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Form Adaptation of Individual Biological Structures to Mechanical Stress

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Observations and experiments of the mechanical stress adaptation of overall shape and of local microstructure in living animal bones and in living trees are reviewed. These adaptations are those of individuals and not of species. A continuum model called the theory of adaptive elasticity is presented to predict the evolution in shape and microstructure of these biological structures. A computational formulation of the predictive model is compared with an animal experiment. The phenomenological representation of the data by the theory is excellent.

INTRODUCTION

This paper is concerned with living biological tissues like bone and wood that adjust to their ambient environmentally applied mechanical loads by slowly changing their overall shape and their local density or microstructure. The ability of plants and animals to adapt their form to their function was a major theme in the famous book by D'Arcy Thompson (1917) entitled On Growth and Form. In the most widely quoted chapter in that book, entitled On the Theory of Transformations, or The Comparison of Related Forms D'Arcy Thompson begins with the paragraph

> "In the foregoing chapters of this book we have attempted to study the inter-relations of growth and form, and the part which the physical forces play in this complex interaction; and, as part of the same enquiry, we have tried in comparatively simple cases to use mathematical methods and mathematical terminology to describe and define the forms of organisms. We have learned in so doing that our own study of organic form, which we call by Goethe's name of Morphology, is but a portion of that wider Science of Form which deals with the forms assumed by matter under all aspects and conditions, and, in a still wider sense, with forms which are theoretically imaginable."

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The topic of this paper was therefore one of the first major topics in the study of the Science of Form.

A theory of adaptive elasticity is described here. This theory attempts to model these biologically and chemically complex stress adaptation processes with a simple continuum model. The model is composed of a porous anisotropic linear elastic solid perfused with, and surrounded by, a fluid. The chemical reactions of the stress adaptation process are modeled by the transfer of mass from the fluid to the porous solid matrix, and vice versa. As a result of the chemical reactions mass is transferred to (from) the solid matrix so that it either increases (decreases) the overall size of the body or increases (decreases) the density of the body. The rates of these chemical reactions are very slow compared to the characteristic time of inertia effects. The rate of change of the overall size and shape of the body is controlled by surface strain, and the rate of change of density at a point is controlled by the local matrix strain. The details of this model, as well as its physical motivation, are described.

STRESS ADAPTATION IN BONE

Functional adaptation is the term used to describe the ability of organisms to increase their capacity to accomplish their function with an increased demand and to decrease their capacity with lesser demand. Living bone is continually undergoing processes of growth, reinforcement and resorption which are collectively termed "remodeling". The remodeling processes in living bone are the mechanisms by which the bone adapts its overall structure to changes in its load environment. The time scale of the remodeling processes is on the order of months or years. Changes in life style which change the loading environment, for example taking up jogging, have remodeling times on the order of many months. Bone remodeling associated with trauma has a shorter remodeling time, on the order of weeks in humans. The time scales of these remodeling processes should be distinguished from developments in bone due to growth, which have a time scale on the order of decades in humans, and the developments due to natural selection which have a time scale of many lifetimes.

It is necessary to describe the nature of bone as a material before describing the remodeling processes that occur in bone. Experiments have shown that bone can be modeled as an inhomogeneous transversely isotropic or orthotropic elastic material, with the degree of anisotropy varying inhomogeneously also.

There are two major classes of bone tissue which significantly contribute to the structural strength of the skeletal system. They are called cancellous and cortical bone. Cortical bone is the hard tissue on the outer surface or cortex of the femur (thigh bone). It is dense, it contains no marrow and its blood vessels are microscopically small. Cancellous bone occurs in the interior of the femur. It consists of a network of hard, interconnected filaments called "trabeculae" interspersed with marrow and a large number of small blood vessels. Cancellous bone is also called trabecular bone or spongy bone. Generally cancellous bone is structurally predominant in the neighborhood of the joints and cortical bone is structurally predominant in the central sections of a femur away from the joints. Bone tissue contains an abundance of extracellular material or matrix. The volume fraction of the matrix is orders of magnitude larger than the volume fraction of bone cells. The matrix accounts for virtually all the structural strength of bone.

The concept of stress or strain induced bone remodeling was first publicized by the German anatomist Wolff (1870), and is often called Wolff's law. The distinction made by Frost (1964) between surface and internal remodeling is followed here. Surface remodeling refers to the resorption or deposition of the bone material on the external surface of the bone. The details of the process of deposition of new lamina at the surface of a bone are described by Currey (1960). Internal remodeling refers to the resorption or reinforcement of the bone tissue internally by changing the bulk density of the tissue. Only cortical bone remodels by surface remodeling, because cancellous bone never appears at the external surface of a whole bone. Both cancellous and cortical bone exhibit internal remodeling.

Surface remodeling can be induced in the leg bones of animals by superposing axial and/or bending loads. Woo et al. (1981) has shown that increased physical activity (jogging) in pigs can cause the periosteal surface of the leg bone to move out and the endosteal surface to move in. Surface remodeling can also be induced in the leg bones of animals by reducing the loads on the limb. In two studies Uhthoff and Jaworski (1978) and Jaworski et al. (1980) immobilized one of the forelimbs of beagles. In the study of Uhthoff and Jaworski (1978), young beagles were used and it was found that the endosteal surface showed little movement while there was much resorption on the periosteal surface. However, in the study with older beagles (Jaworski et al. (1980)), it was observed that the periosteal surface showed little movement while on the endosteal surface there was much resorption. Lanyon et al. (1982) reported on an ulnar ostectomy study in which the bone strain was measured during functional adaptation to hyperphysiological stress states. Mature sheep were subjected to an ulnar ostectomy (removal of a section of the ulnar diaphysis) on their right limb, and the left forelimb was used as a control. The strain in the radii was monitored by means of in vivo strain gaging at the cranial and caudal periosteal surfaces. The top image on the plate is a photograph of the cross-section of the intact ulna and radius from the left control limb. The middle image on the plate shows the radius from the right experimental limb 1 year after the removal of the ulna. The bottom image on the plate represents the surface remodeling predicted by the theory and will be discussed later.

STRESS ADAPTATION IN TREES

Functional adaptation also occurs in trees and plants. Trees adapt their shape and structure to their environmental loading in a manner qualitatively similar to that observed in bones. The exact mechanism of stress adaptation in trees is unknown, but a combination of mechanical stress and the hormone auxin have been suggested by a number of studies, Zimmermann (1964), Zimmermann and Brown (1970).

It has been observed that trees growing in dense forest strands have smaller trunk diameter than trees growing at the edge of the strand and are more inclined to be blown over than those at the edge. It has also been observed that nursery trees grown

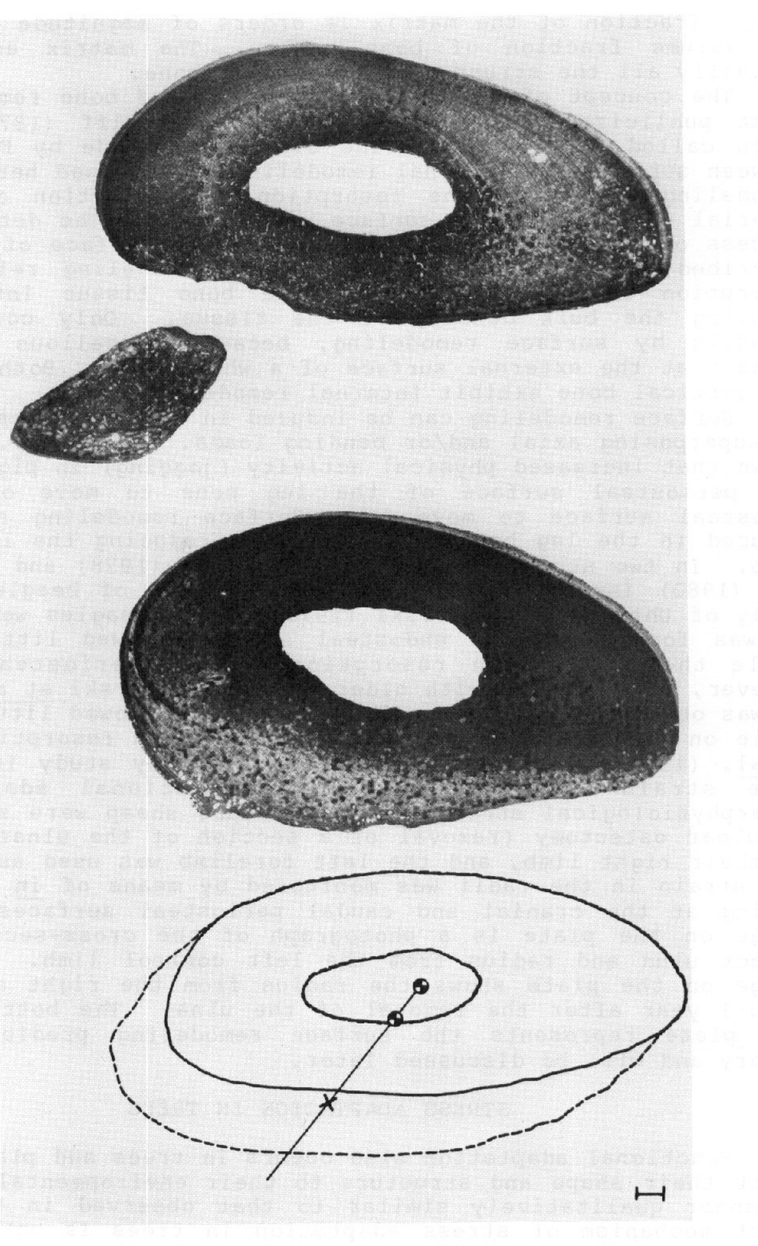

Plate. The ulnar ostectomy experiment with mature sheep (Lanyon et al., 1982). Each illustration represents the bone cross-sections in the sheep forelimb. (Upper) The contralateral control limb at 1 yr showing the radius with the intact ulna. (b)(Middle) The experimental radius at 1 yr, showing marked asymmetric periosteal deposition. (c)(Bottom)The calculated remodeling. The solid lines represent the surfaces of the control bone, (a)above, and the dashed lines represent the predicted geometry at 9 months. The indicated length is 1 mm.

close together in containers are tall and spindly while those placed further apart are greater in trunk diameter. An interesting experiment which quantified this phenomenon was reported by Neel and Harris (1971). These environmental horticulturists obtained eight matching pairs of young sweet-gum trees (Liquidambar). The trees were placed in four gallon cans in a greenhouse. Each morning at 8:30 for 27 mornings, one tree in each pair was shaken for 30 seconds. At the end of the 27 day period the shaken trees had reached a height which was only 20% of the height of the unshaken trees. However, the trunks of the shaken trees were larger than those of the unshaken trees. At a distance of 5 cm from the ground the diameter of the shaken trees had increased by 8.3 mm while those of the unshaken had increased by only 6.8 mm. The wood fiber length and the vessel member length were significantly shorter in the shaken trees. Although the authors did not measure the elastic moduli, the changes in the wood tissue microstructure suggests that the elastic moduli are different in the shaken and unshaken trees. One would reasonably expect the moduli to be higher in the unshaken trees.

The wood tissue that is deposited on an external surface of a tree trunk in response to a superposed bending moment in a particular direction is called reaction wood. Reaction wood is visible when a transverse section of the tree trunk is viewed because it distorts the growth rings. In a tree that has been bent in a particular direction the growth rings will not be circular, but they will be ovals distorted in the particular direction associated with the bending. The additional wood tissue deposited will increase the area moment of inertia of the trunk cross section and decrease the stress experienced by the wood tissue. This phenomenon is illustrated in Figure 1. The upper portion of this figure shows an alpine tree that has been shifted by an avalanche at some time in the past to a horizontal position. In the lower portion of the figure the cross sections of the limb at two different locations are illustrated.

MODELING OF THE STRESS ADAPTATION PROCESS

At this early stage of development, the stress adaptation processes in bone and trees can be described by the same model. The modeling ideas for bone are described in Cowin (1984). The theories of surface and internal remodeling use a simple two constituent model. The solid matrix is modeled as a porous anisotropic linear elastic solid. The basic model is then a porous, anisotropic linear elastic solid perfused with a fluid. In the model of the stress adaptation process chemical reactions convert the fluid into the porous solid matrix and vice versa. As a result of the chemical reactions mass, momentum, energy and entropy are transferred to or from the porous solid matrix. The rates of these chemical reactions depend on matrix strain and are very slow compared to the characteristic time of inertia effects. Thus, inertia effects are neglected and the stress in the matrix considered here is the actual stress averaged over a time period greater than any inertia effects.

At this point the discussion naturally bifurcates into the consideration of the two parts which constitute the complete model, namely the surface remodeling theory and the internal remodeling theory. The distinction between the two theories is

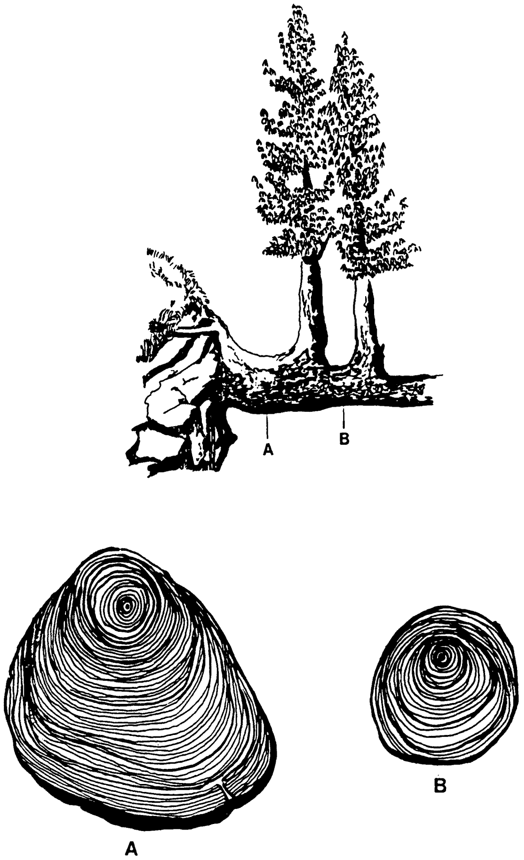

Figure 1. The upper portion of this figure shows an alpine tree that has been shifted by an avalanche at some time in the past to a horizontal position. The lower portion of the figure illustrates the cross sections of the limb at two different locations.

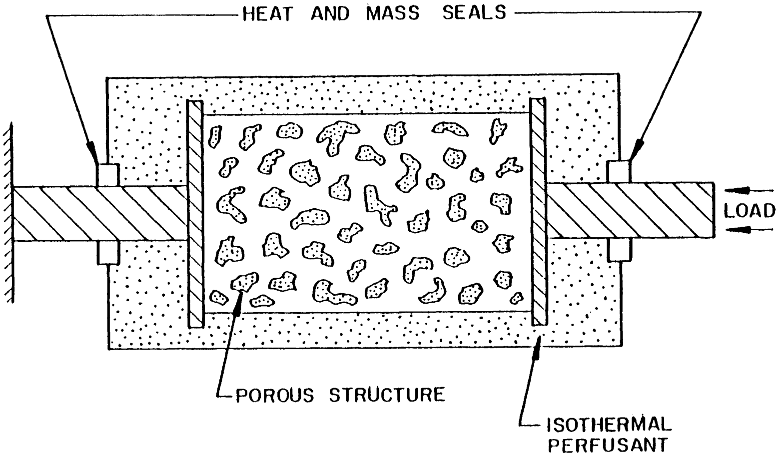

Figure 2. A schematic model of the remodeling mechanism.

made upon the locations at which the chemical reactions occur and the way in which mass is added to or removed from a material body. In the theory of surface remodeling the chemical reactions occur only on the external surfaces of the body and mass is added to or removed from the body by changing the external shape of the body. During surface remodeling the interior of the body remains at constant bulk density. In the theory of internal remodeling the chemical reactions occur everywhere within the porous solid matrix of the body and mass is added by changing the bulk density of the matrix and without changing the exterior dimensions of the body. In both cases the rate and direction of the chemical reaction at a point are determined by the strain at the point. It is important to note that these two theories are neither contradictory nor incompatible, but combine easily for a single body in which there are both overall shape changes and density changes.

The theory of surface remodeling acknowledges the observed fact that external changes in body shape are induced by changes in the loading environment of the body. This theory postulates a causal relationship between the rate of surface deposition or resorption and the strain in the surface of the body. The body is considered to be an open system with regard to mass transport and the mass of the body will vary as the external shape of the body varies. This theory is described by Cowin and Van Buskirk (1979) and Cowin and Firoozbakhsh (1981). The theory of internal remodeling postulates a causal relationship between the rate of deposition or resorption of the solid matrix at any point and the strain at that point in the solid matrix. A schematic diagram of this model is shown in Figure 2. The fact that living bone and living wood tissue are encased in a living organism and that the geological materials are saturated, is reflected in the model by setting the elastic porous solid in a bath of the perfusant. The mechanical load is applied directly to the porous structure across the walls of the perfusant bath as illustrated. The system consisting of the elastic porous solid and its perfusant bath is considered to be closed with respect to mass, heat energy, and entropy transfer, but open with respect to momentum transfer from loading. The system consisting of only the elastic porous solid without its entrained perfusant is open with respect to momentum transfer as well as mass, energy, and entropy transfer. The solid matrix is taken as the control system since the changes in the mechanical properties of the solid matrix alone determine the changes in the mechanical properties of the whole body.

The theory of internal remodeling is developed in a series of papers: Cowin and Hegedus (1976), Hegedus and Cowin (1976), Cowin and Nachlinger (1978), Cowin and Van Buskirk (1978), and Cowin (1986). Due to space limitations the reader is referred to these works for further discussion of the internal remodeling theory. In the remainder of this work the theory of surface remodeling will be developed as an example of the adaptive elasticity theories.

THE THEORY OF SURFACE REMODELING

The model for surface remodeling employed assumes that solid matrix can be modeled as a linear elastic body whose free surfaces move according to an additional specific constitutive relation. The additional constitutive relation for the movement of the free surface is the result of a postulate that the rate of surface deposition or resorption is proportional to the change in the strain in the surface from a reference value of strain. At the reference value of strain there is no movement of the surface. In order to express the constitutive equation for the surface movement in equation form some notation is introduced. Let Q denote a surface point on the body and let U denote the speed of the remodeling surface normal to the surface. The velocity of the surface in any direction in the tangent plane is zero because the surface is not moving tangentially with respect to the body. Let E(Q) denote the axial components of the strain tensor at Q. Small strains are assumed. The hypothesis for surface remodeling is that the speed of the remodeling surface is linearly proportional to the strain tensor,

$$U = C\,(E(Q) - E^{o}(Q)), \qquad (1)$$

where $E^{o}(Q)$ is a reference value of strain where no remodeling occurs and C is the surface remodeling rate coefficient. The surface remodeling rate coefficient and the reference value of the strain are phenomenological coefficients of the body surface and must be determined by experiment. Eq. (1) gives the normal velocity of the surface at the point Q as a function of the existing strain state at Q. If the strain state at Q, E(Q), is equal to the reference strain state, $E^{o}(Q)$, then the velocity of the surface is zero and no remodeling occurs. If the right hand side of (1) is positive, the surface will be growing by deposition of material. If, on the other hand, the right hand side of (1) is negative, the surface will be resorbing. Eq. (1) by itself does not constitute the complete theory. The theory is completed by assuming that the body is composed of a linearly elastic material. Thus, the complete theory is a modification of linear elasticity in which the external surfaces of the body move according to the rule prescribed by Eq. (1). A boundary value problem will be formulated in the same manner as a boundary value problem in linear elastostatics, but it will be necessary to specify the boundary conditions for a specific time period. As the body evolves to a new shape, the stress and strain states will be varying quasi-statically. At any instant the body will behave exactly as an elastic body, but moving boundaries will cause local stress and strain to redistribute themselves slowly with time.

This theory has been applied recently by Cowin et al. (1985) to the results of five reported animal experiments in which the temporal evolution of a change in bone shape after a significant change in the mechanical loading environment of the bone was documented. One of these animal experiments was the sheep ulna ostectomy study reported by Lanyon et al. (1982) and discussed above. Application of the theory of surface remodeling to this animal experiment resulted in the predicted shape shown in the bottom portion of the plate. The solid lines represent the surfaces of the control bone shown in the top image of the plate and the dashed lines represent the predicted geometry at 9 months. The reader is referred to Cowin et al. (1985) for the details of the study. The phenomenological representation of the data by the theory was excellent.

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