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## INTRODUCTION

Polarity can be currently defined as two different qualities opposed at the extremities of an axis or, more simply, as axial asymmetry generating polar axiation. In this connotation, it means heterobipolarity, namely two different poles on an axis as exemplified by the dipolar magnetic bar with its north and south poles; contrarily to theoretically impossible homobipolar magnets, monopoles of the north or south type are predictable as homologues of the isolated + or – electric charges. Polarity is thus fundamentally bipolar and originates from the lasting separation of opposite, elementary electric charges, the proton ( $H^+$ ) and the electron ( $e^-$ ) in the probabilistic, primeval dipole hydrogen ( $H$ ). From that point of view, electric and magnetic bipolarities of Physics rejoin the dual principle of Yin-Yang proposed by oriental Philosophy, a problem of opposed polarities which could be solved by the modified notion of structural stability recently proposed by Zeeman (1988).

In Biology, the term polarity was introduced by Allman in 1864 in connection with the specific orientation of phenomena of animal regeneration with reference to axis in space and, in 1904, the great *Drosophila* geneticist T.H. Morgan called “polarity” the dominance of the apical parts in the axial regeneration of hydranths. In plants, the theoretical aspects of polarity have also been extensively discussed in their relation to problems of regeneration, directional growth and differentiation. In 1878, Vöchting showed that a stem or cutting is polarized. He attributed this property to polarity of individual cellular components and, ultimately, to their molecular structure. In that pioneer view of the molecular essence of polarity, he was followed, in 1935-36 only, by Seifriz, who considered the protoplasm as a continuity of structure consisting of elongated molecules (as in carbohydrates and proteins) to which the polarity and symmetry of organisms could be attributed. Harrison (1936) made the close proposal that protein molecules, because of their bipolar character, might become oriented in the cell possibly in relation to their point of attachment. In 1939, Paul Weiss had already hypothesized for animal eggs “the possibility of a *dynamic* structure, that is, a defined pattern into which the diverse molecular groups would force one another by mutual specific repulsions, attractions and other interactions”. For Needham who had referred, in 1942, to “the difficult question of polarity, perhaps the central puzzle of embryonic development”, constituent molecules of the cell protoplasm were also oriented in a definite structure which, in morphogenesis, was manifested as polarity. Bünning expressed again, in 1952, the opinion that the physical asymmetry induced within the young egg cell or spore must be a polar protoplasmic structure. According to him, the surface of protoplasm would therefore contain a submicroscopic protein skeleton exhibiting a polar orientation.

The structural views of biopolarity were first tempered by Child (1941) who saw the need for introducing metabolic factors without which the structure must remain static, if it can indeed come into existence. According to this eminent precursor, "molecular orientation must result secondarily from the metabolic differential pattern". Turing went further, in 1952, when he proposed his theory of the reaction-diffusion to account for the zygotes and eggs differentiation without invoking their specific protoplasmic structural organization. More recently, Prigogine (1972) attempted to reconcile cell submorphology and biophysics in considering membrane bound polarity, especially conspicuous in some types of cells, as the expression of dissipative processes far from thermodynamic equilibrium.

At the *single* cell level, the intrinsic polarity of macromolecules and their derived microstructures prevails over polarization by gradiental diffusion of morphogens (Grant, 1978). When transiently, apparently apolar spherical cells such as microbial spores or unfertilized eggs are led to recover their internal polarity, an intracellular gradient lines up polar molecules in specific orientation "like iron fillings in a magnetic field or opposite electrical charges at the two poles of an electrophoretic system". Founding this opinion on the pioneer bioelectrochemical studies of Lund (1947), Sinnott (1960) predicted that "polarity may be due to something quite different from a gradient and may be comparable to, and perhaps result from, an inherent polar tendency, presumably electrical in character". The intrinsic polar organization of cells should thus not only be based on the polarity of their macromolecules and microstructures but would also be tightly connected with their somehow hidden sensitivity to electrostatic and electromagnetic signals from the environment (Racusen, 1979; Berry, 1981; Pohl, 1981).

In the *multicellular* organization of embryos, polarity reversal by grafting experiments provided strong evidence to Slack (1976) that "polarity does not result from many small polar substructures from the slope but of graded distribution of morphogenetic substances". On that experimental basis, Meinhardt theoretized, in 1982, that interactions and movements of molecules can also generate spatial differences or polar patterns from more or less homogeneous molecular conditions if two morphogenic substances with different diffusion rates react with each other by Turing's mechanisms. Such processes would provide positional information for the cells and would change their internal state of determination in a systematic way until it corresponds to the external signal, the local morphogen concentration. Morphogen polar gradients could thus direct the overall polarity of tissues up to organismic level. Nevertheless, the questions remain still largely unsolved of "what is the relationship between polarity and the origin of morphogenetic field? How does pattern formation occur within a morphogenetic field and, what does a position effect mean?" (Karp and Berrill, 1981).

From the above fundamentals, we have conceived and surveyed a progressive, evolutive ladder of polarity upgraded through several levels of complexified integra-

tion: from the primary processes of electric bipolarization (chapter I) emerge small molecular dipoles, prototyped by  $H_2O$ , evolved into electrically mono — bipolar, often chiral (D/L-stereoisomers) biomolecules (chapter II); these polarities are repercutated into the macromolecules with the polarly-read sequences of nucleic acids and their translated proteins (chapter III); from these natural polymers emerge microstructures either bipolarly electrified as cell membranes or structurally polarized into head and tail as actin-myosin and tubulin, the components of microfilaments and microtubules respectively; such microstructures exhibit unidirectional growth during polymerization correlated with elongation of mitotic spindles or of surrounding cytoplasm (chapter IV); that cytoplasmic expansion is transient and polarly reversible in the cytoplasmic streaming of amoeboid pseudopods illustrating polar cell movements (chapter V) while it is permanent and axially continuous at polarized cell growth (chapter VI) and differentiation resulting from asymmetrical cell division (chapter VII); it is only at the ultimate organismic level of morphogenesis that intrinsic cell polarity becomes superceded by gradients of morphogens (chapter VIII).

Polarity can, however, not only be considered as an expression of the *spatial* component of development; at the genetic level, it is also thought to be regulated by *temporal* sequences of gene expression. In many cases, the translated products become localized within particular places in the cell such as the various wall specializations of plants (Sinnott, 1960). In our last chapters (V-VIII), we will therefore refer to the elusive problem of intracellular choreography (Fulton, 1984) by which such gene products are asymmetrically distributed at the onset of polarity (Schnepf, 1986).

