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EXPLORING CELLULAR TENSEGRITY: PHYSICAL MODELING AND COMPUTATIONAL SIMULATION

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TENSEGRITY: FROM ARCHITECTURE TO CELL MECHANICS

The term *tensegrity* was first coined by Buckminster Fuller to describe a structure in which continuous tension in its members forms the basis for structural integrity. Fuller most famously demonstrated the concept of tensegrity in architecture through the design of geodesic domes while his student, artist Kenneth Snelson, applied the concept of tensegrity to create sculptures that appear to defy gravity (Figure 1). Snelson's tensegrity sculptures have minimal components and achieve their stability through dynamic distribution of tensile and compressive forces amongst their members to create internal balance [1]. It was upon viewing Snelson's sculptures that Dr. Donald Ingber became inspired by their structural efficiency and dynamic force balance to adopt tensegrity as a paradigm upon which to analyze cell structure and mechanics. It has been 30 years since the premier appearance of the cellular tensegrity model and although the model is still much under debate, empirical evidence suggests that the model may explain a wide variety of phenomena ranging from tumor growth to cell motility [1-4].

Tensegrity structures fall under two distinct categories. The first type, which includes geodesic structures, uses stiff members that are designed to bear both tension and compression. The second type of tensegrity structure, as demonstrated by Snelson's sculptures, is built using distinct tension and compression members[1,2,4]. Although each individual member bears exclusively either tension or compression, the structural ensemble is able to withstand tension, compression, shear, bending, and torsion. In the cellular tensegrity model, both types of tensegrity are used; the geodesic form is typically used to model structures such cell membranes while the distinct tension compression form is used to model intracellular structure (Figure 2).

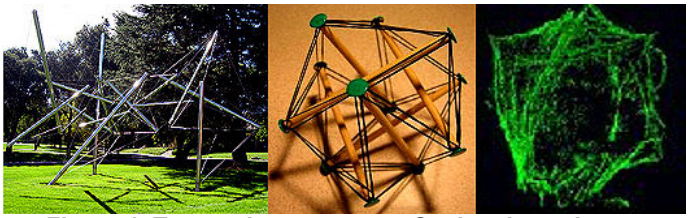

Figure 1. Tensegrity structures: Snelson's sculpture 'Mozart', elastic-wood model, and cell cytoskeleton

In the 1970's, prior to the appearance of Ingber's cellular tensegrity model, a cell was presented as a viscous sac in which organelles floated. It was understood that a cytoskeletal (CSK) matrix

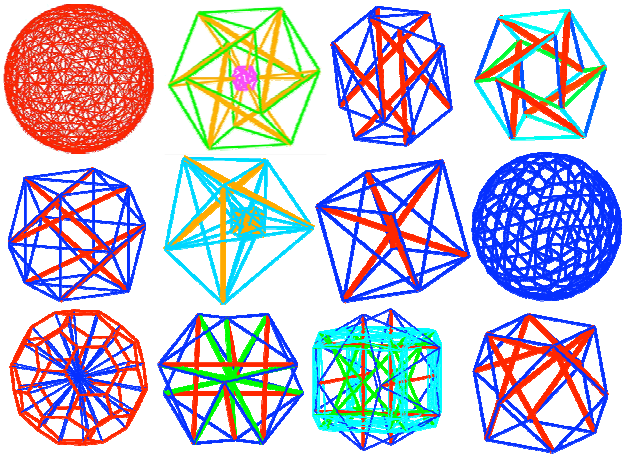

Figure 2. Tensegrity in the cell: Cell membrane models and intracellular structural models.

existed, but it was unclear as to how the CSK affected cell structure and its interaction with the environment. To bridge this gap, the tensegrity model aimed to explain intracellular and extracellular processes via a biomechanics viewpoint. The model uses three distinct biopolymers to describe CSK structure. They consist of compression members (microtubules) and tension members (microfilaments and intermediate filaments) that work together to provide structure and support for the cell and its internal organelles. Microtubules are hollow tubular polymers that are the largest in size out of the three biopolymers and mechanically the stiffest. While *in vitro*, microtubules appear to be straight, *in vivo* they appear often as bent or buckled under compression. Microfilaments, thin stringy structures *in vitro*, are seen to be straight and taut tension members *in vivo*. However, microfilaments can also act as compression members, such as in the formation of filopodia where strands undergo cross-linking to form stiff bundles that extend out from the leading edge of cells. The third structural component, intermediate filaments, are highly flexible and extensible structural polymers that act like guy wires which help keep individual microtubules from buckling. [1-4]

The simple mechanical elegance of the tensegrity model motivated this study, which investigates cellular tensegrity by creating physical models and a variety of computational models that are analyzed for structural integrity and design efficiency. The goal of this study is to gain a preliminary understanding of how tensegrity structures physically respond to external loading, use this learning to analyze the response characteristics of different tensegrity forms and to draw parallels between these observations and cell mechanics.

EXPLORING FORCE NETWORKS THROUGH PHYSICAL MODELS

Physical tensegrity models were built using wooden struts and elastic bands; some were based on Ingber's initial designs and others were created anew. Varying numbers of compression and tension members, i.e., struts and ropes, were used to achieve different shapes with unique mechanical properties (Figure 3). From these models, we conclude that a set minimum number of ropes is required to interconnect struts to establish structural integrity. Failure of a single non-redundant member results in the immediate collapse of the entire structure. However, as a whole, the models display an intrinsic ability to recover from large deformations without irreversible damage. In fact, redundancy and the ability to recover from large strains is widely seen in naturally-occurring tensegrity structures, such as in the intricate network of structural polymers found within cells (Figure 1).

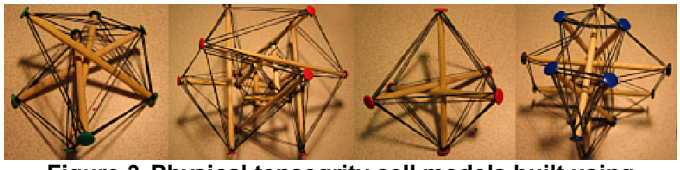

Figure 3. Physical tensegrity cell models built using compressive wooden struts and tensile elastic bands.

Prestress and compliance of ropes significantly impact cell shape and mechanics. Increasing overall prestress increases the stiffness of the cell whereas modifying prestress and/or compliance of selected ropes changes distances between struts, consequently altering cell structure and response to load. However, changing strut stiffness does little to affect the overall structure of the cell unless the struts undergo large strain or buckling.

It is interesting to note that there are distinct locations on the surface of the tensegrity cell that are more mechanotransducive than others. For example, nodes that are at the junction of compression or tension members are better suited to directly transmit force through the cell than arbitrary points within a tension member. This phenomenon is reflected in biological cells where local stress, when applied at distinct signal transduction points on the cell surface, can cause immediate distortion of cell shape and structure. These discrete transduction points are membrane adhesion receptors known as integrins, which couple the CSK with the extracellular matrix and act as direct lines of load transfer in the cell. The immediate deformation in cell structure caused by loading at the integrins alters the mechanics, kinetics and thermodynamics of cellular processes. When stress is applied to other types of receptors on the cell surface which are not mechanotransducers, stress is dissipated locally amongst the flexible members and does neither affect the internal nor the global structure of the cell.

EXPLORING CELL STIFFNESS THROUGH SIMULATIONS

Various computational models of tensegrity structures were created (Figure 2) and in a nonlinear finite element based analysis, the complex interplay between form and function was analyzed to address the fundamental question of how local filament stiffness translate to global structural stiffness. The overall tensile, compressive and shear stiffness were calculated (Figure 4), as well as structural efficiency (defined as stiffness scaled by biomass). By varying prestress and geometric cross-linking, the models displayed a wide range of responses ranging from tremendously stiff to extremely flexible.

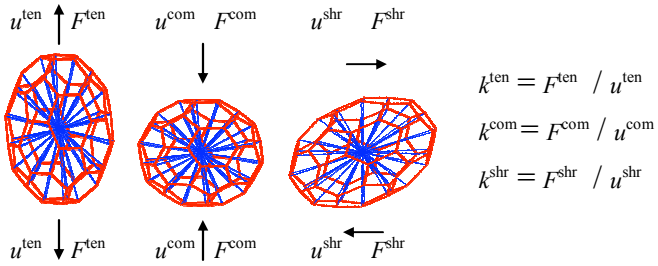

Figure 4. Computational analysis of tensegrity cells designed using compressive struts and tensile ropes.

CONCLUSION

The tensegrity paradigm provides an elegant framework to explore cell mechanics and mechanotransduction. In order to gain understanding of the response of tensegrity cell structures, physical structures and computational models were designed and elaborated. The physical structures gave rise to various forms, either flexible or stiff depending on the magnitude of prestress and the geometric interconnections. The complementary computational simulations enabled a quantitative analysis of the highly nonlinear force network generated within the cell. In conclusion, the tensegrity model is an important contribution to the field of mechanobiology. The cellular tensegrity paradigm provides a unified theory that can be use to describe how mechanical forces are transmitted in cells, allowing for more specific understanding of cellular mechanics and how mechanics can directly affect biochemical responses on the subcellular and cellular levels.

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