D. Strain and substrate motion

Spider strain detection

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Abstract

This chapter is about biological mechano-sensors embedded in the cuticular exoskeleton of arthropods and serving purposes analogous to those of technical strain gauges. Spiders have several thousands of such sensors providing them with a highly resolved picture of the mechanical events in their exoskeleton. The spider “strain gauges”, also called slit sensilla, form tiny slits (length ca. 8 to 200 μm, width 1 to 2 μm) in the exoskeleton, each supplied by two sensory cells. The slits are sites of locally increased compliance which respond to the slightest deformation of the exoskeleton caused by muscle activity, hemolymph pressure, or external sources of load such as substrate vibrations. Slit compression by as little as ca. 1.5 nm and due to strains down to some –10 to –20 με are sufficient to set off action potentials in the sensory cells. A particularly intriguing feature of slit sensilla are lyriform organs representing diverse and sometimes seemingly bizarre close parallel arrays of up to ca. 30 slits.

The following text will highlight some of the properties of the sensors per se and relate their structural characteristics to natural sources of load and the strains produced by them in the exoskeleton. Considering the limitations of direct micromechanical measurements, the modeling of strains and organ deformation by Finite Element analysis has been particularly rewarding. Computational biomechanics has thus contributed substantially to revealing the principles underlying the measurement of strains in a highly refined biological sensory system. It also has paved the way for the future development of bio-inspired artificial strain sensors for technical applications.

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Introduction

The forces contained in the adequate stimuli of all mechanoreceptors generate some strain in the sensory structures. Indeed, stress, which is force per unit area (σ = F/A), and strain (ε = l/l₀), which is relative deformation due to stress, are inseparable from each other. The distinctive feature of the strain sensors treated here is their close relationship to the arthropod exoskeleton. The cuticular exoskeleton of arthropods like insects and spiders serves not only to mechanically support the animal and to provide the necessary leverage for locomotion, but also protects it from unwanted environmental influences, and may camouflage or alternatively advertise its bearer by adopting an appropriate shape and color. In addition, the exoskeleton represents the interface between the outside and inside of the organism and, therefore, carries a wealth of sensory structures on its surface that collect information about the outside world. Importantly, the exoskeleton serves its sensory function not only as a base for large numbers of exteroceptors, but also as a stimulus conducting structure, which propagates stresses and strains to specialized sensors embedded in it and forming a skeletal sense unique to arthropods and alien to humans and other vertebrates. The slit sensilla of spiders form the most elaborate sensory system of this type and will, therefore, be the focus of our attention. Slit sensilla provide spiders with a detailed picture of the mechanical events going on in their exoskeleton which they use as guidance for various patterns of behavior.

Arachnid slit sensilla, like insect campaniform sensilla, are analogues of technical strain gauges. The wealth of strain gauges now commercially available reflects their general importance for many areas of engineering like the construction of buildings, bridges and industrial machines, cars, airplanes and rockets, to name just a few. Like strain gauges the slit sensilla measure the effects of force. In our present biological case these forces act on the exoskeleton and are prompted either by muscular contraction and hemolymph pressure (used to extend the leg), or to external sources like vibration of the substrate and gravity. Both the slit sensilla and campaniform sensilla are tiny holes in the exoskeleton and spots of enhanced compliance which slightly change their shape when the exoskeleton is minimally deformed by such forces. The sensory cells attached to the holes are excited by this deformation.

What follows will not only highlight properties of the sensors (sensilla) per se. An in-depth understanding of the principles at work and of the achievements made possible by their application also asks for the consideration of several components of the entire sensory system and the ways in which they influence, shape and indeed reflect each other. The focus here (albeit treated with different levels of detail) will be on the occurrence and topography of the sensilla, their structural characteristics, the natural sources of load, and the strains in the exoskeleton resulting from them. Having established this background the focus will then be on the mechanical tricks involved in the sometimes bizarre close parallel arrangements of slits forming so-called lyriform organs. The data gained from electrophysiological studies will highlight physiological properties of the sensory cells associated with the slit sensilla.

Finally, some conclusions will be drawn regarding the development of synthetic slit sensilla for technical applications. For earlier reviews on arthropod skeletal strain sensilla, see Barth (1981, 2002), Barth and Blickhan (1984), and Vincent et al. (2007).