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V. POLAR CELL MOVEMENTS

A. Cytoplasmic movements

Rotational cytoplasmic streaming has been widely accepted as being caused by active shearing at interface between the moving endoplasm and the stationary ectoplasm (Kamiya, 1981, see **I**). Microtubule bundles are indispensable for such cytoplasmic streaming in the Characean cells (see Williamson, 1975 in **I**; Nagai and Hayama, 1979).

Directionality of streaming in amoeboid cells is ensued by the polarity of actin filaments and interaction between the mechanochemical electric field and the electric dipoles built by the movement of protons along the filaments "may cause the turning over of the filaments, giving rise to shuttle-streaming and to oscillations of the electric polarization" (Tirosh *et al.*, 1979, *not* 1980 as in **I**).

B. Cell Movements

1. *Cilia-flagella*

The flagellum of *Allomyces* zoospores has an intrinsic polarity when it beats perpendicularly to the long axis of the rhizoplast (Aliaga and Pommerville, 1990).

3. *Amoeboid motion (transient polarity)*

A possible mechanism of motion in *Amoeba* which involves repolarization by two types of K^+ channels of the cell depolarized by the influx of Ca^{2+} through both mechano-sensitive and voltage-gated Ca^{2+} channels has been proposed by Franciolini (1990). In this model, entering calcium binds to the contractile filaments, conferring movement on the *Amoeba*.

4. *Amoeba-flagellate reversible transformation*

In this transition process, well-studied in the life cycle of the slime mold *Physarum*, the amoeba becomes a different cell type and displays polarity while developing a new organelle, the flagellum (Sauer, 1982). Microtubules have been recognized as the major structural components of this amoeba-flagellate transformation (Sauer and Pierron, 1983).

The transition from flagellates to amoeba cells involves disintegration of flagellate-specific microfilamentous structures. A cold treatment or the artificial elevation of intracellular Ca^{2+} concentration disintegrates flagellate-specific microfilamentous cytoskeleton and induces amoeba specific microfilamentous cytoskeleton (Uyeda and Furuya, 1990).

The numerous insights into the role of Ca^{2+} in cell shape changes of *Naegleria* (see **I**, pp. 138-139), and in the yin-yang alteration of actin-based and tubulin-based cell motility in the amoeba-flagellate *Naegleria* have been recently updated by Fulton (1990).

5. *Taxis:*

a) *Chemotaxis*

When growing on the surface of rotting tree bark, the plasmodium of the slime mold *Physarum polycephalum* looks like a fan and is polarized because of its chemotactically-directed search for food in contrast to well-fed laboratory cultures (Sauer and Pierron, 1983). Reversible polymerization cycles of actin (G $\leftrightarrows$ F forms) accompany the shuttles of ecto-endoplasms and are thus involved in rhythmic contractions of the plasmodium.

Polarization is the degree to which a neutrophil leukocyte forms a pseudopod or adopts motile or ''polarized morphology'' (Wilkinson, 1990). In the presence of chemoattractants, all leukocytes can respond by chemotaxis (directional locomotion) and chemokinesis (change in cell speed). As first event, chemotaxis is a change in morphology from a spherical shape to an anteroposterior polarity. According to Wilkinson (1990) ''the same shape change occurs both in isotropic attractant concentrations and in gradients. Any theory of gradient detection must explain how cells in isotropic attractant concentrations adopt a head-tail polarity''. Intrinsic cellular mechanisms would determine polarization and locomotion, while chemotaxis and chemokinesis would be determined statistically by the nature of cells' environment (Wilkinson, 1990).

Polarization and adhesiveness of neutrophils are affected by globulin factors in plasma. Induction of this polarization appears to be linked to promotion of adhesiveness (Bignold *et al.*, 1990).

Large, rapid increases in actin polymerization and in the amounts of actin associated with the cytoskeleton are part of cellular responses to chemotactic and phagocytic factors. Actin appears to be actively recruited to plasma membrane sites, including the anterior ends of locomoting cells, phagocytic cups, and adherens junctions (for review, see Shariff and Luna, 1990).

Chemotactic factors are reported to trigger the formation of new actin nucleation sites with free barbed ends, i.e., the increased actin polymerization during chemotaxis is inhibited by the barbed-end capping agent, cytochalasin D (Shariff and Luna, 1990). The intracellular location of these actin nucleation sites is unknown. The identification of an actin-binding protein (ABP-50) as elongation factor (1a) and its association with the cytoskeleton has been found to be regulated during chemotaxis of Dictyostelium (Yang *et al.*, 1990).

In signal transduction during cyclic-AMP induced chemotaxis in the cellular slime mold *Dictyostelium discoideum* the plama membrane potential plays a possible role. From experiments involving measurements of cyclic GMP and cyclic AMP responses in

cells with a depolarized membrane potential, it was concluded that ''membrane-potential-regulated processes, such as voltage-gated ion channels, do not play an essential role in chemotaxis in *D. discoideum*'' (van Duijn *et al.*, 1990). *Dictyostelium* amoebae translocating in buffer are elongate and, by the addition of cyclic AMP, exhibit expansion zones primarily at their anterior end. Filamentous, F-actin is primarily localized in anterior pseudopodia. In such conditions, the pattern of microtubules organization is unaffected (Wessels *et al.*, 1989). In cultured fibroblasts, selectively stabilized microtubules are oriented toward the direction of cell migration. Such remodelling of microtubular arrays suggests that ''selective stabilization of microtubules is an early event in the generation of cellular asymmetry'' (Gundersen and Bulinski, 1988).

b) *Phototaxis*

In their review of photomorphogenesis in lower green plants, Wada and Kadota (1989) have tabulated orienting phenomena that are dependent upon blue-light absorbing pigment(s) such as polarotropism and hyperpolarization in ferns and mosses. They mentioned the fact that dipole moment theory of red-light-absorbing form of phytochrome spirally arranged in the cell surface plays a role in chloroplast photo-orientation in the green alga *Mougeotia* (Haupt and Bock, 1962).

6. *Structural basis for directionality*

The underlying polarity of the microtubules determines the directionality of force transmission by both orienting the attached force generators and influencing the direction of microtubule assembly and disassembly (Linck, 1989 and **I**). Microtubule-dependent events such as mitosis (IV. F) and motility are coupled to such assembly and disassembly processes (see **I**). In flagella the polarity of assembly was first observed *in vitro* by experiments showing that ''brain tubulin assembles preferentially onto the distal or plus ends of basal bodies and axonemal A-tubules and to a lesser extent onto the proximal or minus ends'' (ref. in **I** and Linck, 1989).

Among important forces responsible for cellular movements there are electric forces and mechanical torsional movements. Tropomyosin would interact by its polar side chains in the possible torsional processes during Ca^{2+}-activation. This would lead to a rotation of the tropomyosin coiled-coils, as demonstrated with a molecular model (Jarosch, 1979).

The ruffling movement of L cells on a glass substratum was analyzed by time-lapse cinemicroscopy. The ruffling movement could be stopped and the leading edge retracted in the presence of cytochalasin B. The ruffling processes changed to pseudopodia-like structures when colchicine was added to the culture medium. Finally ''the cell changed from a fan-like shape to a circular one, loosing its polarity'' (Ohnishi, 1979).

Fish (teleost) chromatophores are capable of rapid pigment transport and possess a finalized intracellular organization, the cytomatrix (Bikle *et al.*, 1966). This granule-moving matrix also implicates mitochondria, nucleus and plasma membrane and is connected with the pigment transport system (Green, 1968). A model for matrix-microtubule interaction has been constructed by McNiven and Porter (1984) using a modification of the technique of Heidemann and McIntosh (1980, see **I**) to determine the direction - clockwise or counterclockwise - of microtubule hooks as probes for arm microtubules polarity (McIntosh and Euteneuer, 1984, see **I**). In summary, the dynamic matrix in chromatophores requires "energy for expansion, is controlled by Ca^{++}, is non-actomyosin dependent and requires microtubules for support and direction" (McNiven and Porter, 1984).