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VIII. MORPHOGENETIC POLARIZATIONS

A. PLANTS

1. *Embryonic polarity*

The origin and perception of positional information in plant embryos, and the temporal and spatial expression of their genes have been recently reviewed by Racusen and Schiavone (1990). They feature that “the spatial distribution of certain gene products is correlated with changes in morphology”.

The gradient of a chemical mediator and its associated transcellular electric fields (Nuccitelli, 1988; also **I**) arise from the diffusion of substances from different regions of an organism. Electric fields have been monitored around plant embryos (Brawley *et al.*, 1984; Rathore *et al.*, 1988). The associated electric currents in carrot embryos appear to be most sensitive to changes in external concentrations of Ca^{2+} and H^+ with expected consequences on the cytoskeletal assembly. “The presence of electric fields implies an asymmetric distribution or activation of ion transporters in the membranes of participating cells” (Racusen and Schiavone, 1990).

Blockage, or removal of the auxin supply (see also **c⁴**) from the apical end of the somatic embryos of carrot promoted rapid elongation in the basal, root portion (Schiavone, 1988).

A recent study of the distribution of membrane-bound calcium has suggested that calmodulin was displaced to one or the other apical poles of developing carrot embryos. Proembryonic masses, showing an unexplained propensity for acting as sites of embryo formation in culture, exhibited a polarized distribution of calmodulin (Timmers *et al.*, 1989).

2. *Organismic polarities*

c² Vegetative shoots

Plants display polar growth: the primary axis of the shoot elongates by the addition of new structure at one pole, therefore structures located at the base of the shoot formed later are located in more apical positions. Such polar developmental pattern or heteroblasty “makes it extremely difficult to distinguish temporal, spatial and quantitative factors in shoot development” (Poethig, 1990).

In experimentally-induced (deficient nutrition), asymmetrically budding plantlets of the Compositae *Bidens pilosus*, the transport of messages involved in the storage of the symmetry-breaking information is associated with the induction of a wave of electric depolarization (Desbiez and Thellier, 1990).

A polarity has been detected in light-induced unrolled grass leaves. "The top end of the basal section of a divided leaf unrolls more than the base end of the distal section" (Virgin, 1990).

c⁴ *Polar auxin transport and tropic curvatures*

The structural polarity of statocytes from roots of *Lepidium sativum* is converted to a physical stratification of organelles by apically-directed centrifugation of the whole plantlet (Sievers and Heyder-Caspers, 1983). After return of the roots to normal gravitational force, the integrity of the distal cells pole and their underlying endoplasmic reticulum complex is reestablished. Direction of the earth gravity vector does not influence the recovery of the normal cell polarity. Therefore, perception of gravity is inevitably correlated with the integrity of statocytes (Wendt and Sievers, 1985).

A gradient of auxin along the longitudinal axis has been suggested by the demonstration of polar transport of this hormone in embryonic hypocotyls of *Pinus* (Greenwood and Goldsmith, 1970) and in similarly prepared hypocotyls of bean and sycamore (Fry and Wangermann, 1976). More recently, Schiavone (1988) explored the developmental significance of polar auxin transport in somatic embryos of carrot by auxin donor-block experiments.

Gravistimulation changes the pattern of electric current surrounding the root tip and alters membrane potentials within the root cap (Behrens *et al.*, 1985). The pattern of current flow around a vertically oriented root of *Lepidium* has been reported to change from symmetrical upon gravistimulation to asymmetrical.

Electrotropism or galvanotropism, modification of the direction of growth of certain plants or organs by an applied electric field has been reported in fungi (McGillivray and Gow, 1986) and other plants such as maize roots which curve toward the positive electrode or anode (Ishikawa and Evans, 1990a). These last authors also reported that, unlike gravitropism, electrotropism does not depend upon the root cap. Gravistimulation also induces hyperpolarization of intracellular potentials along the upperside of the elongation zone and depolarization in cells along the lower side of the elongation zone. This suggests to Ishikawa and Evans (1990b) "the possibility that differential growth may be linked to membrane potential changes in both gravitropism and electrotropism".

Gravity detection can be indirectly evidenced within the root tip and this induces the movement of a growth-modifying signal from the tip toward the elongation zone. There is good evidence that auxin IAA mediates gravitropism (ref. in Evans, 1991). Bandurski *et al.* (1984) had suggested that auxin asymmetric redistribution toward the lower side of the organ may develop by gravi-induced differential release of free IAA from its esterified form and thereby would cause the growth asymmetry. The classical Cholodny-Went hypothesis of gravitropism has recently been reassessed on criteria of interaction of modulation of hormone sensitivity of the gravity receptor and effector redistribution (Evans, 1991).

There is also an asymmetrical distribution of ions, already described for Ca^{2+} (see **I**, p. 237), which involves K^+ ions. Thus, in twining shoots of *Phaseolus vulgaris* maximal concentration in potassium has been correlated with maximum of curvature, suggesting that differential distribution of this ion and lateral polarity is directly connected with circumnutation of shoots in volubile plants (Badot *et al.*, 1990).

c⁵ Flowering shoots

Among the recently investigated changes in the markers of flower induction there are thickening and chemical modification, possibly involving amphipathic molecules, of plasma membranes (Greppin *et al.*, 1990).

Homeotic genes in plants can provide insights into the underlying molecular regulatory mechanisms of flower development. However, unlike in animals, morphogenetic processes in plants cannot easily be related to maternally determined positional information. It has recently been shown that different gradients of diffusible factors and cellular receptors sensing them induce alternative pathways in the developing flower primordia of *Antirrhinum* (Sommer *et al.*, 1990; Schwarz-Sommer *et al.*, 1990).

Homeotic mutations affect the position of the four concentric whorls of the floral organs of *Arabidopsis* (Bowman *et al.*, 1989). The homeotic gene *agamous* "probably encodes a transcription factor that regulates genes determining stamen and carpel development in wild-type flowers" (Yanofsky *et al.*, 1990).

B. ANIMALS

The unfertilized egg has only one axis of developmental polarity, the animal-vegetal (A/V) axis. A dorsal protein and perhaps other gene products are then involved in polarizing the egg in the dorsal-ventral (D/V) axis. A recent review by Melton (1991) underlines important gaps in our knowledge of such polar pattern formation.

"We may not have a morphogen"!... such is the surprising announcement recently made by Brockes (1991) which contradicts a previous statement (Slack, 1987b, in **I** p. 240). Brockes cites the findings of Noji *et al.* (1991) according to which "retinoic acid (RA) induces polarizing activity but is unlikely to be a morphogen in the chick limb bud" and those of Wanek *et al.* (1991) which suggest that "the graded response to exogenous RA may reflect variation in the number of adjacent cells induced to become polarizing cells".

As the effects of maternal mutations that affect a somatic cell fate directly are still unknown, the present interpretation of spatial determination in the early development of animals fits with Wall's "This Side Up" title of his recent (1990) book that the egg contains little developmental information other than instructions needed to specify the poles of the embryo.

1. MONOAXIAL PATTERNS

a) *Mycetozoa (slime molds)*

Much evidence supports the hypothesis that cytoplasmic pH may be an essential regulator of the choice to differentiate the pseudoplasmodial slug of *Dictyostelium discoideum* in either the prestalk or prespore pathway (see I). No gradient of intracellular pH along the anterior to posterior axis of the slug was detected (Furukawa *et al.*, 1990).

Prestalk gene expression in this slime mold induced by the differentiation-inducing factor (DIF), or by conditions that decrease intracellular pH (pH_i), is facilitated but not mediated by cytoplasmic acidification (Wang *et al.*, 1990).

New roles in the early development of *Dictyostelium* have recently been ascribed to the chlorinated molecules of DIF. Among those effects, transient inhibition by DIF-I of cAMP oscillations and cAMP relay during spiked oscillations and transient decrease in cellular cGMP levels in cells taken before oscillation start (Wurster and Kay, 1990). Such effects could possibly affect cytoskeletal organization of the developing slime mold.

c) *Hydrozoa*

Two types of head activator receptors have been characterized on *Hydra* cells (Neubauer *et al.*, 1991).

2. BIAXIAL PATTERNS

Animal eggs are divided into two parts, a dark animal pole (future tadpole) and a lighter, larger, vegetal pole (yolk supply). In such regionally differentiated eggs, it has been suspected that the cytoskeleton confers its form to the egg by the protein vimentin as suggested by disturbances of the early cleavage pattern which result from knocking out vimentin by blocking its messenger RNA (Wylie's experiments, see Cherfas, 1990).

In the sea cucumber (*Holothuria leucospilota*) oocyte, there are two visible structures which serve as markers for the main animal/vegetal (A/V) axis (Maruyama, 1990): the polar cytoplasmic protrusion at its presumptive animal pole which, at maturation, migrates as germinal vesicle to the pole where it breaks down into a pair of asters; a clear spot of special cytoplasm near the cell surface opposite the presumptive animal pole.

a) *Worms*

The soil nematode *Caenorhabditis elegans* has been proposed by Sydney Brenner in 1965 as a model system for studying how an animal's genes specify its development and behavior (see the "Book of the Worm", Wood, 1988; Riddle and Georgi, 1990).

Key attributes include: “small size (1 mm in length), a simple anatomy, the adult hermaphrodite has 959 somatic nuclei and the adult male has 1031, a transparency for microscopic observation of internal structures, ease of laboratory cultivation, suitability for high resolution genetic analysis, and small genome size (10^8 DNA base pairs)”. Among genes that control the development of this worm there are temporal (heterochronic), and spatial (homeotic) ones.

The body plan of the *C. elegans* adult, typical for nematodes, shows a few left-right asymmetries, but the majority of tissues themselves are arranged with bilateral symmetry (White, 1988). By contrast, the embryo exhibits some left-right asymmetries with generally invariant handedness (however, possible reversal of handedness see VIII.3.d). Therefore the left-right embryonic axis must have a consistent polarity (Wood, 1991) “whose origins and subsequent effects on development are not understood” (Brown and Wolpert, 1990).

Dorso-ventral polarity is of morphogenetic importance and had been studied in regeneration processes in *Nereis* (Boilly and Boilly-Marer, 1972). Recently, it has been shown that positional information according to Wolpert (1969, see I) may be changed during regeneration of the nerve cord in that annelid (Boilly *et al.*, 1990).

The influence of head and tail grafts on axial polarity in regeneration of the freshwater plathelminth *Planaria* has been further studied by Kurabuchi and Kishida (1990).

d) Insects

d¹ Egg-embryo patterns

Homeotic genes are involved in the conversion of positional information in the egg into the specific expression of the genes needed for differentiation of the various body segments (Gehring, 1987, see I). The homeotic gene products are DNA-binding proteins which contain a sequence known as the homeobox that is conserved in evolution. They also have regulatory capabilities and there is a need for identification of the subordinate target genes in order to understand specification of individual segmental pathways of development. According to Gould *et al.* (1990) the genes encoding the 35 and 48 transcripts are good candidates for target genes directly regulated by the homeotic gene *ultrabithorax* which encodes homeodomain-containing transcription factors that determine segmental identity in *Drosophila*.

The segment-polarity genes act coordinately by means of local cellular interactions to assign and maintain an identity for each cell in the segment, and to establish segment boundaries. Unique among these genes so far characterized, the *zeste-white3* gene encodes proteins that have homology to serine-threonine protein kinases (Siegfried *et al.*, 1990).

Segmental polarity and identity in the abdomen of *Drosophila* do not depend on the relative concentration of posterior pole plasm activity but rather on the position of

gap gene expression (Lehmann and Frohnhofer, 1989). In the initiation of segment polarity, periodic patterns of pair-rule gene are expressed in response to gap gene products. By the end of the fourteenth nuclear division cycle, "the stripes of the pair-rule gene *even-skipped* (*eve*) sharpen and polarize, a process that is essential for the precisely localized expression of segment-polarity genes" (Warrior and Levine, 1990).

There is a hierarchy of regulation among the three segmentation gene classes active in embryonic development of *Drosophila*: the gap, pair-rule, and segment-polarity genes. Such regulation intervenes in the transition from the early pair-rule to the segment-polarity pattern of expression. During primordial segmentation, there is a two-step conversion of the initial analogue specification of position along the anteroposterior axis into a digital code specified by combinations of active segment-polarity and homeotic genes (Baumgartner and Noll, 1991). Two segment-polarity genes represent the *gooseberry* locus (Bopp *et al.*, 1986) which, according to recent results of the Noll's group, specifies the orientation of the larval segments and consists of two transcription units encoding proteins.

A gradient in the *bicoid* (*bcd*) protein is known to specify a position in the anterior region. The bicoid homeodomain protein morphogen would act by an interaction of its recognition helix with DNA (Hanes and Brent, 1991). The correct formation of a gradient of the *bicoid* protein requires the localization of *bcd* RNA to the anterior pole of the egg of *Drosophila*. However, the mutation in maternal-effect genes lead to an almost uniform distribution of *bcd* RNA in the early embryo (St Johnston *et al.*, 1989).

In addition, experiments resulting in alteration of the normal expression of homeobox genes support the hypothesis that these genes function in patterning. They subdivide the embryo along the head-to-tail axis into morphogenetic fields each of which contains a "gradient-field" of information for specifying an organ (De Robertis *et al.*, 1990).

f) *Amphibians*

The sperm entrance point determines the embryonic axes and therefore the animal/vegetal polarity of the amphibian egg (Nieuwkoop, 1977 and Gerhart *et al.*, 1981, in I).

Like other amphibian eggs, that of *Xenopus* transforms its polarized cylindrical symmetry into bilateral symmetry within the first cell cycle after fertilization by a microtubule-mediated process which involves cortical cytoplasmic rotation (Gerhart *et al.*, 1989, in I).

A so-called "molecule of the moment" (Slack, 1991), activin has recently been uncovered by three research groups and shown to be an inducer of mesoderm polar axiation (vegetalizing factor ?) in the early *Xenopus* embryo. An activin A homologue elicits dorso-anterior tissues as a graded response characteristic of classically postulated morphogens (Green and Smith, 1990).

The anteriorizing effect of a new peptide growth factor can be overridden by both retinoic acid and a homeodomain protein (Cho *et al.*, 1991b).

h) *Birds*

Regional differentiation of the chick neural epithelium along the anteroposterior (A/P) axis is apparent at the neural plate stage while the differentiation of cell types along the dorsoventral (D/V) axis of the neural tube occurred later. Yamada *et al.* (1991) provide evidence that the pattern of cell differentiation along this D/V axis is regulated by polarizing signals derived from the notochord and floor plate. This polarizing activity might be mediated by retinoic acid, an endogenous "morphogen" (?) also involved in the establishment of axial polarity in the developing chick limb.

In a further study of the specification of position in chick wing development, it has been shown that the putative endogenous morphogen, retinoic acid, induces *de novo* transcription of the homeobox *Hox-4* genes (Izpisúa-Belmonte *et al.*, 1991). The primary morphogenetic signal provided by homeobox genes might thus be translated into a "complex network of positional information".

Patterning in the limb does not always depend on a positional signal (Wolpert, 1990). STOP, GO, STAY and POSITION are signals which play a role in such developments and pigment patterns associated with feather germs.

i) *Mammals*

How cells in the developing embryo "know" what structures to become? Molecules called morphogens - literally "shape-givers" - might play this specifying role by spreading across the embryo in a concentration gradient. The transplantation of a polarizing region from a donor to a host chick limb bud induces on that last one a second polarizing region causing the growth of extradigits. In 1987, Thaller and Eichele have shown that the morphogenetic role is assumed by retinoic acid (see I, p. 240 and 265) and many recent publications have suggested that this compound and other derivatives of vitamin A have also a shaping role on the developing mammalian embryo (Hoffman, 1990). Thus, human homeobox genes belonging to the complex of HOX loci are differentially activated by retinoic acid in embryonal carcinoma cells (Stornaiuolo *et al.*, 1990).

3. TRIAXIAL PATTERNS

d) *Worms*

In *Caenorhabditis elegans* bilateral asymmetry becomes evident between 4- and 6-cell stages. Left-right polarity cannot be fixed until after dorsal-ventral polarity is established between the 2- and 3-cell stages (Priess and Thomson, 1987). The worm exhibits left-right asymmetries at all developmental stages. Reversal of this embryonic handedness by micromanipulation (6-cell stage) resulted in mirror-image in otherwise

normally developed, fertile animals with all the usual left-right asymmetries reversed (Wood, 1991).

e) *Molluscs*

The direction of coiling of the shell of snails such as *Limnaea* is one of the best known examples of asymmetry known to be inherited maternally (Sturtevant, 1923, see **I**). Molecular determinants are probably involved in such asymmetry in development (Brown and Wolpert, 1990). However, Galloway (1990b) recently pointed out that this is unlikely because the structure of individual proteins is either right- or left-handed and that gene mutation could not readily produce a change in handedness. Moreover, Galloway states that the primary structure of nucleic acid cannot be ambidextrous. However, and more recently, Holliday (1990) disagrees with that last remark (see **II.D**). Parallelly to other work by Galloway (1990a, see **II**) concerned with the role of microtubules in the right-handedness in *Limnaea*, Holliday (1989) suggested that secondary and tertiary RNA structures, encoded by maternal DNA, may be important cytoplasmic determinants in the egg and developing embryo of this snail.