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Sensory Systems

1. Introduction

Organisms constantly monitor and respond to changes in their environment (both external and internal) so as to maintain themselves under the most favorable conditions for growth and reproduction. The structures that receive these environmental cues are sense cells, and the cues are always forms of energy, for example, light, heat, kinetic (as in mechanoreception and sound reception), and potential (as in chemoreception, the sense of smell and taste) (Dethier, 1963). The sensory structures use the energy to do work, namely, to generate a message that can be conducted to a decoding area, the central nervous system, so that an appropriate response can be initiated. The message is, of course, in the form of a nerve impulse. Sensory structures are generally specialized so as to respond to only one energy form and are usually surrounded by accessory structures that modify the incident energy.

As Dethier (1963) noted, the small size and exoskeleton of insects have had marked influence on their sensory and nervous systems. Smallness and, therefore, short neural pathways provide for a very rapid response to stimuli. However, it also means that there are relatively few axons and, therefore, a limited number of responses to a given stimulus. This has led to a situation in insects where stimulation of a single sense cell may trigger a series of responses. Further, almost all insect sense cells are *primary* sense cells, that is, they not only receive the stimulus but initiate and transmit information to the central nervous system; in other words, they are true neurons. In contrast, in vertebrates, almost all sensory systems include both a specialized (*secondary*) sense cell and a sensory neuron that transmits information to the central nervous system. The cuticle provides protection and support by virtue of its rigid, inert nature, yet sense cells must be able to respond to very subtle (minute) energy changes in the environment. Thus, only where the cuticle is sufficiently "weakened" (thinner and more flexible) will the energy change be sufficient to stimulate the cell. An insect, therefore, must strike a balance between safety and sensitivity. In contrast to mammalian skin, which has millions of generally distributed sensory structures, the surface of an insect has only a few thousand such structures, and most of these are restricted to particular regions of the body.

Two broad morphological types of sense cells are recognizable (Dethier, 1963; French, 1988), those associated with cuticle (and therefore including invaginations of the body wall) (Type I neurons) and those that are never associated with cuticle and lie on the inner

side of the integument, on the wall of the gut, or alongside muscles or connective tissue where they function as proprioceptors (Type II neurons) (Section 2.2). A Type I neuron and its associated cells are derived embryonically from the same epidermal cell. They and the associated cuticle form the sensillum (sense organ). All types of sensilla, with the possible exception of the ommatidia of the compound eye, are homologous and derived from cuticular hairs.

2. Mechanoreception

Insects receive and respond to a wide variety of mechanical stimuli. They are sensitive to physical contact with solid surfaces (touching and being touched); they detect air movements, including sound waves; and they have gravitational sense, that is, through particular mechanosensilla they gain information about their body position in relation to gravity. This is especially important in flying or swimming insects which are in a homogeneous medium; they receive information about their body posture and the relationship of different body components to each other, and they obtain information on physical events occurring within the body, for example, the extension of muscles in movement, the filling of the gut by food, and the stretching of the oviduct when mature eggs are present.

Information on the above is gathered by a spectrum of mechanosensilla associated with which, in most cases, are accessory structures that transform the energy of the stimulus into usable form, namely, a mechanical deformation of the sense cell's plasma membrane (French, 1988).

2.1. Sensory Hairs

The simplest form of mechanosensillum is seen in sensory hairs (sensilla trichodea) (Figure 12.1), which occur on all parts of the body but are in greatest concentration on those that frequently come into contact with the substrate, the tarsal segments of the legs, antennae, and mouthparts. Typically, they are single structures but on occasion they are found in large groups known as hair plates (Figure 12.2). In its simplest form a sensillum comprises a rigid, poreless hair set in a membranous socket and four associated cells; these are the inner sheath cell (also known as the trichogen or generative hair cell), outer sheath cell (tormogen or membrane-producing cell), neurilemma cell, which ensheathes the cell body and axon of the sensory neuron, and the sensory neuron whose dendrite often is cuticularized and includes a terminal cuticular filament (scolopale) (McIver, 1985; Keil, 1997, 1998). In addition to their generative function, the outer sheath cells have an important physiological role in maintaining the appropriate ionic and molecular environment for stimulus transduction and conduction by the dendrites. Specifically, they pump K^+ ions into the space that surrounds the tip of the sensory dendrite to facilitate generation of the receptor current (Section 2.3). A characteristic feature of the tip of sensory neurons are large numbers of microtubules. Because of their position and experiments with antimicrotubule drugs, it has been suggested that the microtubules may play a role in transduction. However, French's (1988) assessment of the evidence led him to conclude that their more likely roles are in the development and structural maintenance of the sensilla.

Within the above-generalized structure, hairs may differ widely in their detailed morphology, physiology, and function (Section 2.3). Nevertheless, they are all designed such