Morphogenetic polarizations

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VIII. MORPHOGENETIC POLARIZATIONS

A. PLANTS

2. *Organismic polarities*

a) *Mushrooms*

These higher fungi grow upwards and should be responsive to the gravitational field. The problem will be to find the gravity sensor and the way its signals are interpreted (also for the model mold *Phycomyces,* see below).

c⁴) *Polar auxin transport and tropic curvatures*

Bioelectric gradients along axial organs demonstrate morphological and physiological polarity in higher plants (Fensom, 1959; Scott, 1967; Zatsepina and Tsaplev, 1980; Goldsworthy, 1986). This electric polarity probably controls the distribution of phytohormones (Clark, 1937). Changing the bioelectric gradients by an external electric field has various consequences on plant growth and development (Lund *et al.,* 1947; Cholodny, 1956; Jaffe and Nuccitelli, 1977; Ellis and Turner, 1978; Medvedev and Markova, 1990).

In studies of gravity-dependent plant responses provided by the special conditions of spaceflights, interfering accelerations are relatively small (below 10^{-3} g) and termed "microgravity" (see Hensel, 1989a).

Plant morphogenesis in general does not appear to be considerably disturbed by microgravity, as shown by the polar differentiation of anise callus cultures into somatic embryos (Theimer *et al.,* 1986). Compared to ground controls the distribution of the amyloplasts is shifted towards the proximal pole in statocytes of space grown roots (ref. in Hensel, 1986). This polarity of statocytes does not require the continuous action of gravity but develops also at microgravity. In statocytes of lentil roots differentiated in microgravity, the nucleus was preferentially located toward the gravity center of the cell (Perbal and Driss-Ecole, 1989). Polar differentiation of statocytes was also disturbed but only at the level of endoplasmic reticulum (ER) in seedlings of *Zea mays* launched from earth after germination, while those germinated at microgravity had aggregated ER in root statocytes (Moore *et al.,* 1987).

By comparison, the normally negatively gravitropic sporangiophores of the terrestrial mold *Phycomyces* (see VII.B.1a²) become disoriented when cultivated aboard an orbiting spacecraft (Parfyonov *et al.,* 1979). The nature of the gravity receptor is still unknown (Shropshire and Lafay, 1987).

As previously suggested, statocytes polarity depends on a genetically prepatterned program (Sievers *et al.,* 1976). Since, agravitropic mutants of roots have been discovered (see Scott, 1990). Such mutants exhibit morphological and physiological abnormalities which suggest that they are unable to respond to the plant growth hormone auxin, indole-3-acetic acid (Hicks *et al.,* 1989). The root cap plays a role in root geotropism (Pilet, 1978) and its removal can also lead to an agravitropism (Moore *et al.,* 1990). Gravity could thus induce a change in cellular structure which somehow generates a chemical and/or electrical signal in the cap.

The starch statolith hypothesis attempts to explain gravity perception in plants. Starchless (phosphoglucomutase deficient) mutants recently produced in *Arabidopsis thaliania* (Caspar and Pickard, 1989) showed a lower response to gravity. The authors concluded that a full complement of starch is necessary for full gravitropic sensitivity (Kiss *et al.,* 1989). However, these mutants can still sense gravity also more slowly and less accurately. According to Bandurski (1990) "if an organism has a dense and heavy statolith then it will use the statolith to provide a very accurate and rapid gravity sensor. If however it does not have such a dense body then the organism uses some more subtle gravity sensing apparatus". Bandurski's guess is then "that the plant uses its own bioelectric fields as a sensor". With his collaborators he had developed a working theory postulating that "the perception of the gravitational stimulus involves a perturbation of the plant's bioelectric field" and that the transduction of the stimulus involves a hormone-transport voltage-gating mechanism (Bandurski *et al.,* 1986).

In the provoking suggestions concluding his recent review on "Plant Movements and the Cytoskeleton", Hensel (1989b) suggests that the cytoskeleton has a general function to generate and maintain polarity of root cap statocytes but that the cytoskeleton is "indirectly involved in perception by generating and maintaining a structural polarity of statocytes". Interestingly "it maintains domains of ion pumps/channels and/or hormone receptors/channels in the plasma membrane". The cortical part of the cytoskeleton would be directly involved in mechanotransduction of statolith weight into shear forces, thus triggering a plasma membrane response.

B. ANIMALS

Polar axiation in the eggs and embryos as well as the mechanisms underlying these processes in annelids, arthropods, amphibia and mammals are further discussed in a symposium on "Cellular Basis of Morphogenesis" published by Wolpert in 1989.

2. BIAXIAL PATTERNS: i) *Mammals*

Homologous gene clusters have been recently compared in insects and vertebrates. Specific homologues of *Antennapedia* (*Antp*)-like homeobox genes in *Drosophila* (see VIII.B.2d, in **I**) have been characterized as *Hox* complexes in vertebrates (Duboule *et al.*, 1986). Corresponding murine genes and insect complexes show the same relative boundary of the expression along the antero-posterior (A/P) axis of the developing embryo (Akam, 1989). A model for the mouse forelimb budding has been proposed by Dollé *et al.* (1989) that accounts for the establishment of the expression of the *Hox-5* domain in relation to the existence of a morphogen released by the zone of polarizing activity.

3. TRIAXIAL PATTERNS (left-right polarities)

Handedness is a fundamental quality already appreciated by D'Arcy Thompson (1942, see **I**).

a) *Helical bacteria*

The twist model of the lytic-deficient mutations of *Bacillus subtilis* has recently reactivated the handedness principle (Mendelson and Thwaites, 1989). Growth of these lytic-deficient mutants does not result in increased numbers of individual bacteria but in long thread-like clones which may have an unusual double-helical morphology. These double-helical threads fold repeatedly to form helical, multicellular "macrofibres" ("macrobes") that, according to Galloway (1990) are structurally analogous to twisted textile yarns. A macrobe is therefore an amplifier of the cell wall structure-determining features of the individual cells and therefore has a helical structure.

On the basis of screw sense, some strains are left-handed, others right. Others again are "conditional" mutants — they may be either left or right, and the degree of twist can vary continuously between left-handed and right-handed extremes depending on environmental factors, such as temperature (Galloway, 1990). Right-hand clones are produced at lower temperatures, left-hand at higher ones (Mendelson *et al.*, 1984). It seems that a protein is needed for left-handed structures but not right-handed.

e) *Molluscs*

Interestingly, a same asymmetric behaviour as in bacteria is seen in the early development of snails: right-handedness in *Lymnaea peregra* needs a protein, left-

handedness apparently does not (see **I**). In the interplay between molecular self-assembly into helicoidal structures and mechanical reorientation due to growth forces (Neville, 1985; Galloway, 1990), a central role has been suggested to microtubules in the formation of helical patterns (Lloyd, 1984).