Elastomeric Proteins

Structures, Biomechanical Properties, and Biological Roles

Elastomeric proteins occur in a wide range of biological systems where they have evolved to fulfil precise biological roles. The best-known include proteins in vertebrate muscles and connective tissues, such as titin, elastin and fibrillin, and spider silks. However, other examples include byssus and abductin from bivalve molluscs, resilin from arthropods, and gluten from wheat. Interest in elastomeric proteins is currently high for several reasons – first, because of their biological and medical significance, particularly in human diseases. Second, the unusual properties of proteins, such as spider silks, provide opportunities to develop novel materials. Third, the development of scanning probe microscopy makes it possible to study structures and biomechanical properties of these proteins at the single molecule level. This book will be of interest to graduate students and researchers from a broad range of disciplines, working on any aspect of elastomeric proteins.

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Preface

Elastic proteins occur in a wide range of biological systems, from plants and invertebrates to humans, where they have evolved to fulfil precise functional roles. The majority of these proteins possess rubber-like elasticity, undergoing high deformation without rupture and then returning to their original state on removal of the stress, with virtually all the energy stored on deformation being returned. The second stage of this process is passive and does not require an input of energy. Such an entropic mechanism is ideal for elastomers that are required to last a long time (e.g., aortic elastin undergoes millions of stress-strain cycles in a human life span). However, not all biological protein elastomers have purely entropic mechanisms.

In simple terms, chains of a protein elastomer must be flexible and independently free to respond rapidly to an applied force and must also form a network of monomers stabilised by cross-links between non-elastic domains. The elasticity will therefore vary with the length of the flexible domain and the extent of cross-linking.

The best-known and most widely distributed protein elastomer is elastin, which is responsible for the elasticity of the aorta and skin of mammals, and is also present in the ligamentum nuchae which is involved in raising the heads of grazing hoofed animals. More recently, fibrillin, which forms the scaffold for elastin in vertebrate tissues, has also been shown to have elastic properties. Resilin is also well known as the elastic ligament attaching the wings to the thoraxes of insects, where it is responsible for the rapid vibration of the wings, and, more recently, the properties of giant protein titin – which is responsible for the elasticity of vertebrate striated muscle – have been elucidated.

Elastic proteins also perform unusual and unique functions, for example: abductin ligaments in clams (bivalve molluscs) open the shell when the muscles relax, generating a primitive swimming action; byssus threads bind mussels to rocks and possess elastic and rigid domains to resist wave action; and spider webs comprise stiff dragline silks that form the spokes and extensible flagelliform silks that form the capturing spirals, absorbing the energy of the impacting insect without catapulting it out of the web.

Biologically active protein elastomers are unknown in plants, but the elastic properties of the gluten proteins of wheat grain have been well documented. Although there is no known biological role for gluten elasticity, it is responsible for the ability to make leavened bread. Thus, an entirely fortuitous property of a plant storage protein has a major impact on food processing. The collagen fibres of tendons are generally considered virtually inextensible but, like steel wire, they also have elastic properties. This elasticity is exploited by animals during rapid running and, in doing so, their tendons act as energy stores for rebounds, thus providing more efficient running.

The ability of proteins to exhibit rubber-like elasticity is provided by their molecular organisation.The relationships between mechanical properties and biochemical structure have intrigued scientists for many years, particularly since the seminal work of Miles Partridge on vertebrate elastin and Torkel Weis-Fogh on insect resilin in the 1960s.

The recent rapid explosion of our understanding of protein elasticity has been based on our ability to determine the molecular sequences and three-dimensional structures of the proteins and to relate them to the mechanical properties of macromolecular arrays and single molecules, the latter using new techniques, such as laser tweezers and atomic force microscopy. These techniques have led to rapid advances, but have inevitably also raised many more questions. For example, it is now considered that the elastic behaviour of elastin may be due to the presence of β-spiral structures rather than randomly free chains as in classical rubbers. In contrast, resilin – which is almost a perfect elastomer and exhibits an entropic mechanism like elastin – does not appear to contain β-spirals. Similarly, the stretching of titin appears to involve immunoglobulin-like domains. Furthermore, some elastomers may possess a two-stage mechanism operating at low and high extensions (e.g., the spider silks).

Although these various elastomers have been shown to have little or no amino acid sequence homology, it is possible to recognise some common properties. For example, most contain regions comprised of repeating blocks of particular sequences, which may adopt similar secondary structures capable of generating elasticity. Similarly, β-turns and β-spiral structures appear to occur in several unrelated protein elastomers and readily account for their elastic properties, but are by no means universal. It has, therefore, become clear that many different structural designs in proteins may be responsible for their elastic behaviour, with the requirements for variable levels of elastic behaviour being satisfied in different ways. This is hardly surprising in view of the diverse organisms in which elastomers occur.

The current interest in elastomeric proteins is enhanced by their importance in medicine (e.g., understanding the role of aortic elastin in atherosclerosis) and by opportunities to develop novel biomaterials with specific properties. Synthetic polypeptides based on the repeat sequence of elastin can be used to study platelet interactions and to prevent tissue adhesions in wounds, whereas synthetic structures based on spider silks are being studied to exploit their high strength and high energy-absorbing properties. Additional applications will arise from a greater understanding at the molecular level of the mechanisms that nature has evolved to confer elastic behaviour.

Most of the papers in this volume are based on those presented at a Discussion Meeting of the Royal Society held in London in May 2001 (and since published in *Philosophical Transactions of the Royal Society Series B* 2002, Volume 357, No. 1418, pp. 117–234). This meeting brought together for the first time leading researchers and covered the latest developments in the relationships between the molecular structures and mechanical properties of elastomeric proteins. However, these papers have been revised and expanded, whereas additional chapters (notably on spider silks, resilin, biomimetics, spectrin, and the comparative properties and functions of elastomeric proteins) have been commissioned to complete the coverage. It is hoped that these reviews will together stimulate additional researchers in protein chemistry, molecular biology, and biomechanics to enter this exciting field.

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