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Autor: Turian, Gilbert
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POLARITY

FROM DIPOLES TO BIOPOLARIZATIONS

II. ADDENDA AND INDEXES

by

Gilbert Turian

Ce travail est la suite et le complément de celui intitulé POLARITY, paru en 1989 dans le volume 42, fascicule 1, des *Archives des Sciences.*

La numérotation des pages poursuit celle dudit travail. Nous conseillons donc à nos abonnés de classer ce supplément à la fin du fascicule 1, vol. 42.

This paper supplements the review entitled POLARITY (Arch. Sci. 42: 1-323, 1989) and should be classified at the end of vol. 42, fasc. 1.

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POLARITY
FROM DIPOLES TO BIOPOLARIZATIONS

II. ADDENDA AND INDEXES

BY

Gilbert TURIAN*

Polarity is a problem of wide interdisciplinary interest that we have attempted to survey in its widest span from its atomic to its embryogenic, plant and animal levels in the Archives of 1989 reprinted as book **I** (Turian, 1989).

Primeval polarity is bipolar, founded on the separation of two equal but opposite electric charges. Consequently, even apolar molecules are intrinsically electrically polarized but with a symmetrical distribution of their opposite (+ and −) electric charges and therefore they lack in electric polar moment. Similarly, apolar morphological biostructures are examplified by spherical cells (certain eggs, etc.), initially deprived of heterogeneously distributed components, and which being identical with their mirror image can be also considered as achiral.

The whole universe is electrically neutral and, by necessity, contains rigorously equal numbers of opposite electric charges (10^{40} of protons and of electrons, see Souriau in Brack *et al.*, 1989) even though it is filled with electric dipoles from the minute water molecules to giant cosmic dipoles, a basic requirement for its physico-chemical and biological functionings. However, in its wider expression, polarity spans not only pure electric and magnetic phenomena but also chemostructural (chiral), biomolecular (cytoskeletal elements) and spatio-temporal developmental processes. Our survey had therefore to encompass them in their whole span from monopoles to multipoles as following:

1) *monopoles,* electric (+ or −) or magnetic (still elusive north or south isolated poles) as well as homochirals (l- or d-enantiomers) and monopolar, elongating biostructures such as microfilaments (actin), microtubules (tubulins), multinucleate cells such as hyphae and neurites;

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* Laboratoire de Microbiologie générale, Sciences III, Université de Genève.

2) *dipoles,* basically electric (+ and −) or magnetic (north and south poles), but also heterochirals (l + d-enantiomers) as well as morphogenetic homodipoles in the twice-budded or -germinated yeasts or fungal spores and heterodipoles in the developing eggs of plants and animals;

3) *tripoles,* electric (+ − + as in thunderclouds, see addendum) or morphogenetic as in iris flowers!

4) *quadrupoles,* electric (radio-frequency electric traps and nuclear coupling, see addendum) or morphogenetic as in four- (multi-) budded yeasts and germinated fungal spores;

5) *multipoles* as exhibited by cells such as amoebae or fungal spores outgrowing n (>4) pseudopodia or germ tubes, respectively.

During the second half of 1989 and first trimester of 1990, we have noticed a few omitted significant papers as well as newly published ones, related to dipoles and biopolarities. We have registered them below by following the sequence of the eight preceding chapters and, parallely, added two subject and taxonomic indexes. Their item entries cover the main book (**I,** 1989) and these first addenda (**II,** 1990).

I. ATOMIC POLARIZATIONS

A. Origins

A fourth state of matter is the plasma state which is formed when a gas is heated to such high temperatures that it becomes partly or fully ionized: "electrons are torn off the atoms in the gas, leaving a stream of negatively charged free electrons and positively charged ions"(Peratt, 1990). Suggestively, the term plasma proposed in 1932 by Langmuir evokes "the unstable almost lifelike behavior of the ionized material". According to plasma cosmology, "the universe has been and remains a veritable sea of charged particles interlaced with complex magnetic fields and electric currents. Many among the cosmologists therefore conclude with Peratt (1990) that "the universe may have evolved not with the Big Bang but from a vast sea of plasma". However, the theory of primordial explosion and of the shaping of the universe by gravitational rather than by electromagnetic forces keeps strong proponents (Rees, 1990).

In the evolutive perspective from the inert to the living matter, the atom of hydrogen (H) could be viewed as forming "le couple divin"(Turian, 1990) displaying the electron, mobile as a male cell around the passively "courted" proton, as female cell, a most fertile association indeed concretized in the bioenergetics through the ATP-generating redox scale ($2H^+ + 2e^- + O = H_2O$, see **I**, IV.B.2.c).

B. Symmetry – Polarity

The whole world appears to be chirally asymmetric from the scale of elementary particles upward. This leads Hegstrom and Kondepudi (1990) to ask the questions, as we did (**I**) for related polarities "How do the asymmetries arise? Are chiral symmetries at one level linked to those at another, or are they independent?"

Chiral asymmetry must therefore be first studied at the scale of elementary particles. Indeed, there is symmetry within an atom only when it is regarded as governed by the electromagnetic force and its associated property of conservation of parity. The additional weak force (involving W^+ and W^- gauge bosons) gives rise to a violation of parity and consequently an asymmetry between the electrons and the nucleus in the atom (Bouchiat and Pottier, 1984). Chiral asymmetry at the subatomic level is thus fundamentally connected to parity nonconservation. One result of this asymmetry is that nuclear β decay, which is governed by the W force, produces mostly left-handed electrons. Consequently, electrons of matter are polarized with a left helicoidal coil while positrons of antimatter are right-directed. However, such chiral

effects of the electroweak W and Z charges leading to a distinction between left and right chirals are strictly valid only when the electrons are travelling at the high energies near the speed of light (Hegstrom and Kondepudi, 1990).

An important consequence of chiral asymmetry at the *subatomic* level is that it causes a chiral asymmetry at the higher level of *atoms*: under the influence of the Z weak force, the electron orbit becomes a right-handed helix in the vicinity of the nucleus. However, the asymmetric Z force is so small that its effects on the chemical properties of *molecules* has not (yet) been observed (Hegstrom and Kondepudi, 1990). That such a mechanism affecting the production rate of L- and D-amino acids can indeed exist in nonequilibrium chemical systems was shown theoretically by Kondepudi and Nelson (1985, see **I**).

The problem of equivalence which has been upheld about left and right (see II.D) also arises "with respect to positive and negative electricity" as commented by Weyl (1952) in his book entitled "Symmetry" in which he also discussed relationships between quantum mechanics and symmetry. This author also assumed that "the primary polarity as well as the subsequent *bilateral* symmetry come about by external factors actualizing potentialities inherent in the genetic constitution" (see VII-VIII in **I**).

As already expressed by Pierre Curie "symmetric systems behave in a symmetric fashion". However, such Curie's principle is contradicted by the occurrence of spontaneous symmetry breaking which occurs when a perfectly symmetric system takes up a state with less symmetry (Field and Richardson, 1989). An example of the phenomenon is the change of form produced by compression of a cylindrical shell initially endowed with a perfectly *circular* symmetry.

The principle of "cosmologie symétrique" has been further discussed by Brack *et al.* (1989) in relationship with the equivalence between matter (proton + electron) and antimatter (antiproton + antielectron). Among previous books concerned with the principle of symmetry there are those cited by Weyl (1935), namely Jaeger (1917) and Hambidge (Dynamic Symmetry, 1920), completed by Jaeger (1925) and, more recently, those by Nicolle (1950) and Caillois (1973) as well as Hargittai and Hargittai (1986).

C. Electric bipolarization

2) *Electric dipoles*

The hydrogen atom (H) can be considered as the primordial electric dipole when we consider that its electron or unit of negative charge is probabilistically positioned on a peripheral orbit around the positive proton according to the classical image of a planet circling the sun (Fig. 1B, in **I**). However, when the atom is placed under

strong stimuli such as a constant magnetic field or exposed to electromagnetic radiation in the form of microwaves, either of these strong stimuli disturbs the orbit of the electron and pushes it into chaotic, unpredictable motion. Eventually, the electron atom is ionized, i.e. its electron has so much energy that the pull of the proton can no longer hold it, and the electron is torn away. According to quantum mechanics, the electron is not considered as a particle orbiting the proton, but as a rather nebulous "wave packet". Ionization high energy will delocalize the wave packet, namely "the electron will become "spread out" over several energy levels", an event corresponding to "the chaos in the classical motion of the electron" (Pool, 1989).

Protons and neutrons, the two types of nucleons, can be examined "by observing electron or muon scattered off them with a large transfer of momentum to one of their constituent particles or partons" (Roberts, 1990). As for the proton, its simplest properties are dependent on the three valence quarks, two "up" (u^+) and one "down" (d^-) (see **I**, I.C.2), each of which carries a spin of 1/2. These are polarized so that the u^+ quarks contribute 4/3 of the proton's total angular momentum (also 1/2), and the d quark $-1/3$. The distribution of polarized quarks can never exceed the distribution of unpolarized quarks (further discussion in Roberts, 1990).

The neutron (1 quark u^+ and 2 quarks d^-, see Cline, 1988) has also an electric-dipole moment, the upper limit of which has been recently measured (Smith *et al.*, 1990). The interest of neutron's electric-dipole moment is that "it would violate the combination of charge conjugation invariance and parity known as CP symmetry. As such, any electric-dipole moment would take the opposite sign for the antineutron, and thus discriminate between matter and antimatter" (Ellis, 1990).

Quantum theory holds that two photons emitted by a particular light source share their similarly oriented polarization. According to Clauser and Freedman's experiments recently recorded by Linden (1990), "a change in one photon did alter the polarization of the other" as if they were not separate objects and thereby obeying to the laws of quantum mechanics also applied to other "wave particles" such as leptons (electrons, etc).

In a search for understanding the charging of storm clouds, and contrarily to previous conclusions from Wilson and Simpson (see Williams, 1988) that electrical structures of thunderclouds were either a positive dipole (Wilson) or a negative dipole (Simpson), their actual structure is tripolar rather than dipolar. The correct explanation for this tripolar structure of thunderclouds is now known to lie in the microphysics of charge transfer between graupel particles (soft hail) and ice crystals (Williams, 1988).

3) *Polarized conductivity*

In a semiconductor the electrons move through an array of constituent atoms arranged in a crystalline lattice. Electrons move with great ease through gallium

arsenide circuits. This compound is made into bipolar transistor devices by depositing it in three layers: electrons n-type doping, holes p-type base and n-type collector. These compose light-emitting diode of gallium arsenide alloyed with aluminium. Gallium arsenide photodetectors respond faster than silicon ones. They can also detect light by reversing the reaction and the resulting photodetector converts the flash signal to electronic pulses. Such optoelectronic computing systems can be linked by optical fibers which greatly increase the efficiency of the digital computing circuitry (Brodsky, 1990).

D. Magnetic polarization

1) *Cosmological level*

The sun's magnetic field can affect many aspects of the sun's surface and atmosphere. It oscillates along a 11-year variation of sunspot number. Measurements of sunspot spectra (Zeeman effect's analysis) showed that the strength of the magnetic fields around sunspots is thousands of time stronger than the earth's field. Most spots occurred in paired groupings that resemble giant magnetic dipoles roughly parallel to the solar equator. According to Foukal (1990), the great astronomer Hale already announced in 1924 that this switch in polarity occurred at each activity minimum, in the midst of a 22-year solar magnetic cycle and was a basic feature of the sunspot cycle. The largest areas of single magnetic polarity are the sites of spot formation. These solar magnetic changes may have their effects on the earth's periodic climate changes.

2) *Magnetic fields*

The discovery of ferroelectric crystals such as barium titanate ($BaTiO_3$) offered an electrically switchable, two-state device with which one could encode the 1 and 0 states required for the Boolean algebra of binary computer memories. A tetragonal ferroelectric crystal has two polarization states in which the centrally located Ti^{4+} ions are involved through their displacement up or down with respect to the other ions (Ba^{2+} or Pb^{2+}, O^{2-}). In a crystal of $PbTiO^3$, for example, there would then occur regions in which the polarization is up and regions it is down, called "ferroelectric domains" (Scott and Paz de Araujo, 1989). Most important for memory applications, the polarization of the entire crystal can be switched from up (+1) to down (0) by reversing the applied field. This ferroelectric memory progressively fades when the amount of switched charge decreases with use or by retention failure when the stored charge decreases to a level where the + or − state of polarization cannot be sensed.

All ferroelectric materials display a hysteretic behavior relating polarization and applied field, so that there is a nominal threshold (coercive field) above which the polarization changes sign.

4) *Spin polarizations*

Dipolar interaction between two nuclear spins depends on size and orientation of the magnetic moment as well as on the distance. In NMR spectroscopy which is based on the Zeeman phenomenon (Ernst *et al.*, 1987), nuclei with a kinetic moment of spin I higher than 1/2 have a quadrupolar (Q) electric moment. The nuclear quadrupolar resonance (NQR) is bound to a nonspherical symmetry in the distribution of electric charges on the nuclear volume. This NQR can only be observed on a limited number of nuclei but is helpful in the study of the electric structures of chemical bonds (Lucken, 1969).

E. Light polarization

A light ray can be polarized by reflection on a polarizer and the intensity of the reflected ray received on an analyzer varies with its incident angle. The proportion of polarized light in the light ray or the rotation of the polarization plane of light are measured with a polarimeter (Pariselle, 1936).

II. MOLECULAR DIPOLES AND CHIRALS

A. Electric dipole moments

Dipolar electric moments and dielectric polarization have been surveyed by Errera (1928, 1935). Further study of the dielectric response of matter to an applied electric field has contributed to the measurement of molecular dipole moments (Price, 1969). The induced dipole moment per unit volume or polarization consists of two components: a *polarizability* one which arises from the distorsion of the electronic distribution of the substance, and an *orientation* component. Farley and McClelland (1990) have demonstrated that even in collisionless molecules, "hot isolated polyatomic molecules can reorient in response to an external field, thereby giving rise to this second component of polarization".

B. Mineral dipoles

1) *Dipolar water*

Among recent and complementary knowledge about water biophysics and relevant to polarity, mention can be made of Saenger's 1987 review. It mainly concerns the relationships between hydration water and hydrogen bonds. Hydrogen bonding dynamics involves flip-flops and movement of water along the surface of macromolecules. Water would not have its particular properties if the molecules were not associated by hydrogen bonds O-H···O. If the O-H group is involved in hydrogen bonding it becomes polarized (see II in **I**). In the association of water molecules to the surface of proteins or nucleic acids, hydrogen bonding of type (water) O-H···*Y* is the main attractive force. When the O-H···O bonds all run in the same direction, this is called *homodromic*; it is indicative of the influence of the cooperative effect. When a water molecule donates two hydrogen bonds this gives rise to *heterodromic* situation, where hydrogen bonds are randomly oriented.

According to the idealized structural model for water presented by Finney (1982), the simplest picture of the molecule "assigns partial charges to the two hydrogens and the two lone pairs which are considered to be disposed in an approximately tetrahedral manner. Each molecule is capable of forming four hydrogen bonds to neighbouring molecules" (see also **I**). Among the three proposed models of the water-water hydrogen bond, the PE model (water molecule electron distribution in terms of an electrical multipole expansion, see Barnes *et al.*, 1979) represents the water molecule electron distribution in an electrical multipole expansion. According

to Finney (1982), "the experimental dipole moment and quantum mechanical quadrupole are used, together with a dipole polarizability to try to handle the cooperative effects". Switching on polarizability in the PE model would therefore affect only the dipole-dipole and dipole-quadrupole energy terms (Finney, 1982).

The local dipolar field of protons of liquid water is averaged out by fast isotropic rotation and translational diffusion, and this gives a single narrow line in the NMR spectrum. In a molecular or biological system which can restrict water motion, causing an anisotropic averaged orientation, the NMR spectrum of the preferentially oriented water molecules can be given by a line pair or doublet. Lenk *et al.* (1980) have reported such NMR doublets spectra due to "structured" water in plant systems.

A typical example of efficient proton translocation across or along the surface membrane is the movement of protons across a cell membrane after their generation in some oxidation process. A high level of proton conductivity is extremely rare in crystalline solids. Thomas and Farrington (1982) have proposed that the proton conduction mechanism in one of the very best crystalline proton conductors so far studied ammonium/hydronium β"-alumina is a useful model mechanism for biological proton transfer. This proton conduction mechanism deduced from an accurate single crystal neutron diffraction study involves a classical Grotthus-type mechanism (see below).

In relationship with bilayer membranes (see IV.B.2) it should be pointed out that "an ion in water is stabilized by the favorable interactions of the water dipoles, the hydration energy. To remove an ion from water and place it in the middle of a membrane is unfavorable because of the loss of this hydration energy". The most successful model for quantifying this is the Born model described in Gennis (1989). In addition to this Born energy, a second component due to the polarization arises at the dielectric interface. An "image energy" results from the "presence of a charge on one side of the interface which causes the dipoles in the medium on the other side to reorient".

Cell water is modified by solvation which arises when water abuts a cell surface. Molecules become restricted in their motions and a greater proportion of them have four (rather than three or fewer) hydrogen bonds with their neighbours. Water modified in this manner is called vicinal (see **I** and Drost-Hansen and Singleton (1989).

Virtually all of the water in cells is considered to exist as polarized multilayers arising from fixed charges on extended protein surfaces. Cardinal sites exist on these particular proteins, the degree of binding for a given ion being influenced by a number of factors. Clegg (1982) further commented "ATP binding at the cardinal site leads to cooperative alterations and the selective accumulation of K^+ over Na^+, and generates the polarized multilayers of water; ATP splitting and the removal of ADP results in a movement of the system to a lower energy state in which the ion selectivity is lost as is the polarization of water".

Protons can be transferred along lipid/water interface in the absorbed water molecule network by a Grotthus-type mechanism (ref. in Tocanne and Teissié, 1990, see also IV.B.2.a).

C. Organic dipoles

2) *Multiple molecules (polar chains)*

Charge transfer molecular interactions are of high significance in biology (Sklifkin, 1980). Electrons are delocalized in molecular conjugated systems (alternate single and double bonds). The polarization of these molecules is enhanced when they carry hydroxy-substituent(s) which behave as electron-attracting groups. Consequently, Pont and Pezet (1990) could suggest that "the polar interaction of these molecules with membraneous proteins could lead to a destruction of the cellular membranes by depolarization" (see IV.B.2.d). This could account for the biocidal effects of highly conjugated phenol derivatives such as the natural hydroxystilbenes which are efficient protectors of grape berries against the grey mold *Botrytis* (Pont and Pezet, 1990).

D. Chiral molecules

Pasteur (1884, see **I**) audaciously extrapolated from molecular asymmetry the famous aphorism "la vie est apparue dans une brisure de symétrie". If we equate asymmetry and polarity, this would therefore mean that polarity is basic to the arisal of living matter.

From atoms to human beings, nature is asymmetric with respect to chirality (Gardner, 1979) and "clues are beginning to emerge that connect chirality on different levels". Thus, and as resulting from the weak nuclear Z force between electrons and nuclei, all atoms are also chiral. Consequently, the interaction that causes the helical motion does not conserve parity, and the mirror-image atom with a right-handed helical electron flow does not exist in nature (Hegstrom and Kondepudi, 1990, see I.B).

Chirality has its fundaments in the asymmetry between electron and positron; this asymmetry follows up in the hydrogen atom and reaches its full expression in the carbon asymmetry (see II.D). The basic molecules of life all have a specific handedness. They are therefore asymmetric (see I.B): its amino acids are left-handed, whereas its sugars are right-handed (see **I**). Chiral compounds which dissociate into enantiomers display a sharp difference in biologic activity. Chemists have been able

to induce a selection between two enantiomers and to develop methodologies for asymmetric syntheses initiated from prochiral center (Mosher, 1971, in Morrison, 1983-1985; see Oppolzer, 1987 and Holmstedt *et al.,* 1989). Chiral auxiliaries have been produced around asymmetric centers using organo-copper reagents. New bondings have thus been obtained with the concourse of highly stereo reactions in compounds such as diverse drugs (R(+)-S(−) thalidomide, etc.), pheromones, and perfumes (Oppolzer, 1987).

III. MACROMOLECULAR POLARITIES

A. Free Macromolecules

1. a) *Deoxyribonucleic acid (DNA)*

a[1] *Structure.* As noticed in **I** (Fig. 5) the two polynucleotide strands of the DNA double helix have opposite polarities and transcription only occurs from the sense strand (+) in the 5'→3' direction.

The bipolar pattern of the DNA double helix has important consequences on DNA recombination processes which involve restriction enzymes (Arber, 1974; Nathans and Smith, 1975). The recognition sequence for representatives of these site-specific endonucleases such as *Eco*RI and *Hind*III is a palindrome, i.e. a sequence of six inverted repeat base pairs showing a twofold rotational symmetry. The inverted polarity of the two DNA strands imposes a positioning of the cleavage sites outside the axis of palindromic symmetry. The ensuing asymmetric cutting produces single-stranded ends containing four bases of complementary sequences.

Seemingly, small variations in molecular structure or electrostatic potential at specific sites can make a critical difference in how the nucleic acid is organized and how it is recognized by other molecules in the intracellular environment. This is becoming increasingly clear from scanning tunnelling microscopy studies of calf thymus DNA and poly(rA)·poly(rU) which have shown that the helical pitch and periodic alternation of major and minor grooves can be visualized and reliably measured (Arscott *et al.*, 1989).

a[4] *Mutations.* Those causing variegation are due to the action of transposons, a group of genetic elements known to move from one location in the genome to another. Certain strains of *Saccharomyces cerevisiae* contain an intron endowed with the ability for transposition in the gene coding for mitochondrial RNA which is absent from the corresponding gene of other strains; most of the progeny between intron plus and intron minus are positive (Dujon *et al.*, 1974). This phenomenon, termed "polarity of recombination" by Bolotin *et al.* (1971) resembles a duplicative transposition which is characteristic for prokaryotic transposons.

As recently outlined by crystallographic structural studies of contacts in repressor-operator complexes, "positioning contacts" appear to be important conserved features within families of helix-turn-helix proteins (Pabo *et al.*, 1990).

b) *Ribonucleic acid (RNA)*

Antisense RNA molecules can selectively turn off genes and be used as antisense expression vectors to produce pigment variegations in flowers (Weintraub, 1990).

2. PROTEINS

As one of the recently described DNA-binding motifs, the zinc finger protein coordinates with a Zn^{2+} ion through paired cysteine and histidine residues along the amino-to-carboxyl protein dipole (Johnson and McKnight, 1989).

The thermodynamics of membrane-located proteins containing large (hundred of Debye units) permanent dipoles has been outlined by Schwarz (1978). Ordered water molecules can contribute directly to the properties of proteins by influencing their interaction with ligands. In their studies of atomic structures of the complexes of the L-arabinose-binding protein with sugars, Quiocho *et al.* (1989) have found that "two hydrogen-bonded water molecules in the site contribute further to tight binding of L-arabinose but create an unfavourable interaction with a methyl group of D-fucose".

5. ENZYMES

The distribution of charges within the charge-relay system (or "catalytic triad") at the active site of the serine proteinases has been further investigated. An Asp--Asn mutant in rat trypsin has been engineered by Craik *et al.* (1987). As reported by (Blow, 1990), this mutant showed that "the polarization of the histidine by the buried aspartate enhanced the reactivity of the serine". Warshel *et al.* (1989) have used the technic of computational chemistry "to estimate the effect of the charged carboxylate group and the polarized histidine on the reactivity of the serine side-chain surrounded by water".

B. AGGREGATES

2. c) *Polar viral morphopoiesis*

Packaging of bacteriophage λ DNA involves polarity of chromosome entry into the prohead (**I**, p.70) from the *Nu1* end to the *R* end (Becker and Murialdo, 1990).

IV. SUBCELLULAR POLARIZATIONS

B. Surface membranes

2. a) *Biochemical properties*

The bilayer membrane can be modelled electrically as a thin slab of non conducting material separating two aqueous solutions and thereby acts as a simple parallel-plate capacitor (Gennis, 1989). "Its dielectric constant is a measure of the polarizability of the material and the degree to which any permanent electric dipoles which may be present in the material respond to an electric field (voltage difference)".

The amphiphilic phospholipids form spontaneously well-organized bilayer structures in water which are the basic architecture of biomembrane. Evidence has been obtained with membrane model systems, which support the view that lateral proton conduction occurs at water/lipid interfaces (Tocanne and Teissié, 1990). The polarity at these interfaces in terms of dielectric constant is different of that of bulk water. This means that, "in terms of micropolarity or water molecular dipole moment, the lipid/water interface region is more than likely anisotropic both in terms of structural organization and electrical properties" (see B.2b).

As for the very low permeability of the lipid bilayer to cations as compared to anions (see Tocanne and Tessié, 1990) it is ascribed to the positive polarization potential of the surface membrane (see B.2.d) which would constitute an energy barrier against the transport of positively charged compounds across membranes.

Permeability coefficients have been determined for several kinds of small molecules. Among them, water can relatively easily penetrate the membrane bilayer. As commented by Gennis (1989) "It may seem surprising at first to learn that water can so readily penetrate the phospholipid bilayer". However, "there is no substantial water to be found inside the membrane beneath the carbonyl groups".

2. c) *Energy transduction*

In 1961, two proposals were made as to the way in which electron-transfer reactions of the cytochrome chain — the chain used in the oxidation of NADH by molecular dioxygen — could be connected to ATP formation without the intervention of chemical intermediates (Williams, 1989). Both mechanisms invoked the transduction of the energy of the oxidation/reduction reaction to a proton gradient before the gradient generates ATP. The two mechanisms, sometimes termed the delocalized (Mitchell) hypothesis and the localized (Williams) hypothesis, are very different: in the first, protons generated by oxidation appear only in aqueous phases;

even ATP is generated by an electric field acting on the ATP synthetase and not by proton flow; in the second, protons move in proteins within matrices and aqueous phase equilibrations are ignored in the development of proton gradients, in proton diffusion and in the ATP-synthesis step. To distinguish between these mechanistic possibilities, long series of experiments (Wikström, 1989) have been carried out on separate parts of the cytochrome chain, especially on the last stages of the electron-transfer reactions, those of cytochrome oxidase.

Electric currents produced by oxido-reduction reactions, also called Faraday currents, can be assayed by electrochemical methods such as those of polarography. The polarograph apparatus works with three electrodes (see Monnier *et al.*, 1979): an indicator capillary electrode on which oxido-reduction reactions occur at the surface of mercury drops, a reference electrode allowing to impose to the first one a constant potential while varying the voltage, and an auxiliary electrode insuring passage of current. Registered curves of intensity-potential of chemicals such as metal ions allow their quantitative assay. Dissolved O_2 can also be measured by the polarographic technique (Fork, 1972).

In artificial fuel cells, gases are combined electrochemically such that the exothermicity is converted directly to electrical energy and the only reaction product is water. Dyer (1990) observed gas — electrical energy conversion processes occurring whithin very thin films of gas-permeable, ionically conducting membranes of hydrated aluminium oxide, as a prototypical membrane. Both polarity and the magnitude of the voltage were unexpected. The covered inner platinum electrode was positive and the polarity of the cell could be changed in $H_2 + O_2$ mixtures only when the outer platinum catalyst was changed to a nickel catalyst. This shows the strong dependence of cell polarity on the metals used and their sequence, suggesting that "different electrochemical kinetics might establish the polarity observed" (Dyer, 1990).

2. d) *Electric potentials*

Many possible factors can contribute to the amount of electrical work to move a charge through a membrane (Gennis, 1989): a) associated work with dielectric constant; b) internal dipole potential by orientation of the dipoles at the membrane surface resulting in a positive potential in the center of the phosphatidylcholine bilayer; c) surface potential which, in most biomembranes, is negatively charged, usually due to the presence of acidic, anionic phospholipids; the electric potential at the shear plane which is the plane defining what migrates in the electric field is called the zeta potential (McLaughlin, 1977); it someway controls the electrophoretic mobility of charged vesicles (electrokinetic effects); d) transmembrane potential which is defined as the difference in the electric potentials of the two bulk aqueous phases separated by the membrane. The asymmetric charge distribution generates

transmembrane potentials which are usually negative inside and can be measured with fluorescence polarity methods using probes such as merocyanine or anilinonaphthalene.

The membrane surface potential (ΔV) is the sum of an electrical term (Ψo) and a dipolar or "polarization" term (ΔVp) which exhibits high positive values (about 300 to 500 mV). The variously oriented and rotating strong dipoles of lipid polar heads would contribute to the surface polarization potential and this view (Tocanne and Teissié, 1990) has been correlated with the concept of "molecular electrometer" as developed by Seelig *et al.* (1987) on the ground of ^{2}H-NMR experiments using parameters such as the deuterium quadrupole splitting.

In fungi, marked changes in the membrane potential detected by [^{3}H]tetraphenylphosphonium (TPP^{+}) uptake rate have been caused by illumination of dark-grown mycelium of *Trichoderma viride.* An initial hyperpolarization of the plasma membrane was found to be accompanied by a rise in the intracellular ATP concentration and by changes in the intracellular level of cyclic AMP (Gresik *et al.*, 1988).

In higher plants, blue light is known to activate the electrogenic proton pump to hyperpolarize the plasmalemma (Assmann *et al.*, 1985 and Shimazaki *et al.*, 1986). Plasma membrane hyperpolarization caused by auxin (IAA), accompanied by short time oscillations in the electric potential of corn coleoptile cells, is paralleled by cytosolic pH drops as well as changes in Ca^{2+} activity (Felle, 1989). Moreover, the activity of the plant plasma membrane enzyme NADH oxidase which transfers the electrons from NADH to oxygen in the absence of added electron acceptors has been linked to membrane polarization (Novak and Ivankina, 1983). In Conjugatophycean green algae photoreception, a tetrapolar gradient of phytochrome created by light perception is achieved by the dichroitic orientation of plasma membrane-bound phytochrome molecules; blue-light also appears to mediate a tetrapolar gradient of the sensor pigment proper mediating tetrapolar actin anchorage sites on the plasmalemma (Grolig and Wagner, 1988).

Gating and ion selectivity of calcium channels have been further studied by electrophysiological experiments. Subtypes of calcium channels have been classified according to their voltage threshold for activation and by their inactivation characteristics (Wray *et al.*, 1989). Current dependence of channel gating has been tentatively ascribed to the formation of dipoles along the trajectories of ion movement that exist during dipole relaxation time (Kostyuk *et al.*, 1989). This new approach would assume that "ion transition through the open channel produces local displacements of charged molecular groups lining the wall of its steric region". During the process, the frequency of ion transitions would increase drastically and become comparable with frequency of dipole relaxation (Kostyuk *et al.*, 1989).

Release of Ca^{2+} from the sarcoplasmic reticulum (SR) following depolarization of transverse tubules (T-tubules) triggers contraction of the skeletal muscle. The foot

structure of the SR is part of a molecular bridge which spans a short gap between the T-tubules and the terminal cisternae of the SR. Large cytoplasmic extensions of the molecule evidently attach to the dihydropyridine receptor complex in the T-tubules (Agnew, 1989). There is also evidence that the dihydropyridine receptor in the T-tubule membrane of skeletal muscle functions not only as slow calcium channel but also as an essential component of coupling, probably as the voltage sensor (Takeshima *et al.*, 1989). A model of the structure of the dihydropyridine-sensitive calcium channel has been proposed (Catterall *et al.*, 1989) in analogy with current models of the structure of voltage sensitive sodium channels.

Chloride (Cl^-) channels (normal and pathological) were activated by patch excision which caused large membrane depolarization. This allowed Welsch *et al.* (1989) "to use depolarization as a "tool" to determine if a Cl^- channel was present in a patch". Active chloride transport can be light-driven by retinal proteins. These bacterio- or halorhodopsins function as inward-directed electrogenic pumps for Cl^- ions (Zimányi and Lanyi, 1989). Parallely, these pumps transport protons out of the cell interior, thereby generating an inside-negative membrane potential.

Opening and closing of chloride channels studied in the electric ray *Torpedo californica* are unequally timed. This asymmetric electric conduction increases with transmembrane electrochemical gradient for the chloride ion thus demonstrating that the channel-gating process is not at thermodynamic equilibrium (Richard and Miller, 1990).

2. e) *Action potentials*

They are not only generated in animals (see **I**) but also in fungi, algae and higher plants in response to light, heat, cold, chemicals, electrical stimulus, and wounding as reviewed by Pickard (1973) and Simons (1981). Davies (1987) considered action potentials as multifunctional signals in plants and proposed a unifying hypothesis to explain apparently disparate wound responses. Action potentials could also be a unifying factor to explain the involvement of an interaction between Ca^{2+} flux and auxin transport in the role of gravity in geotropisms (De la Fuente, 1984, also VIII.A.2.c[4]).

Cell electrophysiology and membrane transport in plants have been recently reviewed by Bentrup (1989) who stated that "the evergreen question of the role of Ca^{2+} during the characean action potential will remain elusive as long as the characean plasmalemma is not routinely accessible to patch clamp technics". In the *Characeae,* depolarization occurs by diffusive Cl^--efflux and repolarization by diffusive K^+-efflux (Köhler *et al.*, 1986; Gradmann, 1989).

The role of K^+ in the mechanisms of action potentials has been further analyzed in the green alga *Eremosphaera viridis* by Köhler *et al.* (1985, 1986) who showed that it is caused by a transient opening of a K^+ channel which is not gated by the membrane potential.

In animals, action potentials experimentally evoked by electrical activity can suppress neurite elongation and growth cone motility (Cohan and Katter, 1986) and thereby may influence structure and connectivity within the nervous system (see also VI.A.2.i).

Following electrical activity in excitable cells, there is an increase in intracellular Ca^{2+} concentration. Silver *et al.* (1990) also report that clustering of L-type Ca^{2+} channels causes intracellular Ca^{2+} hotspots at the neural growth cone. Enzymes with a micromolar requirement for Ca^{2+} at the hotspots are therefore activated by the ensuing depolarization. The role of voltage-dependent calcium influx in controlling nerve cell outgrowth remains puzzling because "also raised intracellular Ca^{2+} concentration triggers outgrowth of the growth cone margin, neurite elongation requires low intracellular Ca^{2+} concentration". According to Silver *et al.* (1990), the fact that "electrical activity can selectively raise intracellular Ca^{2+} concentration in the growth cone, leaving neurite calcium concentration low would resolve this paradox".

C. Endomembranar and vesicular systems

1. Endoplasmic reticulum

In the endomembranar sorting process, proteins destined for transfer are sequestered within membrane vesicles that bud off from a donor organelle and then fuse with the appropriate acceptor organelle. Vesicle fusion in several distinct branches of this complex distribution network as well as transfer of vesicles between the rough endoplasmic reticulum (ER) and the Golgi complex require the same cytosolic protein, a tetrameric, *N*-ethylmaleimide-sensitive protein (NEM) called NSF (Beckers *et al.*, 1989). Such transfer requires ATP and is inhibited by NEM or the monoclonal antibody against NSF. NSF is required in a late, calcium-dependent transfer step; this step is most likely the fusion step. Surprisingly, the deduced protein of cloned and sequenced NSF product showed sequence similarity with the product of a yeast gene *(SEC18)* previously shown by Schekman and Novick (1982) to control the transfer of vesicles between the rough endoplasmic reticulum and the Golgi complex; more recent studies suggested it has a function in endocytosis (Riezman, 1985). These results raise the possibility that "fusions between different organelles derived from the rough endoplasmic reticulum may all be catalyzed by the same set of proteins" (Schatz, 1989).

2. Golgi apparatus

This compact structure colocalizes with the microtubule organizing center (MTOC) in a perinuclear region of fibroblasts. Intact interphase microtubules but

not microfilaments appear to be required for this specific location of the Golgi apparatus. This has been demonstrated by the scattering of Golgi elements after treatment with the microtubule depolymerizing drug nocodazole, and by the subsequent reclustering of the Golgi elements when nocodazole is removed (Ho *et al.*, 1989). A protein may be involved in linking the Golgi apparatus to the microtubule network and the MTOC in vivo (Allan and Kreis, 1986). A fungal antibiotic, brefeldin A, produces a reversal of traffic polarity i.e. a rearrangement of Golgi elements into the ER, thereby inducing a secretion block (Bosshart *et al.*, 1990). Such "violation of the one-way system" has been further discussed by Armstrong and Warren (1990).

D. Organelles

3. Chloroplasts and phototransducing membranes

Most of the chloroplast proteins are imported from the cytosol and polarly directed into six different compartments (Smeekens *et al.*, 1990). Two sorting systems are involved in this import and intraorganellar transport of nuclear-encoded protoplast proteins. Additional sorting informations located at N- termini are contained in thylakoid lumen proteins. The information present in transit peptides, decoded by the chloroplast import machinery, is not yet known.

The electron transfer reactions in photosystem II take place within the so-called reaction center grouping numerous antenna pigment molecules (chlorophyll, etc.) as well as organic ions and charged atoms (manganese, calcium, etc.). The stepwise transfer of electrons through this reaction center succeeds in pulling far apart the mutually attractive positive and negative charges. The task of the photosystem II is thus to act as a tiny capacitor, storing energy by separating and stabilizing positive and negative charges on either side of the thylakoid membrane (Rutherford, 1989). The water-splitting reaction produces four protons and four electrons released simultaneously with O_2 in that water-oxidizing clock which is a cyclic mechanism of four states (Gowindjee and Coleman, 1990).

E. Cytoskeletal components

That the cytoskeleton is someway involved in plants intracellular movements, perception mechanism and transmission effects has again been emphasized by Hensel (1989b) who concluded that "the function of the cytoskeleton is to generate and maintain cell polarity".

As for fungal cells, they have been comprehensively surveyed in 1987 and 1989 by Hohl.

1-2. Microfilaments (actin-myosin)

Both actin and myosin filaments have definite polarities and well-ordered structures (see **I**). Actin filaments can move in opposite directions on tracks of myosin heads. They always move foreward but never backward reversing the polarity of the movement. According to Toyoshima *et al.* (1989) "The direction of movement is therefore determined by the polarity of the actin filament".

Myosin heads can form reverse chevrons and, when tethered in a single thick filament of a mutated *Drosophila* flight-muscle sarcomere, can bind with opposite rigor crossbridge angles to flanking thin filaments, which are apparently of opposite polarities (Reedy *et al.,* 1989).

The driving force for the rearrangements of the actin cytoskeleton in cell motility, division and differentiation is provided by actin-binding proteins. The addition of actin subunits to the barbed end of actin filaments and the nucleation of polymerizing actin *in vitro* are controlled by capping protein. Recent experiments suggest that capping protein regulates polar distribution *in vivo* of actin filaments. The actin cytoskeleton is disrupted in yeast capping protein mutants, indicating that "the asymmetric distribution of actin in budding yeast (see VI.A.1.a[2] in **I**) depends on the proper functioning of several actin-binding proteins with apparently different functions" (Amatruda *et al.,* 1990).

The uniform angle and conformation of myosin subfragment 1 (S1) bound to actin filaments (F-actin) "attest to the precise alignment and stereospecificity of the binding of these two contractile proteins. Because actin filaments are polar, myosin heads must swing or rotate about the head-tail junction in order to bind" (Reedy *et al.,* 1989). Adams and Pollard (1989) have shown for the first time that the single-headed myosins called myosin-I can bind directly to NaOH-extracted membranes isolated from *Acanthamoeba* and to vesicles of pure lipids with an affinity sufficient for extensive binding in the cell. Membrane-bound myosin-I may provide a mechanism for many cellular movements previously thought to involve filamentous myosin-II (see V, in **I**) and for the specification of sites of cell surface growth (Drubin *et al.,* 1990).

For a general review about cytoskeleton microfilaments, see Kristen (1987).

1-3. Microfilaments-microtubules (actin-tubulin)

In the cortex of the giant coenocytic green alga *Caulerpa,* amyloplasts are transported along microtubular strands as shown by the fact that both microtubule- and dynein-specific inhibitors block movements of these organelles. In contrast, chloroplast movement is blocked by cytochalasin but not by colchicine thereby showing that immobilization and movement of chloroplasts are dependent on intact microfilaments of actin but not on microtubules (Menzel and Elsner-Menzel, 1989).

F. Nuclei and mitotic figures

2. Polewards chromosome movement

The bipolar attachment of chromosomes to the spindle occurs well before all the chromosomes congregate metaphasically. In the normal functioning of the mitotic spindle most of its growth and disassembly take place at the end of the microtubule away from the pole. All microtubules have the same polarity and the fibers behave differently depending on the structure in the spindle to which they bind. Most important as microtubule-organizing center is the centrosome which serves as a seed to start microtubule polymerization; thereby it defines their polarity. That polarity, or asymmetry, is crucial to the functioning of microtubules (see I) by at least two of its functional consequences: at the ends it causes the (+) end to add and lose subunits faster than the (−) end; along the surface it influences the orientation with which proteins will bind to the microtubule surface (McIntosh and McDonald, 1989).

The molecules involved in the mechanical forces moving polewards chromosomes begin to be unraveled (Vale and Goldstein, 1990). Among such mitotic motors there are kinesin motors and perhaps the newly discovered dynamin motor (Shpetner and Vallee, 1989) which forms cross-bridges and induces ATP-dependent sliding between antiparallel microtubules *in vitro* (McIntosh and Koonce, 1989). Kinesin is a microtubule-interactive, force-generating ATPase acting as a plus-end motor in intracellular transport of vesicles along microtubules (Vale, 1987, and others, see in **I**). The inherent asymmetry of the polymer (actin or tubulin) and the motor is necessary for the unidirectional movement of the motor along the polymer. It is toward the barbed (or +) end of the actin filament that myosin motors such as myosin I (single ellipsoidal head) move.

A superfamily of kinesin motors acting in fungal nuclear fusion and division has now been described in *Saccharomyces cerevisiae* (Meluh and Rose, 1990) and in *Aspergillus nidulans* (Enos and Morris, 1990). Such kinesin motors bear either round or rectangle heads at the end of the α-helical coiled coils. Short single-headed kinesins analogous to myosin I, kinetochore-specific kinesins, and perhaps kinesins may also be expected to be involved in morphogen or RNA transport as force-producing proteins (Vale and Goldstein, 1990).

V. POLAR CELL MOVEMENTS

B.1. *Cilia-flagella*

In the green unicellular alga *Chlamydomonas,* a component of contractile flagella roots is the centrosome-associated phosphoprotein centrin. This type of structural organization contributes to define its cell polarity through cell axiation (Fig. 1, in Salisbury, 1989).

2. *Gliding movements*

Bacterial gliding motility appears to be dependent on the establishment of transmembrane potential and any depolarization (*not* depolymerization as wrongly written in **I** p. 132) by protonophores such as 2,4-DNP or CCCP results in a cessation of motility.

3. *Amoeboid motion (transient polarity)*

Both the single headed myosin I and the double headed myosin II are mechanochemical enzymes which generate force through the hydrolysis of ATP when complexed with F-actin.

Fukui *et al.* (1989) show by immunofluorescence microscopy that non-filamentous myosin-I occurs at the leading edges of the lamellipodial projections of migrating *Dictyostelium* amoebae, which are devoid of myosin II, whereas filamentous myosin II is concentrated in the posterior zone of the cells. The authors suggested on the basis of these locations of the two forms of myosin and their known biochemical and biophysical properties that "actomyosin I may contribute to the forces that cause extension at the leading edge of a motile cell, while the contraction of actomyosin II at the rear squeezes the cell mass forward. Myosin I isoenzymes might have similar roles in metazoan cells, for example at the leading edges of neuronal growth cones, and in the extension of lamellipodia and pseudopodia of leukocytes, macrophages and fibroblasts." These observations suggest that "actomyosin I-dependent force-generating activity occurs at the leading edge (as in pseudopodia extension) and that actomyosin II-dependent force-generating activity occurs at the trailing end of a migrating *Dictyostelium* amoeba (causing the cell mass to move forwards)". This could explain "how myosin II-minus mutants can form smaller-than-normal pseudopodia at a relatively normal rate. Membrane-bound *Acanthamoeba* myosin I can generate force against actin cables however, and both *Acanthamoeba* and *Dictyostelium* myosin I will crosslink actin filaments and generate force between crosslinked filaments".

None of Fukui *et al.* (1989) observations is compatible with the participation either of other processes in amoeboid movement, such as membrane flow or the remodelling of the actin matrix, or of myosin I and myosin II in other motile activities. The significance of Fukui's team results is that they show the presence in the leading edge of a migrating cell of myosin I, which in conjunction with F-actin is known to be capable of producing force and movement.

To explain the rearward movements of membrane proteins in locomoting polymorphonuclear leukocytes, the experimentally best supported model implies the cytoskeleton (see **I**, pp. 133-137). The retrograde lipid flow hypothesis has been proposed by Bretscher (1984) as an alternative explanation for the rearward movements of membrane proteins. However, recently used techniques of low-light-level fluorescence microscopy and digital image-processing of photobleached images disprove that lipid flow model (Lee *et al.*, 1990). By further implicating cytoskeleton in proteins movements, they also validate the conclusion of Sheetz *et al.* (1989) that such a membrane flow in the leading edge of amoeboid cells does not drive rearward movements of membrane glycoproteins.

About the motor of amoeboid motion, there is much evidence linking actin-based system to the generation of motile structures in the cell (Bray and Vasiliev, 1989). Nevertheless, a mutant of *Dictyostelium discoideum* deficient in α-actinin and in which movements are unimpaired has been obtained by Gerisch's group (Wallraff *et al.*, 1986; Schleicher *et al.*, 1988). "Motile life without myosin" also exists as shown by mutants of *D. discoideum* that lack normal myosin-II (Knecht and Loomis, 1987; De Lozanne and Spudich, 1987, see **I**, p. 134). Since, André *et al.* (1989) have described a strain of this slime mold lacking severin (actin-filament fragmenting protein) even though still able to move. A relative interpretation of these findings is that "there is an extensive overlapping redundancy in the activity of actin-binding proteins *in vitro* and more than one way to crosslink, fragment or even to move actin filaments" (Bray and Vasiliev, 1989). There is analogy between the behavior of such parallely distributed processor of the locomotive cytoskeleton of *Dictyostelium* amoebae and of the cytoskeletal network intervening at yeast budding (see VI.A.1.a[2]).

VI. POLAR CELL GROWTH

A.1. Monopolar Outgrowth (emergence)

In our present state of knowledge, cytoplasmic *microtubules* are dispensable for bud outgrowth (see **I**) but required for specific, single or double budding of yeast cells or fungal spores to direct their mono- or dipolar axiation toward the site(s) of bud formation. By contrast, polarly localized actin *microfilaments* appear to be an absolute requirement for the budding processes.

a[2] *Yeast budding*

The cortical actin cytoskeleton seems to specify sites of growth of the yeast cell surface (Adams and Pringle, 1984, see **I**; Novick and Botstein, 1985). An actin-binding protein (ABP1p) might be involved in the spatial organization of cell surface growth and the identification of C-terminal protein domains suggests that such domains might serve to bring together signal transduction proteins and their targets or regulators, or both, in the membrane cytoskeleton (Drubin *et al.*, 1990).

The cytoskeletal network in the budding yeast cell *(Saccharomyces cerevisiae)* behaves as a parallely distributed processor, as suggested by the finding of a protein (SPA2) associated with actively growing regions of the cell surface (Snyder, 1989). Such polarization of the growth process is disturbed in mutant cells displaying an inability to stop growing under nutrient-limiting conditions which often results in multiple budding (multipolar growth, see **I**, p. 187).

b[1] *Fungal spores*

In the germinating spores of *Mucor rouxii* the change in growth pattern from spherical to polarized correlates with the degree of DNA methylation and this, in turn, may be controlled by polyamine levels. The establishment of the polarized phase of growth in *M. rouxii* probably occurs through the regulation of the genes involved in the synthesis of products necessary for apical growth of the hyphae (Cano *et al.*, 1988).

c) *Dimorphism*

Quite recently, Crombie *et al.* (1990) have shown that the sites of budding and germ tube formation on yeast cells of *Candida albicans* were polarized preferentially towards the cathode. Buds were found to be less polarized than germ tubes at any given applied voltage. Moreover, polarization of germ tubes was biphasic.

2. Tip growth

b) *Fungal hyphae*

In the models of hyphal tip growth, electric current does not always enter the growing end (*Allomyces* hypha drives an outward protonic current, see Youatt *et al.*, 1988 in **I**). As recently commented by Gow (1989) "Most of the evidence suggesting that ionic currents are involved in establishing and maintaining polar growth is essentially correlative, and it is not yet clear whether the current is a cause or consequence of polarity". However, Gow leaves open the possibility that "Cytoplasmic proton and calcium-ion gradients and fixed-charged gradients resulting from asymmetric transport of calcium into a cell may be involved in localizing growth". The same conclusions have recently been reached about differentiation at egg germinations of brown and red algae (Quatrano and Kropf, 1989; Waaland, 1989; see VII.C.3.a).

In hyphal tips of the oomycete *Saprolegnia ferax,* Heath and Kaminskyj (1989) observed that "all the organelles and the microtubules are non uniformly distributed, each showing a characteristic longitudinal gradient starting at a different point behind the tip". A few microtubules can reach the extreme tip but they were more abundant sub-apically. The authors concluded that "the correlated patterns of organelle and cytoskeleton organization from this and previous work show that neither the microtubules nor the detected arrays of actin are sufficient to account for most organelle arrangements".

The role of microtubules at the onset and maintenance of polarized growth of hyphae is still unclear. Intact microtubular tracks are required to initiate dominant, monopolar outgrowth from macroconidia of *Neurospora crassa* (Caesar *et al.*, 1988, see in **I**). However, further elongation of hyphae deprived of microtubules can still occur contortionally, with a damped polarity (Howard and Aist, 1980, see **I**).

Germlings of the bean rust fungus *Uromyces appendiculatus* treated with the microtubule-binding drug griseofulvin continued polarized apical growth even though showing changes in the morphology of their apical and subapical regions (Hoch *et al.*, 1987).

i) *Animal neurites*

A major question in developmental neurobiology is how developing nerve cells accurately extend processes to establish connections with their target cells (see Lasek and Black, 1988). This unsolved problem of polarized growth involves "both the nature of cues for growth cone guidance and also the question of how growth cones survey their environment for cues and respond by altering their direction of migration" (Bentley and Toroian-Raymond, 1986, see I). According to Lamoureux *et al.* (1989) "there is also controversy over whether axonal elongation is the result of a pulling growth cone and the role of tension in axonal elongation".

Earlier in this decade, the consensus was that axons or neurites elongated from tension generated by forward motility of the growth cone (Landis, 1983; Letourneau, 1982). It was presumed that contractile filopodia were the source of the tension moving the growth cone (Bray, 1982; Trinkaus, 1985). But this view was challenged by experiments showing that neurites elongate, albeit abnormally, in the presence of cytochalasin, which inhibits growth cone and filopodial movements (Marsh and Letourneau, 1984).

Bentley and Toroian-Raymond (1986) also reported an examination of the migration of pioneer growth cones deprived of filopodia by culture in agents which disrupt actin microfilaments. Under these conditions, axons continue to extend but a large percentage of growth cones are highly disoriented. Their results indicate that filopodia are not necessary for axonal elongation *in vivo* but that they are important for correctly oriented growth cone steering.

Additionally, high resolution, video-enhanced observations of growth cone activity argue against filopodial shortening as a source of tension, suggesting instead that an extrusion of cytoplasm rather than a pulling process, is the key event in neurite elongation (Goldberg and Burmeister, 1986; Bray, 1986; Aletta and Greene, 1988, ref. in Lamoureux *et al.*, 1989). Studies of slow axonal transport (Lasek, 1986) indicate that much slower cytoskeletal pushing underlies axonal elongation and direct measurements of neurite force as a function of growth cone advance show that they are linearly related and accompanied by apparent neurite growth (Lamoureux *et al.* (1989). No increase in force occurs in neurites whose growth cone fails to advance.

According to Mitchison and Kirschner (1988) there are three phases of axonal development: an actin based-system in which the leading edge becomes orientated, a consolidation phase in which filopodial microtubules become stabilized in their direction of future growth and a conversion phase to stable microtubules bundled within the axonal tube. The protein factor tau stimulates the conversion phase. However, tau expression is insufficient to induce polarity but tau antisense oligonucleotides can inhibit neurite polarity (Kosik and Finch, 1987).

Pulse-labelling studies performed both in mature nerve and in cell culture provided most of our knowledge of the axonal transport of cytoskeletal proteins. In 1975, Ochs has put forward his unitary hypothesis of axonal transport according to which proteins achieve different transport rates by having different affinities for a single moving vector. Tubulin and actin molecules are the essential components of the axonal cytoskeleton and considered by some (Black and Lasek, 1980) as a static complex travelling down the axon, a view challenged by others (ref. in Okabe and Hirokawa, 1990) who observed a gradual recovery of photobleached zones rather than their movement or spreading along the axon, both in neurons injected with fluorescein-labelled tubulin and actin. Therefore, these cytoskeletal components can be considered as "dynamic structures that continue to assemble along the length of the axon" (Okabe and Hirokawa, 1990).

In most recent and interesting experiments, Schnell and Schwab (1990) have shown that axonal regeneration and elongation in the rat spinal cord can be produced by the neutralization by monoclonal antibodies of myelin-associated neurite growth inhibitors.

VII. POLARIZED CELL DIFFERENTIATION

B. APICAL DIFFERENTIATIONS

1. *Monopolar patterns*

a) *Fungal exosporulation:* a^2 *Sporangia*

A unique capability of excised segments of sporangiophores of the terrestrial mold *Phycomyces* is to regenerate new sporangiophores with sporangia (Götze, 1918). The excised segments in the sporangiophore preferentially regenerate at the apical end. In addition to this segmental polarity, there is a polarity of the whole sporangiophore. Moreover, the fact that "polarity is not destroyed by acropetal or basipetal centrifugation seems to indicate that the plasma membrane or the cell wall (see also proposal for algal axiation in C.3.a) plays a crucial role in the polarity". Galland and Ootaki (1987) conclude from their comprehensive review that the molecular basis for this polarity is still obscure, and one of the challenging problems in *Phycomyces* differentiation remains to discover what molecules constitute the actual gradient and where are they located?

The tip of the growing zone of the sporangiophores of *Phycomyces* (Bergman *et al.,* 1969) is the site where the gravitropic bending occurs (Sachs, 1879, in Shropshire and Lafay, 1987, see VIII.A.2.c^4).

a^3 *Basidiospores*

Basidia of *Coprinus cinereus* continue differentiation when explanted to water agar and vegetative hyphal tips monopolarly elongate from the four apical sites of the basidium expected to produce sterigmata (Chiu and Moore, 1990).

C. APICO-BASAL DIFFERENTIATIONS

3. a) *Algal eggs (rhizoid-thallic poles)*

In model systems of early embryogenesis of the Fucales, the site of inward current precedes and accurately predicts the site of rhizoid outgrowth (see **I**) and the polar axis can be oriented by external vectors (light, etc.) and two unequal cells result from the first division. Experiments with inhibitors (i.e. the cytochalasins) clearly implicate microfilaments in the process of axis fixation. Moreover, such polarization of two-celled embryo cannot occur in absence of a cell wall, demonstrating that the

presence of this cellular component is an absolute requirement for axis fixation. From these results, Quatrano and Kropf (1989) derive their actual working hypothesis that "axis fixation involves transmembrane bridges at the presumptive rhizoid pole, from the cell wall to the microfilament cytoskeleton".

Using repair shoot cells and rhizoids of the red alga *Griffithsia,* Waaland (1989) tested Jaffe's hypothesis (1968, 1979, see **I**) that transcellular currents are responsible for establishing and maintaining sites of localized secretion and growth. However, in repair shoot cells, the inflowing current continued even when the cell repair hormone rhodomorphin was withdrawn and elongation stopped. Thus, in *Griffithsia* "transcellular currents *per se* do not appear to control localized organelle accumulation and localized growth".

6. *Higher animal cells*

b) *Epithelia (apical-basolateral poles)*

The apical and basolateral, macroscopic domains of polarized epithelial cells are mostly large, morphologically distinct regions of the cell surface which are separated by proteinous barriers.

The rapid diffusion and equilibration of lipophilic NH_3 across cell membranes and the accumulation of NH_4^+ seem to be governed by pH differences between compartments. Kikeri *et al.* (1989) reported that renal tubule cells from the medullary thick ascending limb of Henle have an apical membrane which is not only virtually impermeable to NH_3, but is also highly permeable to NH_4^+. They proposed a model which would explain how this renal epithelium can mediate vectorial movement of NH_4^+ between compartments of equal pH.

A hierarchy of sorting information with multiple sorting signals — apical and basolateral — present in different domains of a given plasma membrane protein has been suggested from the evidence that covalently attached glycosyl-phosphatidylinositol (GPI) acts as a "dominant" apical targeting signal. Polarized epithelial protein sorting might therefore rely on glycolipids (Lisanti and Rodriguez-Boulan, 1990).

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).

c[4]) *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.1a[2]) 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).

EPILOGUE (complement to pp. 271-273 in **I**)

The predictor question — What is life? — asked by the brilliant physicist Erwin Schrödinger in 1945 has since been partially answered by the cracking of the enigma of the genetic code. However, it still leaves open the question of "How does this one-dimensional code specify a three-dimensional organism?", a question relevant of topobiology (Edelman, 1988). At this epigenetic level, organizational principles of inanimate objects appear to be still valid even though complexified for animate ones. Preeminent among such universal principles is polarity emerged from the primary asymmetries of particulate matter (see I.B) and multi-expanded into the numerous biopolarities.

To bridge genetics and epigenetics still remains the great question of how genes control the transduction of the intrinsic molecular polarities into those cellular and organismic biopolarities? The bridge starts to be completed at the cellular level with the recent unravelling of genes controlling polarity of cytoskeletal macromolecules such as actin, myosin and tubulins (see IV.E), themselves someway related to known cell positioning as examplified by our *Allomyces* "sexual dipoles" (Plate **I**). However, the link remains elusive at the organismic level where some types of interaction should intervene between macromolecular polarities and DNA-controlled directional (head or foot in the Hydra model) morphogenetic gradients.

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