



The time evolution of L and D enantiomers from an achiral or racemic substrate in an open flow-reactor system, with an autocatalytic production of each isomer and an enantiomeric cross-inhibition: left, for identical values of the activation parameters of corresponding enantiomeric intermediates and right, for a small bias favouring the production of the L-isomer. Metastable racemic production is represented by the unique point in the left hand graph, to which either an achiral or a racemic substrate leads, and from which the two homochiral production branches diverge. Modified from reference 1.

and [D] refer to the concentrations of the enantiomers². One root of the cubic equation, correlating with a small input concentration of the substrate into the flow-reactor system, corresponds to a vanishing enantiomeric excess, $(\alpha/\beta) = 0$, giving a racemic product. The other two roots ($\alpha/\beta = +1$ or -1) correlate with high substrate input concentrations, and correspond to the two homochiral reaction branches, giving only the L-isomer or the D-enantiomer. At the transition point, where the racemic production process becomes metastable and bifurcates into the oppositely handed reaction channels, the system develops a magnified hypersensitivity to minor inequalities between the activation parameters of corresponding enantiomeric intermediates in the two homochiral reaction branches. Thermal fluctuations at the temperature, T , of the system randomize and annul any initial trend towards the D or the L production branch unless the difference in activation energy, ΔE , between the enantiomeric intermediates satisfies the relationship $(\Delta E/kT) > 10^{-17}$ (ref. 2).

At ambient temperature, the electrostatic advantage ratio for the L-series of amino acids and polypeptides, $(\Delta E_{ew}/kT)$, meets the lower limit of the relationship, so that

selection of the reaction branch for the L-series becomes determinate over a limited range of conditions. With realistic rate constants for the elementary kinetic stages of the model mechanism, the homochiral reaction branch for the L-series is selected with a 98 per cent probability if the passage through the critical hypersensitive transitional bifurcation state is slow. Over 10^4 years this would correspond to an increase in the input concentration of the substrate by 10^{-2} to 10^{-3} moles in a flow reactor with the volume of a small lake, approximately one kilometre in diameter and some four metres deep. This estimate takes into account quantifiable disordering effects, such as the known rates of spontaneous racemization of the amino-acid enantiomers, and the minor enantiomeric photodiscrimination of solar radiation at twilight, when there is a small net circular polarization, oppositely handed at dawn and dusk². □

1. Frank, F.C. *Biochim. biophys. Acta* **11**, 459 (1953).
2. Kondapudi, D.K. & Nelson, G.W. *Nature* **313**, 438 (1985).
3. Mason, S.F. & Tranter, G.E. *Proc. R. Soc. A* **397**, 45 (1985).
4. Japp, F.R. *Nature* **58**, 452 (1898).
5. Morozov, L.L., Kuzmin, V.V. & Gol'danskii, V.I. *Sov. Sci. Rev. D physiochem. Biol.* **5**, 357 (1984).

Stephen Mason is in the Department of Chemistry, King's College, London WC2R 2LS, UK.

Cell biology

Baseless flagellation

from Jeremy S. Hyams

COMPARED with its enigmatic alter ego, the centriole, the basal body is a fairly straightforward organelle. Basal bodies sit, appropriately, on the base of eukaryotic cilia and flagella. Unlike the structures associated with the base of bacterial flagella, they are not actively involved in motility. Rather, they provide the template for the assembly of the 9 + 2 axoneme and, through their association with various rootless structures, anchor the beating cilium or flagellum against the generated torque. This rather comfortable view of

basal body function may, however, have to be re-examined in view of a paper by H.J. Hoops and G.B. Witman on the green alga *Chlorogonium*¹.

In design, the flagellar apparatus of *Chlorogonium* resembles that of its better studied relative *Chlamydomonas*². The two flagella arise from the anterior of the cell in a 'V' configuration. The basal bodies which from the crotch of the V are maintained by a group of striated fibres and serve as the focus for a series of microtubule rootlets that head off towards the

cell's posterior. During forward swimming the two flagella sweep away from each other in a motion which, superficially at least, resembles a human swimmer's breast stroke. Unlike *Chlamydomonas*, where the flagella are resorbed before mitosis, *Chlorogonium* contrives to swim during cell division, the parental flagella remaining attached to the anterior-most daughter cell. Electron microscopy of these dividing cells reveals that the basal-body complex detaches from the flagella to become associated with the poles of the spindle.

Remarkably, not only do the flagella continue to beat in the complete absence of their basal apparatus but the cells still exhibit their normal photophobic and phototactic responses. In *Chlamydomonas*, these responses involve distinct changes in the pattern of flagella beating. During the photophobic response the flagella switch from the asymmetrical ciliary mode used during forward swimming to a symmetrical flagellar waveform that drives the cells backwards³. Phototaxis, on the other hand, involves the inactivation of one flagellum whilst its partner continues to beat, causing the cell to turn⁴.

Experiments on detergent extracts of either isolated flagella or whole cells have shown that both responses are mediated by calcium ions^{4,6}. A rise above 10^{-6} M in the intracellular concentration of calcium triggers the photophobic reaction^{6,7}, whilst a differential response of the two flagella to submicromolar levels of calcium probably underlies phototaxis. The two flagella of *Chlamydomonas* can be distinguished on the basis of their position relative to the asymmetrically positioned eyespot. The flagellum furthest from the eyespot is inactivated below 10^{-8} M calcium whilst the other flagellum continues to beat. Conversely, the flagellum closest to the eyespot is inactivated by 10^{-7} - 10^{-6} M calcium whilst the other flagellum remains active.

By obtaining similar results with dividing *Chlorogonium* cells, Hoops and Witman show that the complex behavioural responses of green algae are intrinsic to the flagella themselves and independent of accessory structures associated with the flagellar base. Taken together with the recent identification of a rhodopsin in *Chlamydomonas*^{8,9}, these new findings suggest that our understanding of tactic responses of eukaryotic microorganisms may soon approach the sophistication of equivalent studies on prokaryotes. □

1. Hoops, H.J. & Witman, G.B. *J. Cell Biol.* **100**, 297 (1985).
2. Ringo, D.L. *J. Cell Biol.* **33**, 543 (1967).
3. Boscor, J.S. & Feinleib, M.E. *Photochem. Photobiol.* **30**, 499 (1979).
4. Kamiya, R. & Witman, G.B. *J. Cell Biol.* **98**, 97 (1984).
5. Bessen, M., Fay, R.B. & Witman, G.B. *J. Cell Biol.* **86**, 446 (1980).
6. Hyams, J.S. & Borisy, G.G. *J. Cell Sci.* **33**, 235 (1978).
7. Schmidt, J.A. & Eckert, R. *Nature* **262**, 713 (1976).
8. Foster, K.W. *et al. Nature* **311**, 756 (1984).
9. Berg, H.C. *Nature News and Views* **311**, 702 (1984).

Jeremy S. Hyams is at the Department of Botany and Microbiology, University College London, Gower Street, London WC1E 6BT, UK.