Mechano-electric Transduction

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Adequate deformation of a mechano-sensitive cell region is transduced to a conductance change of the plasma membrane which leads to a local current flow and to a change in membrane voltage usually called "receptor potential". This transduction is probably a universal property of living cells and is found in highest perfection in hearing and vibration receptors. In recent years mechano-transduction is studied especially in ciliated protozoa and epithelial mechanoreceptor cells (also ciliated) of insects and vertebrates which offer direct access to the sensitive cell region. This report concentrates on the latter sensory cell.

The time delay between the onset of a mechanical stimulus and of the membrane conductance response is between 40 µs (frog vestibular receptors (1)) and 100 µs (insect mechanoreceptor (2)), both at room temperature. This is consistent with a close sensor-to-gate coupling as it is assumed in the electrically controlled Na-channels which switch with a similar latency. The channels, operated by the mechanical stimulus, discriminate poorly between alkali cations, in vertebrate as well as in insect receptors (3, 2, 4).

I. Insect epithelial mechanoreceptors

For the first time, the mechanical energy and its components of force and displacement which stimulate a single mechanoreceptive cell region, could be determined by using thread and clavate hair sensilla of crickets. Epidermal mechanoreceptors of insects become stimulated by indentation of their ciliary outer segment at the site of a modality-specific plasmatic structure, the tubular body. Thread hair sensilla, which are sensitive to the small stimulus energy of slow air streams, are advantageous for measurement of stimulus energy because of two peculiarities: a) The hair is a two-arm lever which transmits force and displacement directly to the receptor terminal; b) the delicate suspension of the hair within the integument absorbs only about 50 % of the energy deflecting the hair; the remainder works on the receptor terminal and the structures lying in series, as removal of the cellular structures indicate. By fastening a magnetic sphere on the hair, which establishes an oscillating system, and by measuring hair deflections in an opto-electronic device the torque producing a certain angle of hair deflection can be determined and an upper limit for force and depth of indentation of the receptor terminal can be calculated taking into account the length of the basal lever arm.

Deflection of a thread hair through 0.1-0.2° causes maximal depolarization of the receptor and requires $1\text{-}3\cdot10^{-16}$ Ws (corresponding to the energy of 200-600 quanta of green light). Oscillations through 0.005° which provide some 10^{-19} Ws per period still produce graded responses. The corresponding upper limits of receptor indentation are about 10 and 0.5 nm, respectively.

The receptor membrane of the stimulus receiving zone is stabilized against strain and bending by cuticular structures. Within this area of 0.5 µm², about 1,000 cones, each 18 nm long, protrude from the inner membrane surface ("membrane integrated cones", MIC); they connect to the peripheral microtubules of the tubular body. Thus, a chain of solid structures is established between the hair base and the cuticle of the integument in which the MICs are the most compliant elements. Since only the hair suspension is located in parallel to the MICs this construction causes a considerable percentage of the total mechanical energy to become absorbed within the MIC-membrane-complex.

The amplitude of the dynamic conductance response is a logistic function of the stimulating force. If its exponential component is due to the Boltzmann-distribution of thermal energy the molecular sensor elements involved need at least 1 kT per sensor for an e-fold conductance increase. We found an e-fold conductance change produced by about 10^4 kT delivered to the hair; i.e., the number of kT available for the receptor cell is a few times the number of MICs. We are testing the hypothesis that each cone-membrane-complex represents one sensor-channel unit.

II. Vertebrate epithelial mechanoreceptors

A group of microvilli (MV, "stereocilia") is located at one side of the unmodified ("kino"-)cilium. A force parallel to the cell surface directed from the MV towards the cilium increases membrane conductance; a force in the opposite direction reduces the resting conductance (5).

We test the validity of the principle of construction found in insect receptors on frog vestibular organs. We observe that the stimulating force exerted by the gelatineous otolithic layer is directly transmitted by filamentous connections only to the cilium. However, as Hudspeth has demonstrated, bending or displacements solely of the cilium do not change receptor conductance (6). The pull at the cilium is transmitted to the neighbouring MV, again by filamentous connections. We found all MV systematically connected at their tips to their nearest neighbours by extracellular bridges of a new type (inter-MV-bridges). Thus, the energy of a natural stimulus leading to receptor depolarization is transmitted as strain within a zone which is composed of MV-tips and inter-MV-bridges. Since each MV is a stable rod (actin skeleton (7)) with some preference for bending at its base, the amount of energy available for absorption within a single zone of inter-MV-contact is stepwise reduced from bridge to bridge.

The sum of all MV-membrane areas underlying the inter-MV-bridges is about 1.5 μm^2. Nearly all the stimulating tension is concentrated within the first inter-MV-bridges, and, depending on the ratio between MV-bending resistance and dilatability of the inter-MV-contacts, a considerable amount of energy will be absorbed within these contacts. This concentration of force across a small membrane area (about 1 μm^2) and possible energy absorption close to the membrane is reminiscent of the stimulus-receiving region of above insect receptors. Other than in those receptors tension instead of pressure across the membrane correlates with the conductance increase, and actin filaments instead of microtubules establish the support behind the membrane. Notwithstanding these differences we consider the inter-MV-contact area the most likely location of the transducing structures.

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