleus. This allows 12 spheres to compact differently around a smaller central space as 12 interlocking pentagons (Figures 17b and 18a, b). Joining all the spheres together creates an icosahedron — another platonic solid, but this one is different (Figure 18c). Adding more spheres to the outside will not create a higher order, like in the previous shapes, because the spheres won't all touch (Figure 18d). A 2nd order icosahedron won't close-pack around the basic shape, or a 3rd order around a 2nd, because they would be unstable (Figure 18e and f), and can only exist in their own right as a single outer shell. The icosahedron enlarges by subdividing each of its faces into more triangles, which is why it remains stable (Figure 18g). (The relative volume compared to the tetrahedron in Table 1 is 18.51.)

In order to understand the full significance of simple geometry, we must look at another way that the universe uses to deal with complexity, namely, integration.

Tensegrity

The concepts of tensegrity [tensional integrity] have become increasingly recognized over the last thirty years as a useful model for understanding some of the structural properties of living organisms. Their appreciation follows from investigations in the 1940s by Snelson (website) who constructed sculptures with parts that appeared to defy gravity and float in the air. His structures so impressed the architect Fuller (1975) that he incorporated them into his developments in building design, and set about exploring the principles underlying their formation. Fuller defined two types of tensegrity structure based on the icosahedron, and termed them geodesic and prestressed.

The geodesic dome

The outstanding feature of all geodesic structures is that they have a rigid external frame maintaining their shape, made from multiple struts or trusses arranged in geometric patterns. These are usually triangles, pentagons or hexagons, with triangulated structures being the most stable. The term 'geodesic' actually refers to the shortest path between two points on a surface (equivalent to the struts), so strictly speaking this definition should only refer to the triangulated structure. Aside from this, the 'geodesic' dome can enclose a greater volume with minimal surface area, with less material than any other type of structure apart from a sphere. When the diameter of a sphere doubles, the surface area increases 4-fold and the volume 8-fold, which makes such structures very efficient in terms of construction material. The 1st order tetrahedron and octahedron are geodesic structures which enlarge by adding more spheres to the outside, but they then cease to be hollow structures. In contrast the icosahedron, whose spheres enclose a small central space, creates an outer geodesic shell which enlarges by adding more triangular faces within it (Figures 18g and 19). The icosahedron has several attributes that are advantageous for biological structures (Levin, 1995). It is the closest of

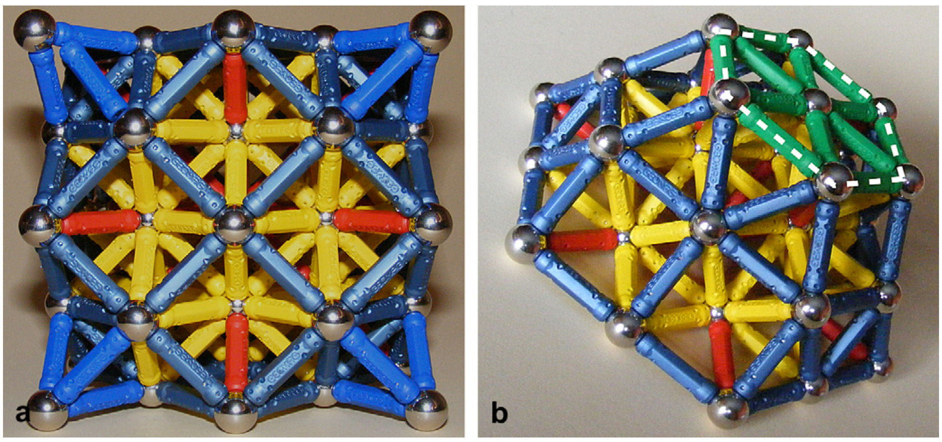

Figure 14 (a) 'Cubic' close-packing in a cube. The orientation of energy bonds in each layer of spheres remains the same (compare Figure 13). (b) 'Hexagonal' close-packing shows the third layer of spheres (white dotted) rotated by 60° on the layer below.

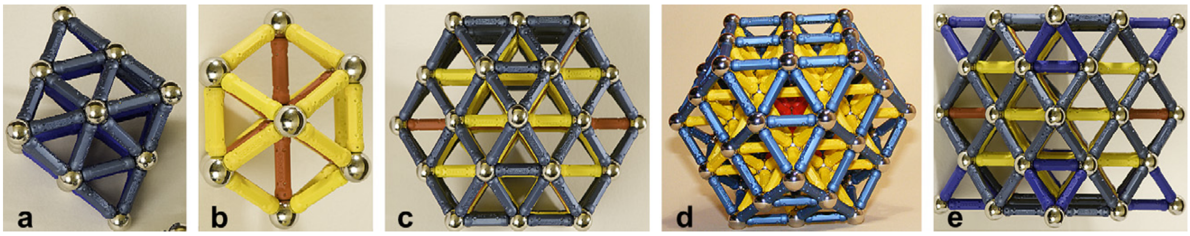

Figure 15 Hexagonal shape in (a) octahedron; (b) 1st order cuboctahedron; (c,d) 2nd order cuboctahedron; and (e) cube (viewed from edge).

all the regular polyhedra to being spherical — making it efficient in terms of construction material; and it is fully triangulated — giving it stability. It has 12 vertices, 20 triangular faces and 30 edges, with five faces and their edges meeting at each vertex; and demonstrates six 5-fold, ten 3-fold and fifteen 2-fold symmetries.

Fuller introduced his geodesic domes during the 1950s; and because their strength increases as they get bigger, it has been possible to build some very large structures. Some of these can be seen in the *Eden project* in Cornwall, and protective coverings on radar installations. Some natural structures are: 'Buckyballs' — a form of carbon named after Fuller — with 60 atoms linked together to form 20 hexagons, interspersed with 12 pentagons — the same as the pattern on a football (actually a spherical truncated icosahedron); viruses; the silica shells of radiolaria; pollen grains; clathrins (endocytic vesicles beneath the cell membrane); and the cellular cytoskeletal cortex (Figure 20).

In 1956, Crick and Watson, the discoverers of DNA, pointed out that the only way to build a hollow protein shell out of identical subunits is a shape with cubic symmetry. Since then it has been amply confirmed that the icosahedron is the best shape for producing the outer capsid shell of the 'spherical' viruses, because it is a minimum free-energy structure, and spontaneously assembles through the actions of intermolecular forces (Figure 20b) (Crick and Watson, 1956; Kushner, 1969; Caspar, 1980; Van Workum and Douglas, 2006). These viruses form larger structures, which get

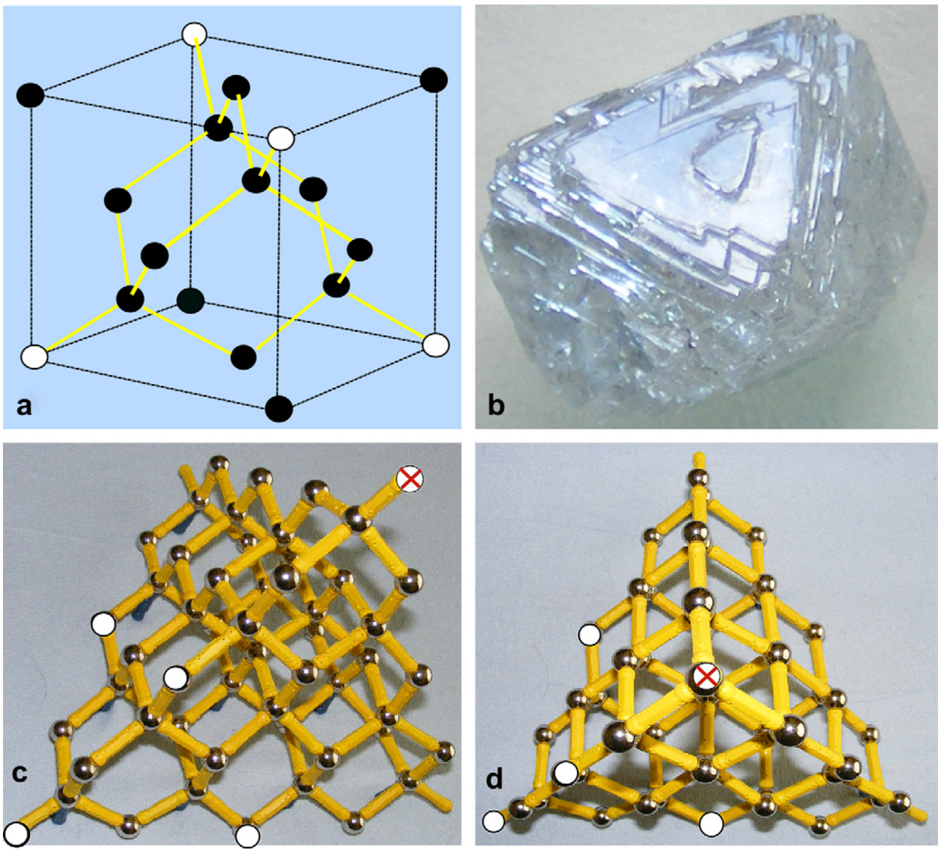

Figure 16 (a) Multi hexagonal lattice of carbon atoms in diamond, shown within the 'standard' cube; (b) octagonal diamond crystal; (c) enlarged lattice showing tetrahedral apexes (white, compare with (a)); and (d) tetrahedron viewed from apex (cross).

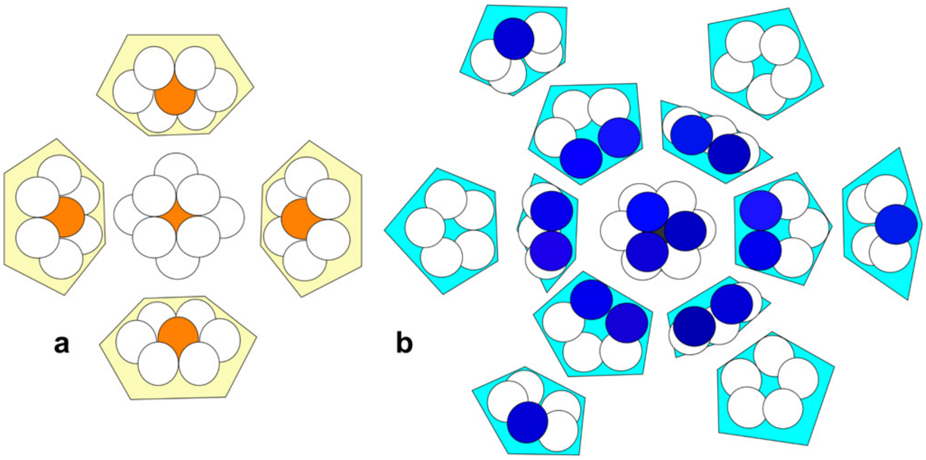

Figure 17 (a) 12 spheres close-pack around a central nucleus to form a cuboctahedron with 4 interlocking hexagons; and (b) around a central space to form an icosahedron with 12 interlocking pentagons (front 3 spheres have been shaded for clarity).

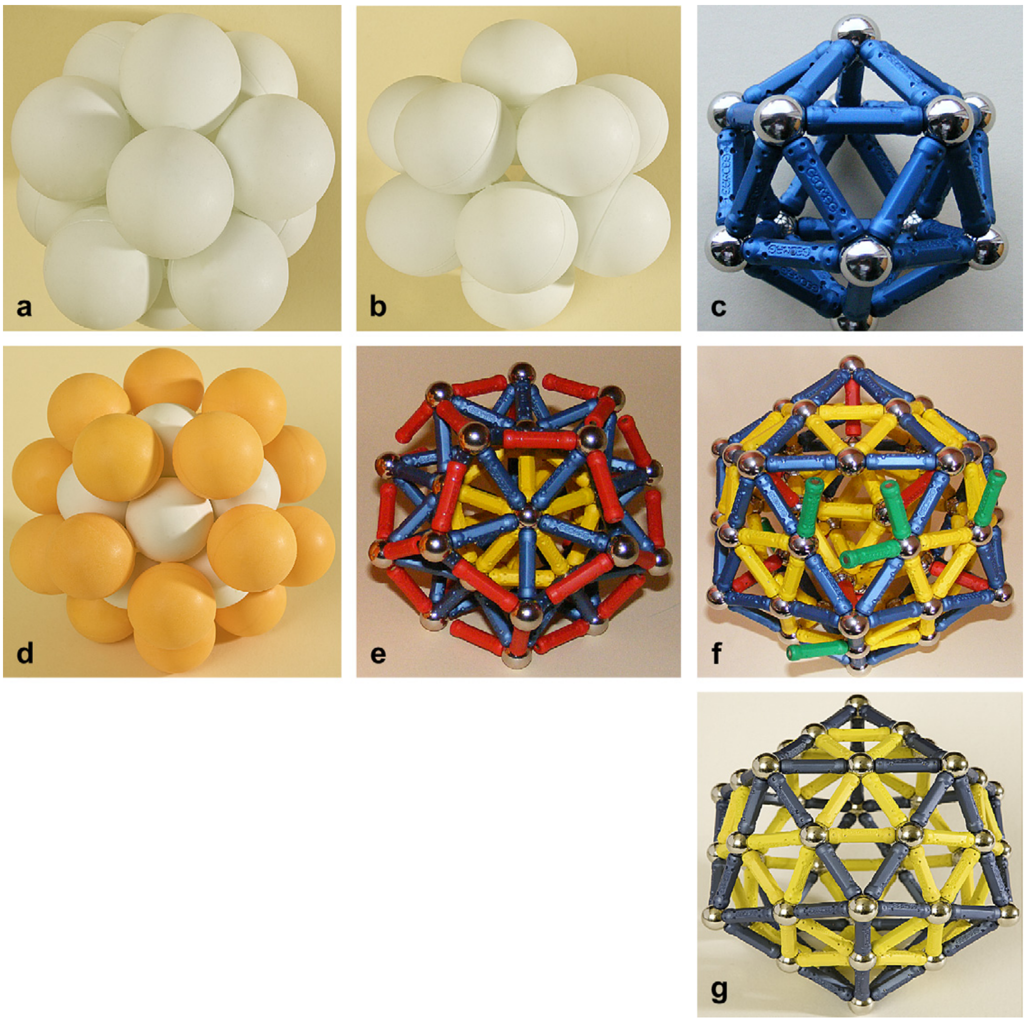

Figure 18 Close-packing around a central space (a,b) forms an icosahedron with hexagonal outline (c). Packing more spheres around the icosahedron (d) forms an unstable dodecahedron (e) or icosahedron (f). An icosahedron enlarges by subdividing its surfaces into more triangles (g).

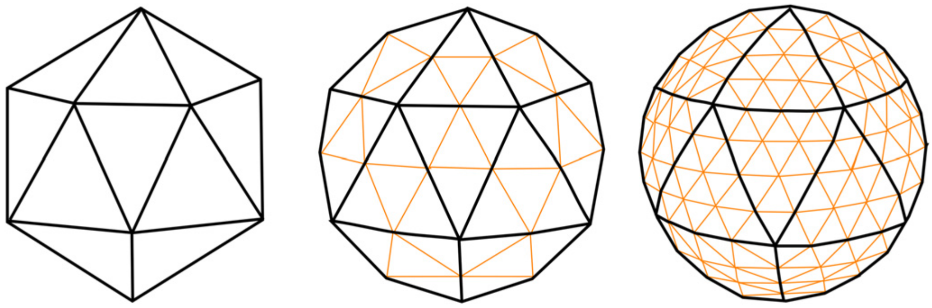

Figure 19 Icosahedron subdivided into 2nd and 3rd order geodesic icosahedra.

even closer to a sphere, by using more protein subunits (capsomers) to subdivide their triangular faces (Figure 19). The maximum number of identical subunits which can be arranged is 60, and to become larger, some subunits must distort slightly in order to form stable bonds. This 'quasi-equivalence' is necessary for preserving the icosahedral template, with multiples of 60 subunits allowing many more triangular faces, but there are always just 12 vertex pentagons (it is the 5-fold symmetry which creates the geodesic dome) (Caspar, 1980). (The icosahedron has also been found to play an important part in the structure of many electron-deficient substances, including metals and alloys Pauling, 1964, 1990; Teo and Zhang, 1991.)

Multiple icosahedra can arrange neatly together in a thick planar sheet because of their hexagonal outline (Figures 7b and 18c), making the hexagon the link between space filling in 2D and the icosahedron in 3D. They can stack in a column or helix; branch or pack around each other (incompletely) to create curved surfaces; and form more complex patterns and shapes in 3D (Figure 21).

In contrast, tetrahedral and octahedral based trusses are not omnidirectional in form and function; they have a smaller volume to surface area ratio; they do not close-pack at all well and their shapes do not self-generate. Cubes and dodecahedra are also inherently unstable unless they are triangulated; and as they rarely feature in biology, will not be considered further at this point. However, they are still significant to later discussion.

Applying pressure to any point of a geodesic dome causes force to be transmitted around the edges, with both compression and tension operating within different parts of each strut, which means that they must be made of a material that can deal with both types of loading. Pre-stressed tensegrities, on the other hand, have these two components separated, optimizing the material properties of each (Ingber, 2003a).

Prestressed tensegrity

The description of biological structures as tensegrities first appeared in the literature in the early 1980s, with independent contributions by Ingber et al. (1981) and Levin (1982). Prestressed tensegrities consist of a set of struts under compression, and an arrangement of cables under isometric tension. The resultant pull of the cables is balanced by the struts, providing structural integrity with the compression elements appearing to float within the tension network. A load applied to this type of structure causes a uniform increase in tension around *all* the edges and distributes compression evenly to the struts, which remain distinct from each other and do not touch (Skelton et al., 2001; Masic et al., 2006). Fuller described it as: ''...*continuous tension and discontinuous compression*'' (Fuller, 1975, sec.700).

The geodesic icosahedron can be converted into a pre-stressed tensegrity structure by using six new compression members to traverse the inside, connecting opposite vertices and pushing them apart (Figure 22) (Fuller, 1975, sec.700; Levin, 1982). The edges can then be replaced with cables so that the outside is entirely under tension. (Some

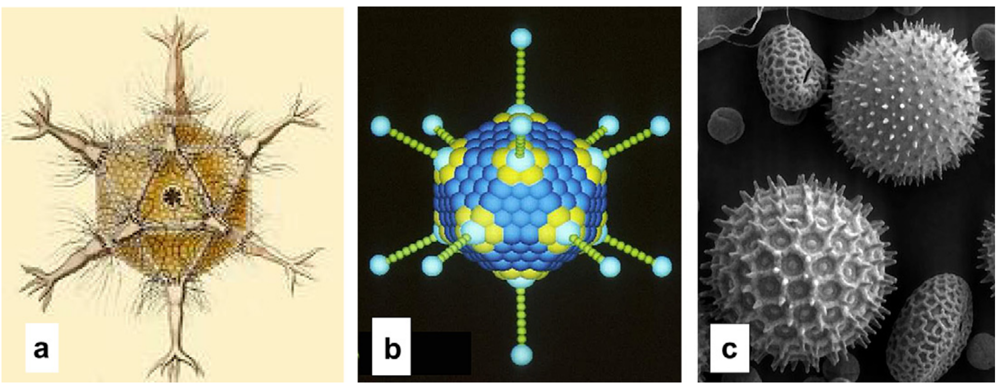

Figure 20 Geodesic icosahedrons in (a) Radiolarian (Wikipedia); (b) Adenovirus (Wikipedia); and (c) Pollen grains (Dartmouth College, Wikipedia).

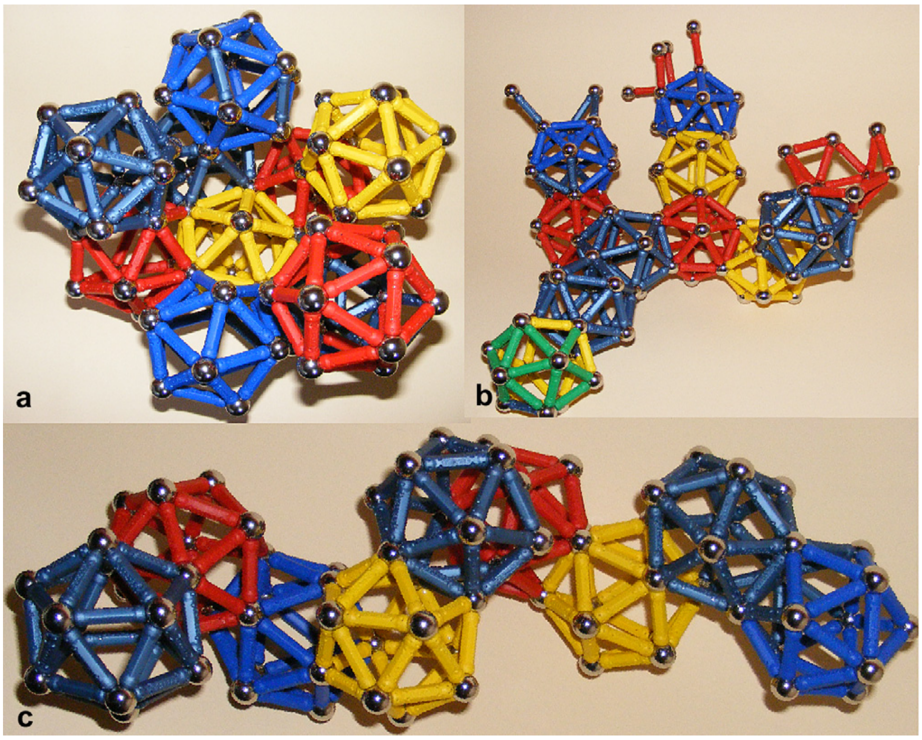

Figure 21 (a) Incomplete icosahedral packing; (b) icosahedral branching; and (c) icosahedral helix.

of the edges have disappeared in the transition to prestressed tensegrity because they are now redundant and not essential to this new structure.)

To summarize the significant aspects of this type of design (Van der Veen, 2003):

1. *Stability* — achieved through the configuration of the *whole network*, and not because of the individual components. It is also omnidirectional, with the different elements maintaining their respective properties regardless of the direction of applied load.

2. *Balance* — the tension and compression components are separated and balanced mechanically throughout the *entire structure*, which will optimize automatically so as to remain inherently stable.

3. *Integration* — a change in any one tension or compression element causes the whole shape to alter and distort, through reciprocal tension, distributing the stresses to all other points of attachment.

4. *Energetically efficient* — giving maximum stability for a given mass of material. In mechanical terms it cannot be anything other than in a balanced state of minimal energy throughout (Masic et al., 2006; Skelton et al., 2001).

Since its discovery, the tensegrity concept has developed in four main areas — sculpture (Snelson); building

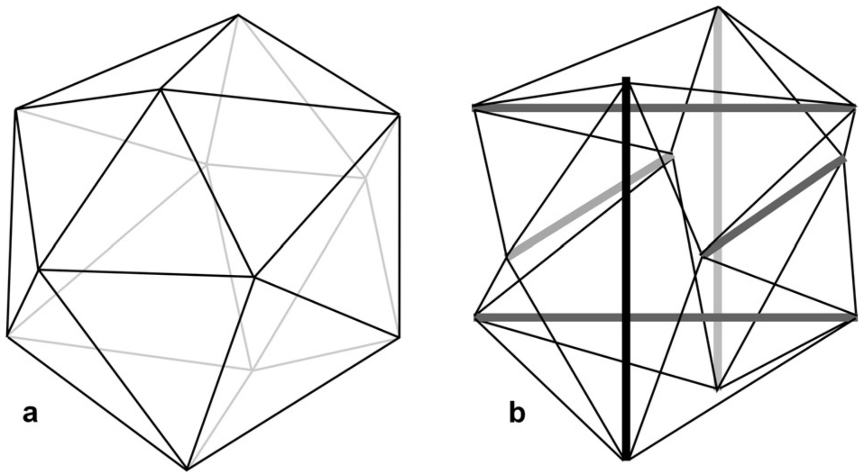

Figure 22 (a) Geodesic icosahedron; and (b) prestressed tensegrity icosahedron.

(Fuller); space research and structural biology. Space research has shown a great deal of interest in tensegrities because of their lightness and other unusual structural properties. Defining their complex mathematics will probably lead to new developments in biological research, with physical and computerized modelling becoming valuable tools for exploring their potential in the future (Connelly and Back, 1998; Skelton et al., 2001; Coughlin and Stamenovic, 2003; Masic et al., 2006; Yu et al., 2008).

The 'geodesic dome' has been considered distinct from 'prestressed' tensegrity for the purpose of description so far — one has all the struts touching, and the other has them all separated; although *tension* maintains their *integrity* in both cases, and they are really both prestressed (Fuller, 1975, sec.703.03). They seem to be poles at opposite ends of a continuum, although even this distinction is an illusion, and as will be explained. A definition which satisfies all researchers has so far remained elusive, particularly in biology, where distinctions become blurred, and the following examples use a broad and inclusive approach.

The complexity of shape

Shape is a direct result of all the forces acting on the component structures during development, from a single molecule to the complete organism. At a 'simple' level, the arrangement of spheres (atoms) is through the spontaneous attraction (tension) of inter-atomic forces. Three spheres form a triangle and four spheres form a tetrahedron (Figure 8). More spheres can be added to create an octahedron, cuboctahedron or cube (Figures 11 and 13); but these distinct shapes are generally only stable as fixed inorganic crystals.

In contrast, the molecular dynamics within living organisms is in continuous flux as conflicting forces attempt to resolve themselves. Eventually they can settle into a balanced and stable state of minimal-energy, at least until some other force exerts its influence. Prestressed tensegrities are a most attractive proposition in living systems, because they create an energy 'sink' for the interacting force fields (a 'basin of attraction' in dynamics terminology), and make possible an enormous number of flexible and stable structures through changes in the lengths of their compression members (Connelly and Back, 1998; Skelton et al., 2001; Nelson et al., 2005; Ingber, 2006a,b, 2008).

Their non-linear stress—strain curve is considered an essential element in biological materials, where it has been related to the differing properties of components in their nano and microstructures (Figures 24 and 29) (Gordon, 1978, p. 164; Lakes, 1993; Skelton et al., 2001; Puxkandl et al., 2002; Gao et al., 2003; Gupta et al., 2006); one of the smallest of these is the helix.

The helix

The α-helix is a series of curves which all have the same radius, drawn out like a long spring (Figures 24—29). Probably the most famous of all is DNA — deoxyribonucleic acid — a double helix of two chains running in opposite directions. The discoverers of DNA rightly predicted that helixes would be one of the simplest of shapes to spontaneously assemble through intermolecular forces (Crick and Watson, 1956; Kushner, 1969; Caspar, 1980; Van Workum and Douglas, 2006). Helical structures are stabilized through a balance between the attractive (tensional) and resistant (compressional) forces within the molecule, which makes them tensegrities. They can also flex without buckling, lengthen without breaking, and are capable of rotation without deformation (Stecco, 2004, p. 185). All known filamentous viruses are helical (most of the rest are icosahedral) (Figures 20b and 21c).

In proteins, sequences of amino acids can fold into α-helixes and further twist around each other to form double or triple coiled-coils (super-coils) (Figure 25), or fold with other α-helixes (or β-sheets) to form globular structures. Of the huge number of possible amino acid combinations, protein folding is limited to a set of about 1000 different forms because of some basic self-assembly rules, analogous to the laws of chemistry or crystallography, which correspond to an energy minimum (Denton et al., 2002).

The cytoskeleton

Within the cytoplasm, the prestressed cytoskeleton is a lattice consisting of microtubules — tightly packed helices

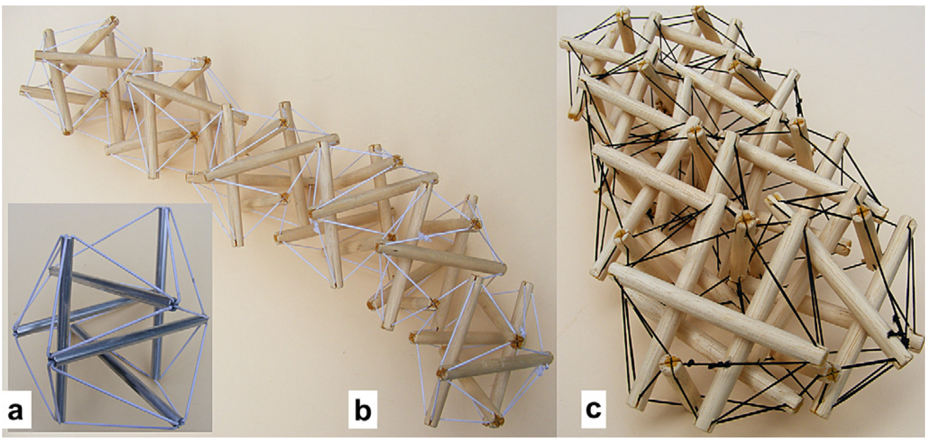

Figure 23 Prestressed tensegrity models (a) icosahedron; (b) icosahedral chain; and (c) icosahedral thick planar sheet.

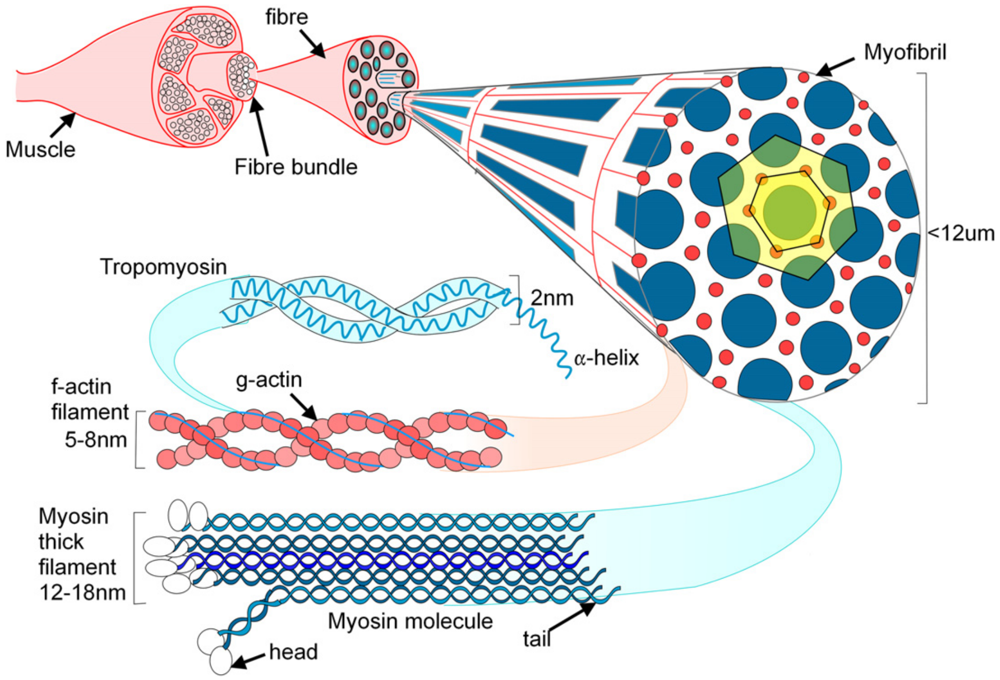

Figure 24 Diagram to show hierarchies of different components in the structure of muscle — α-helix of tropomyosin, double coiled-coil of tropomyosin; globular g-actin, combined double helix of f-actin and tropomyosin; double α-helix of myosin molecule, myosin thick filament; hexagonal packing of actin and myosin in a myofibril, self-similar packing of myofibrils into a fibre, a fibre bundle and ultimately muscle.

of globular tubulin protein under compression (Figure 26); microfilaments — double helices of the protein F-actin under tension (Figure 27); and helical protein intermediate filaments which stabilize and integrate the whole structure, from cell membrane to the nucleus (Ingber, 2008; Maguire et al., 2007; Brangwynne et al., 2006). Experimental support for the cytoskeleton as a tensegrity structure now seems overwhelming (Ingber, 2008), although some studies have been unable to confirm it (Heidemann et al., 1999; Ingber et al., 2000).

The cellular cortex

The cellular cortex is essentially made from triangulated *hexagons* of the helical protein spectrin (Figure 25), coupled to underlying bundles of the helical protein actin (Figures 7g and 27) (Liu et al., 1987; Weinbaum et al., 2003; Li et al., 2005; Zhu et al., 2007). The erythrocyte, with a diameter of 8 μm, has a composite membrane which distorts as it flows through smaller capillaries, but allows the cell to recover its biconcave shape. The network is organized into ~33,000 repeating units, each with a short central actin protofilament linked by 6 spectrin filaments under tension, to a lipid-bound suspension complex (Sung and Vera, 2003; Zhu et al., 2007). About 85% of these units appear as hexagons, with ~3% pentagons and ~8% heptagons, which suggests that the hexagonal arrangement is a preference, and not perfect (Liu et al., 1987). The erythrocyte membrane may be considered as many prestressed tensegrity actin/spectrin units within a geodesic dome, which is itself a bilayered structure of phospholipid molecules with outer heads under tension separated by

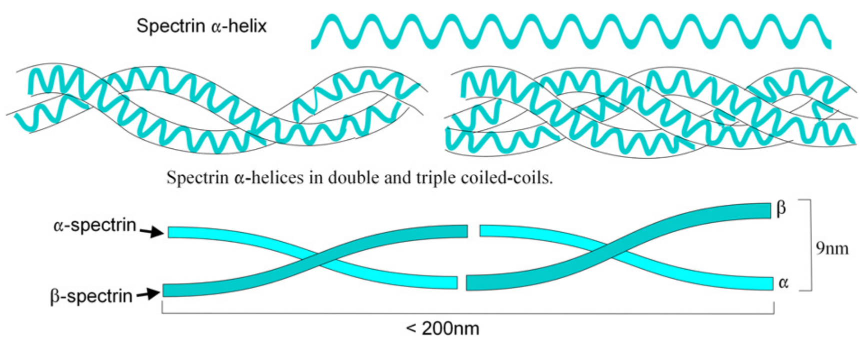

Figure 25 Spectrin tetramer — each strand of α- and β-spectrin consists of a series of double and triple coiled-coils (super-coils).

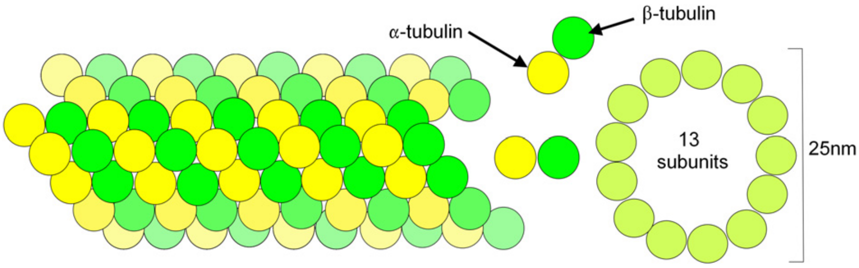

Figure 26 Microtubule polymer of globular tubulin.

hydrophobic tails under compression. It has also been modelled around an icosahedron (Li et al., 2005). Deformation of the membrane network may cause turbining of the actin protofilaments through the suspension mechanism, thereby facilitating oxygen transfer from one side of the membrane to the other (Sung and Vera, 2003; Zhu et al., 2007).

This arrangement of different components at varying size scales is a common feature in biology, where the functions of each one contribute to a higher collective function within a hierarchy of structures (Figures 24 and 29).

Structural hierarchies

The nano-structures of collagen and spider silk have both been described as prestressed tensegrities (Skelton et al., 2001) within a hierarchical fibrous structure (Figure 28) (Termonia, 1994; Knight and Vollrath, 2002; Du et al., 2006). Collagen, the most abundant structural molecule based on the helix, is the main constituent of the extracellular matrix, fascia, tendons and ligaments. More than twenty different types have been described in different tissue specific combinations which are particularly able to resist tensional stresses. At the nano-scale three helical procollagen polymers wind around each other to form a triple helix of tropocollagen. These molecules then arrange laterally in a quasi-hexagonal configuration with cross-linking to form collagen microfibrils, and pack sequentially in a hierarchy to form a subfibril, fibril and collagen fibre (Figure 29) (Jager and Fratzl, 2000; Puxkandl et al., 2002; Gao et al., 2003; Gupta et al., 2006; Perumal et al., 2008).

Collagens and spider silk are also examples of liquid crystal elastomers — different states, or mesophases of matter, that lie between liquids and solid crystals (Ho et al., 1996; Knight and Vollrath, 2002). They are flexible and malleable, with fibres that show a high degree of orientational order and varying degrees of translational order, and are sensitive to mechanical loading and changes in electro-magnetic fields; which may influence their synthesis and define fibre orientation during morphogenesis and tissue remodelling. Even though spider web fibres are secured at their ends to what is effectively a continuous compression component, the whole web has been classed as a tensegrity on structural engineering grounds (Connelly and Back, 1998).

Fractals

The self-similar geometrical structure of collagenous tissues has been demonstrated in the fractal character of their polarization properties, with degenerative-dystrophic changes revealed by alterations in these properties (Ho et al., 1996; Angelsky et al., 2005). This observation may be of value in pre-clinical pathological diagnostics, and a correlation between these findings and tissue palpation would be useful research in the future. Fractal analysis is commonly applied to natural structures, where similar shapes and patterns appear at different size scales, linking hierarchies throughout the body (Mandelbrot, 1983; Skelton et al., 2001; Jelinek et al., 2006); the branching patterns of blood vessels, the bronchial tree and nerve fibres all display this property (Zamir, 2001; Palagyia et al., 2006; Phalen et al., 1978; Thomas et al., 2005). These characteristic shapes are developmental remnants of non-linear dynamic systems which were sensitive to small changes in the local environment, created instabilities in growth and caused the typical branching pattern which extends from the micro to the macro scale. They are part of 'deterministic chaos' or chaos theory (Goldberger et al., 1990).

The matrix

The extracellular matrix, surrounding virtually every cell in the body, provides a branching structural framework which extends through the fascia to the whole organism. It

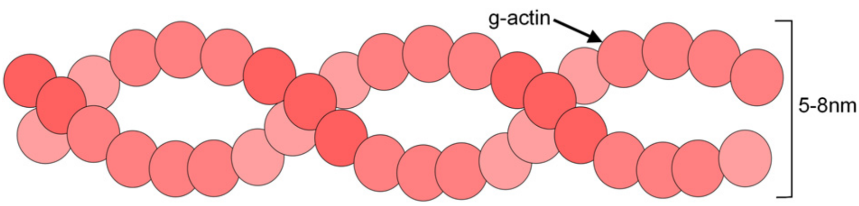

Figure 27 F-actin polymer filament.

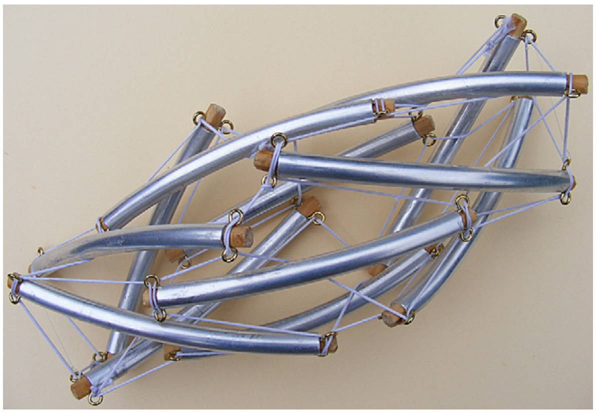

Figure 28 A model fibre showing the prestressed tensegrity nano-structure with similarities to collagen and spider silk.

attaches to the cellular cytoskeleton through adhesion molecules in the cell membrane, allowing a transfer of mechanical forces between them and changes in the cytoskeletal tension (Ingber, 2003a,b,2008). Multiple intracellular signalling pathways are activated as a result which provide multiplexed switching between different states such as cell growth, differentiation or apoptosis. Conversely, local tensional stresses within the cytoskeleton transfer to the extracellular matrix and produce effects on other cells at some distance. Long-distance transfer of mechanical forces between different tissues could then spatially orchestrate their growth and expansion, allowing complex multicellular tissue patterns to emerge through interactions among a hierarchy of different components.

Multi-modular hierarchies of form and function can thus be linked, with simplicity evolving into complexity, and the whole system mechanically functioning as a unit (Stecco, 2004, p. 25; Nelson et al., 2005; Ingber, 2006a, 2008; Parker and Ingber, 2007). As a self-organizing tensegrity construction system, the matrix could repair and replace itself at a local level, by allowing small and incremental changes compatible with the mechanical demands of all its components. Stecco (2004, p. 31) described the fascia as a tensioned network which may coordinate the motor system in a way that the central nervous system is incapable of, although this work has yet to be confirmed.

Modelling icosahedral tensegrities

The icosahedron is particularly useful in modelling the tensegrities of biological structures, because it demonstrates both geodesic and prestressed properties which can be connected to form an infinite variety of shapes (Figures 21, 23 and 31). Even the tension and compression elements can be made from interlinked icosahedra, themselves constructed from smaller icosahedra, repeating further in a self-similar structural hierarchy (Fuller, 1975, sec.740.21;

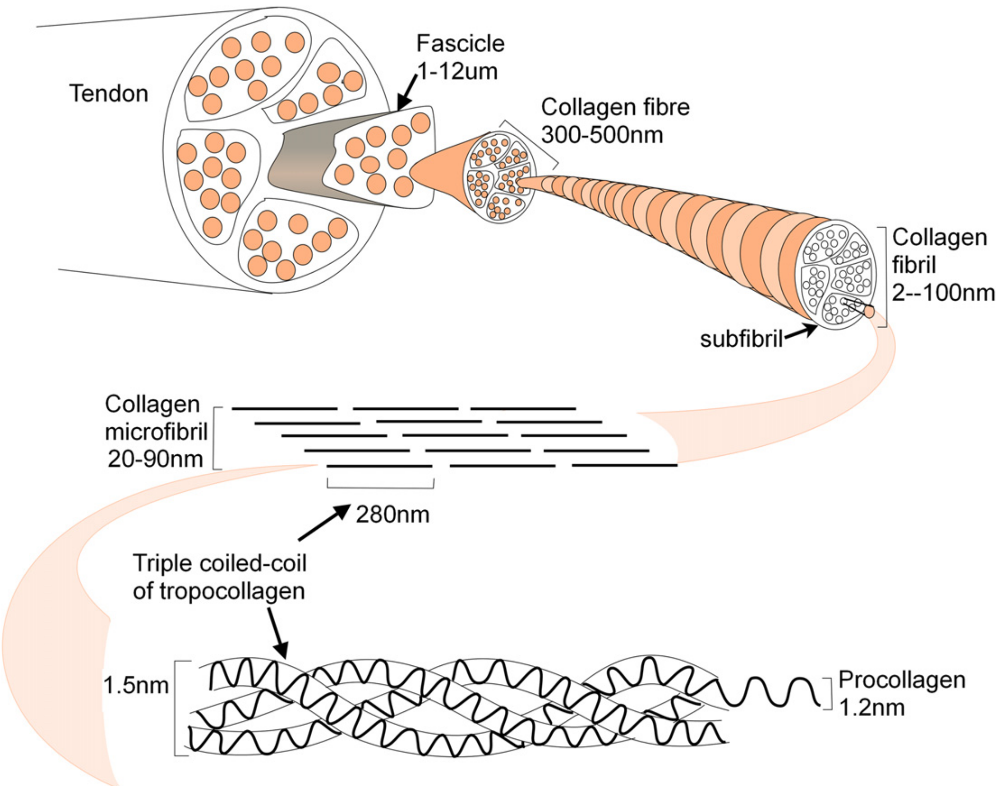

Figure 29 Diagram to show a hierarchy of components in the structure of tendon — α-helix of procollagen, triple coiled-coil of tropocollagen, collagen microfibril, and the self-similar packing arrangement in subfibril, fibril, fibre, fascicle and ultimately tendon.

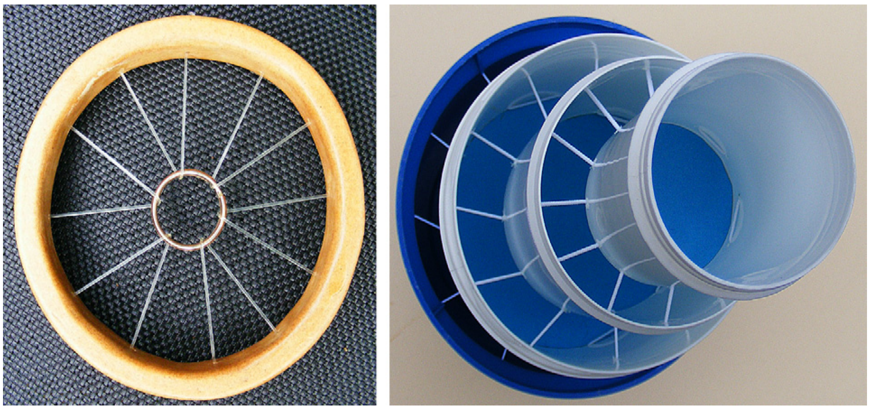

Figure 30 Wheel showing central hub suspended within outer rim; and wheels within wheels model successive joints in the arm.

Ingber, 2003a; Levin, 2007). Curved compression elements (Figure 32) differ from straight struts (Figure 22) because their outer convex surfaces are actually under tension and inner concave surfaces under compression, but like the struts in a geodesic dome, biological materials deal with both types of loading as a result of their nano and micro structures (Gordon, 1978; Lakes, 1993; Puxkandl et al., 2002; Gao et al., 2003; Gupta et al., 2006; Brangwynne et al., 2006). Inferences that this is ultimately due to their *tensegrity* construction have been made (Skelton et al., 2001; Levin, 2007; Ingber, 2008). In addition, when spheres are added to the outside of an icosahedron they do not close-pack completely, and an instability develops (Figures 18d–f and 21a). This apparent 'flaw' in the packing arrangement allows another possibility for modelling an infinite variety of shapes, as different parts of the structure branch outwards, and the spaces in between can fill with smaller icosahedra.

It may now be seen that the distinction between 'geodesic' and 'prestressed' tensegrities is really just relative to the scale at which they are observed, a corollary which should be added to any definition. Even the close-packing of atoms (spheres) should be considered as a 'tensegrity with invisible struts' because their centres of mass are held a minimum distance apart (Connelly and Back, 1998). Distinctions of structure and function in biology may essentially be points on a continuum and artefacts of textbook classification. Although 'geodesic' structures *appear* limited to the cellular size level, 'pre-stressed' tensegrities almost certainly dominate beyond this. At the macro scale the fascia, muscles, ligaments and capsules provide the tension; while the bones and tissue bulk of muscles, organs and fluid-filled vessels resist compression.

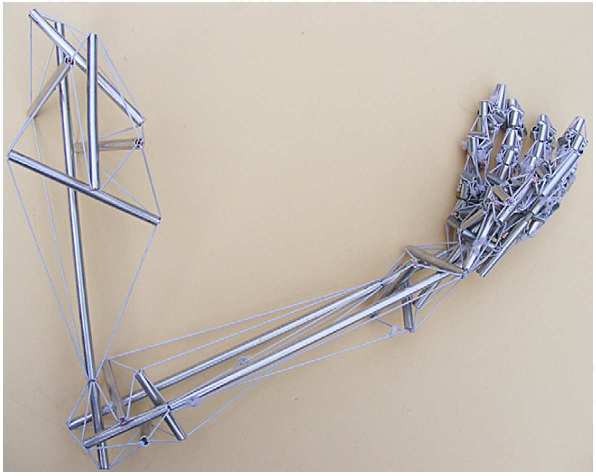

Figure 31 Right upper extremity modelled as a sequence of interconnecting icosahedral tensegrities with compression struts of different lengths.

Tensegrities within tensegrities

Levin was the first to describe the higher complexities of the human body in terms of tensegrities, using the analogy of a bicycle wheel, where the compression elements of the central hub and outer rim are held in place by a network of wire spokes in reciprocal tension (Levin, 1997, 2005a; Connelly and Back, 1998). This type of wheel is a self-contained entity, maintained in perfect balance throughout, with no bending moments or torque, no fulcrum of action, and no levers (Figure 30). He suggested that the scapula may function as the hub of such a wheel, in effect as a sesamoid bone, and transfer its load to the axial skeleton through muscular and fascial attachments (Levin, 1997, 2005a).

The sterno-clavicular joint is not really in a position to accept much compressional load, and the transfer of compression across the gleno-humeral joint has been found to be at maximum only when loaded axially at 90° abduction (Gupta and van der Helm, 2004). As compression can only take place normal to the glenoid surface i.e. at 90° (it is essentially a frictionless inclined plane), the joint must rely heavily on ligamentous and muscular tension in all other positions. A humerus hub model would function equally well with the arm in any position. Similarly, the ulna could be a hub within the distal humeral 'rim' of muscle *attachments*, where load bearing across the joint may be significantly tensional, allowing compressional forces to be distributed through a tensioned network, and the hand to lift loads much larger than would otherwise be

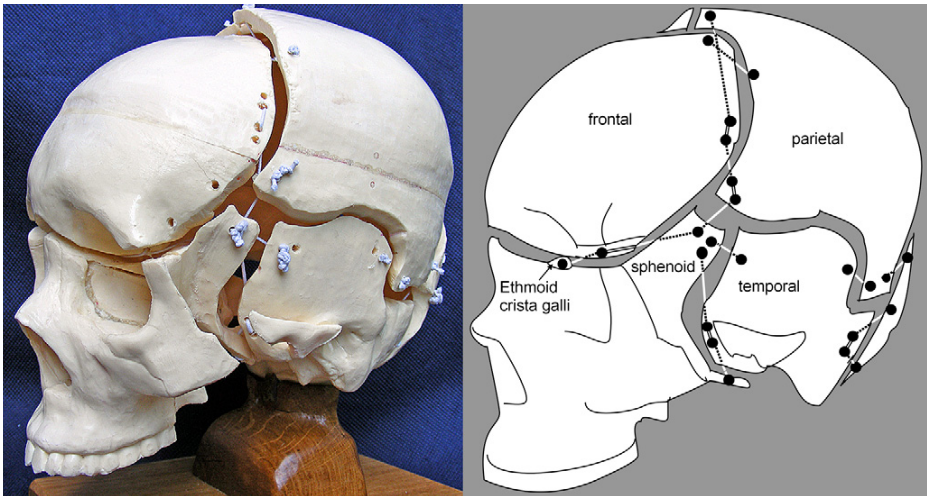

Figure 32 A model of the cranial vault as a tensegrity structure (Scarr, 2008).

the case (Figure 31). In this respect, zero compression across the femur and meniscii has been observed during arthroscopy in an extended knee joint under axial loading in vivo (Levin, 2005b).

The pelvis is also like a wheel with the iliac crests, anterior spines, pubis and ischia representing the outer rim; and the sacrum representing the hub, tied in with strong sacro-iliac, sacro-tuberous and sacro-spinous ligaments. Similarly, the femoral heads may function as hubs within the 'spokes' of the ilio-femoral, pubo-femoral and ischio-femoral ligaments (Levin, 2007).

Most joint movements display helicoid motion around a variable fulcrum, and this is demonstrated in the simple tensegrity elbow in Figure 31, a physiological feature not found in most other models.

Omnidirectionality

According to Wolff's law, tensional forces remodel the bony contours and alter the positions and orientations of their attachments, contributing to the complexity of shapes apparent in the skeleton (Kushner, 1940; Kjaer, 2004). As part of a prestressed tensegrity structure, each attachment would influence all the others, distributing forces throughout the system and avoiding points of potential weakness (Skelton et al., 2001; Masic et al., 2006); in contrast to a pure geodesic chain or truss which is vulnerable to buckling (Figure 21c). Such a mechanism would be an advantage in long-necked animals such as giraffes and dinosaurs, where the load from the head is distributed throughout the neck (Figure 23) (Levin, 1982). The erect spine and bipedal weight bearing capability of humans have traditionally been viewed as a tower of bricks and compressed disc joints, transferring the body weight down through each segment until it reaches the sacrum, but this is a relative rarity amongst vertebrates. Most other species have little or no use for a compressive vertebral column, which is frequently portrayed as a horizontal truss and cantilever support system (Thompson, 1961, p. 245; Gordon, 1978, p. 239). As the main difference in vertebrate anatomies is in the detail, it seems reasonable to suppose that they have some structural properties in common (Levin, 1982, 2002). Tensegrities are omnidirectional, i.e. they are stable irrespective of the direction of loading; and the spine, pelvis and shoulder all demonstrate this property (within physiological limits), enabling dancers to tip-toe on one leg, and acrobats to balance on one hand.

Continuums of structure

Prestressed and geodesic tensegrities may coexist at the same level within a particular functional unit and have been described in the cranium, where the bony plates of the vault substitute for curved prestressed compression struts and do not touch each other; alongside a geodesic cranial base (Figure 32). Prestressed tension is provided by the dura mater — a tough membrane covering the brain — which regulates bone growth, maintains the separation of vault bones at the adjoining sutures, and integrates the whole structure into a single functional unit. It has been suggested that the brain *influences* the vault to grow outwards, through the dura mater, rather than physically pushing it out (Scarr, 2008).

Balanced mobility

Balanced and symmetrical tensegrities automatically assume the configuration that minimizes their stored elastic energy, with changes in shape that require very little control energy; in contrast to classical structures where significant energy is required to work against the old equilibrium (Skelton et al., 2001; Masic et al., 2005). Their high yield strain allows large shape changes to be accomplished at no loss in stiffness (Masic et al., 2006), a distinctive feature in biological structures. The icosahedron has been described as an intermediary in a potential oscillating system (Fuller, 1975, sec.460.08) with similarities to an energy efficient pump (Levin, 2002). If the vector equilibrium (cuboctahedron) (Figure 11a) is constructed without radial vectors and joined with flexible connectors, and is compressed between two opposite triangular faces, it will contract and rotate symmetrically (due to the instability of the square faces) and assume the shape of the slightly smaller icosahedron (each of the square faces now becomes a rhomboid, or essentially, two triangles). Further compression causes the equator to twist and fold, and the structure transform itself through an octahedron, to the tetrahedron, and back again. The icosahedron is at the lowest energy state within the system, and the point around which changes in shape occur. Fuller called this mechanism the 'jitterbug' (Fuller, 1975, sec.460.00). An organism utilizing such a system would be able to move with the minimum of energy expenditure, and remain stable whilst changing shape.

Symmetry and natural laws

> ''The ability… to generate elaborate and beautiful forms… comes from a simple but fundamental principle which governs the deep structure of the physical universe: symmetry. …Albert Einstein… argued that truly fundamental laws of nature must be the same at all times and in all places: that is, the laws must be perfectly symmetric… Principles of symmetry govern the four forces of nature (gravity, electro-magnetism, and the strong and weak nuclear forces that act between fundamental particles).'' (Stewart, 1998, p. 38)

The ubiquitous nature of symmetry offers a simple explanation for stable crystal lattices and other regular patterns, because of the balance of forces. Instabilities in the dynamics of living systems also generate complex patterns and shapes within hierarchies of structure, as self-similar shapes (fractals) scale up through dilation — one of the four principal types of symmetry transformation.

> ''Instability breaks the overall system symmetry, but it appears to be a localized fissure that is offset by… a balancing asymmetry elsewhere in the system. Essentially, the sum of all the asymmetries is symmetrical… Thus, we have patterns of symmetry that reflect the underlying symmetrical nature of the universe, and patterns (and forms) that are generated by instabilities in the system.'' (Kreigh and Kreigh, 2003)

That different structures should emerge at different levels in complex organisms is typical of evolutionary selection. Over hundreds of millions of years chance mutations in the genetic code occasionally gave rise to new characteristics which conferred an advantage to the organism, whilst existing traits which remained useful were retained, through natural selection. This bifurcation in development creates *asymmetries* which must be balanced in order to permit new higher-order *symmetries* (Stewart, 1978, p. 114).

Organization is still part of the self-assembly capacity, but the resulting form may have a very different appearance from its component substructures (Figures 24 and 29) ''…and be arranged into almost any contingent artifactual arrangement we choose'' (Denton et al., 2003). Correlations with '60° geometry' at the macro scale *may* then be more coincidental (Phalen et al., 1978; Thomas et al., 2005); and description such as 'close-packing of the knee in full extension' means something different to 'close-packing of spheres'.

Summary

The tetrahedron is one of the simplest of shapes in 3D because of its close-packing efficiency, minimal-energy configuration and triangular stability. It gives rise to the octahedron and square in the octet truss, and nuclear close-packing in the cuboctahedron and cube; all manifesting within each other, and all resulting from '60° geometry'. The hexagon, and cubic symmetry of these shapes links them to the polyhedron most suited to fulfill structural evolution in biology, which is the icosahedron, possibly part of the substructure predicted by Ramsey (Graham and Spencer, 1990). All these polyhedra undergo a phase transition as they morph into prestressed tensegrity structures, giving endless shape possibilities, but their well-defined geometries are now obscured. The cuboctahedron links them to the 'vector equilibrium' and dynamic 'jitterbug', where energy efficient transformations of shape become significant. Self-assembling helical proteins carry the tensegrity principle into the nano-structures of the cell and extracellular matrix; and through structural hierarchies to the whole body. The genes orchestrate a battery of physical and chemical processes, but the natural laws of physics still provide the construction rules (Stewart, 1998, p. 25; Denton et al., 2003; Harold, 2005; Ingber, 2006b); and shape becomes determined more by Darwin's ''natural selection for biological function'' (Denton et al., 2003).

Conclusion

> ''…ideal geometries…pervade organic form because natural law favours such simplicity as an optimal representation of forces''. Stephen Jay Gould (Thompson, 1961, xi)

Energy consumption is the key to understanding the structural complexities of living organisms, and as energy-efficient structural mechanisms, tensegrities seem to apply at every level from the atom to the whole body. The icosahedron links the simple geometry of the platonic solids to the tensegrities of complex shapes, and lends itself to their modelling. It also becomes a transient in energy efficient transformations of shape, through the 'jitterbug' system described by Fuller.

As a tensioned tensegrity network, the fascia may have a coordinating function throughout the body; and as manual therapies make contact at the whole body level, it provides a pathway for therapeutic interventions right down to the molecular scale.

Acknowledgements

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