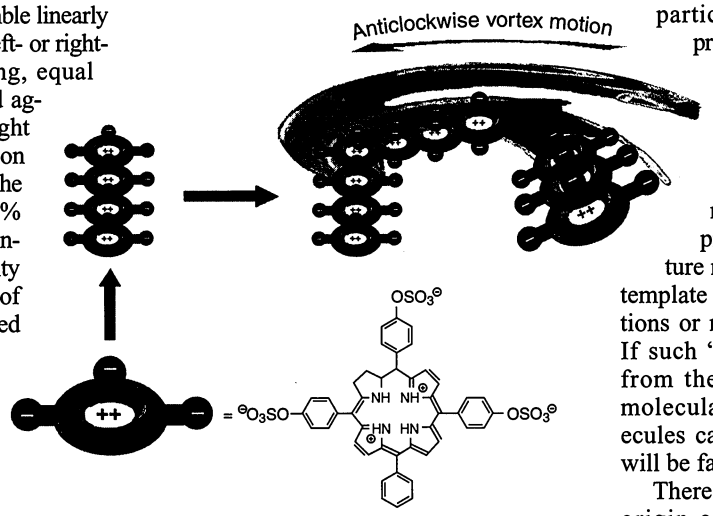
The individual disks can assemble linearly in a growing strand or can form left- or right-handed helices. Without stirring, equal amounts of left- and right-handed aggregates are formed, as one might expect. Depending on the direction of the vortex during aggregation, the porphyrin disks arrange with 85% probability in opposite helical orientations. In other words, the chirality of the supramolecular ensemble of disk-shaped molecules is controlled by the direction of stirring during the aggregation process. The left- or right-handed orientations of the stacked porphyrins can be readily detected by the strong difference in absorption between left- and right-circularly polarized light.



Chiral selection under the influence of vortex motion. In this hierarchical model, aggregation of disk-shaped porphyrins involves two stages. First, zwitterionic porphyrins spontaneously assemble into stacks as a result of electrostatic and hydrogen-bonding interactions. Next, small aggregates assemble into fiberlike structures. The helical orientation in the fiber (anticlockwise shown) in the second stage of the assembly process is controlled by the direction of the vortex motion.

In these experiments, the sensitivity to the asymmetric force at the bifurcation point of the aggregation process seems to be crucial. The random choice at this point to form left- or right-helical aggregates is biased by the vortex motion. Another important feature is the formation of rigid and stable assemblies. In a dynamic assembly, removal of the vortex would lead to equilibrium and loss of chiral selection.

The authors propose a hierarchical organization model (see the figure) to explain their results. In this model, the porphyrins assemble into small aggregates, which are progressively incorporated into growing fibers. Chiral selection takes place at the second stage of this process, where the vortex motion controls the trajectory of the aggregates to be incorporated into the growing helical fiber in a clockwise or counterclockwise manner. The small chiral bias is amplified in the aggregation process.

It is important to realize that the chiral selection thus occurs at the supramolecular level. Exactly how a particular handedness is imposed by the stirring direction remains unclear; nor do we know how general this phenomenon is or what its implications are for chiral selection at the molecular level. Nonetheless, this appears to be the first unequivocal demonstration of chiral selection induced by stirring. The present findings will likely stimulate further studies of the effect of vortex motion on other assembly processes, particularly of helices, which play a prominent role in many supramolecular structures, including peptides, oligomeric metal complexes, hydrogen-bonded assemblies, liquid crystals, and gels (*8*).

It will not be easy to control molecular chirality by this approach. The supramolecular structure may, however, act as a homochiral template for subsequent asymmetric reactions or may function as a chiral catalyst. If such "transfer of chiral information" from the vortex motion via the supramolecular aggregate to individual molecules can be realized, the consequences will be far-reaching.

There are many theories regarding the origin of biomolecular homochirality, from photochemistry to the electroweak force (*4–6*). It has been suggested that vortex motion during key aggregation processes at some stage of chemical evolution may have led to biomolecular homochirality. Ribó *et al.* provide some support for this theory. More experimental work is needed to establish whether we must consider simple stirring as a serious candidate for chiral selection in prebiotic stages of evolution. This promises to be an exciting endeavor.

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PERSPECTIVES: PLANT BIOLOGY

One for All?

Brian E. Ellis and Godfrey P. Miles

The genomics revolution provides almost daily confirmation of the relatedness of eukaryotes, especially when it comes to core activities such as cell division and signal transduction. Against this background of common heritage, it is the differences among eukaryotes that become particularly interesting. In this issue of *Science*, reports by Ullah (page 2066) and Wang (page 2070) highlight one of the striking differences between signaling pathways in plant and animal cells—the degree to which each kingdom relies on heterotrimeric GTP-binding proteins (G proteins) to transduce signals from plasma membrane receptors to the cell interior (*1*, *2*).

In animals, the heterotrimeric G-protein complex—made up of Gα, Gβ, and Gγ subunits—links an extensive array of heptahelical transmembrane receptors to downstream effector molecules. These effectors control a wide range of cellular activities, including cell division, pathogen defense, tolerance to stress, apoptosis, and the generation of action potentials in nerve cells (*3*). The heterotrimeric G-protein complex is inactive when guanosine 5′-diphosphate (GDP) is bound to the Gα subunit. After activation of a G protein–coupled receptor (GPCR) by its ligand, the G-protein trimer interacts with the activated receptor, GDP is exchanged for guanosine 5′-triphosphate (GTP) and the G-protein complex dissociates into GTP-Gα and Gβγ subunits. Both GTP-Gα and Gβγ serve as mobile second messengers that modulate the activities of target enzymes (such as protein kinases, phosphatases, and phospholipases) either within the plasma membrane or in the cytoplasm. The GTP bound to Gα is eventually removed through hydrolysis by the intrinsic GTPase activity of the Gα subunit, and the resulting GDP-Gα reassembles into an inactive GDP-Gα·Gβγ complex.

Mammalian genomes reflect the advantages of this signaling complex, encoding more than 20 Gα, 5 Gβ, and 12 Gγ isoforms and more than 1000 different GPCR recep-

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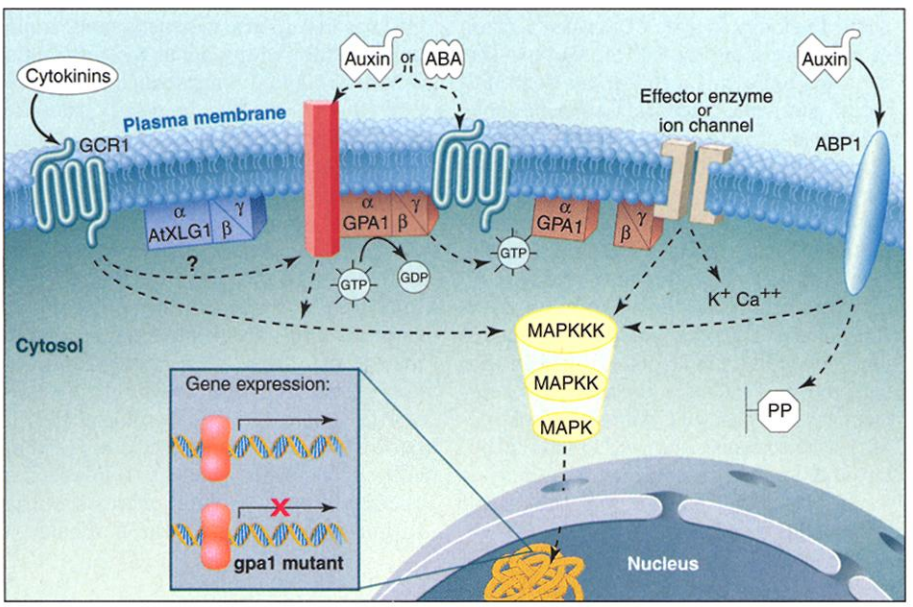
tors. This large suite of interacting molecules affords an enormous array of regulatory combinations. The situation in plants is remarkably different, even though the human genome and the genome of the plant *Arabidopsis* are similar in size. *Arabidopsis* appears to make do with one classical Gα, perhaps two Gβ, and one known Gγ subunit, and possesses only a limited number of GPCR-related membrane proteins. Despite this apparently much lower capacity for G protein–associated signal processing, there is considerable pharmacological and other evidence that plant G proteins are crucial for sensing and responding to environmental and hormonal signals. For example, a dwarf mutant in rice has a deletion within the coding sequence of its Gα protein suggesting that this lesion renders the mutant unable to respond to plant growth hormones (*4*).



Less known than unknown. Plant heterotrimeric G proteins are involved in signal transduction pathways activated by the hormones auxin and ABA. GCR1, the first heptahelical G protein–coupled receptor identified in plants, has been linked experimentally to a signaling pathway activated by the hormone cytokinin, but has not yet been connected to a specific G protein. It remains to be determined whether auxin and ABA use heptahelical receptors or other types of receptors when signaling through the plant Gα subunit, GPA1. Downstream signaling could be transmitted through either GPA1 or the Gβγ dimer. How these downstream signals are connected to plant MAPK modules, and what part, if any, is played by an atypical Gα subunit AtXLG1 in phytohormone signaling are still unclear. Solid arrows denote an established interaction, dashed lines a potential interaction.

With their study, Ullah *et al.* (*1*) provide compelling evidence that G-protein signaling is important for plant responses to phytohormones (see the figure). They show that silencing the *Arabidopsis* gene encoding Gα (*GPA1*) results in an extended G_1 phase of the cell cycle and a reduced frequency of cell division (mitosis) in aerial tissues (such as leaves and stem) of the *gpa1* mutant plants. They also found that overexpression of *Arabidopsis GPA1* in cultured tobacco plant cells produced a shortened cell cycle and a corresponding increase in the frequency of cell division, a phenotype that mimics the behavior of wild-type cells treated with the plant hormone auxin. Despite the centrality of auxin to plant growth and development, the molecular basis of its activity has remained frustratingly elusive. The results of the Ullah *et al.* study, however, indicate that at least one mode of auxin signaling requires participation of the single prototypical plant Gα protein. In this signaling pathway, Gα may be directly involved or GDP-Gα may be required to sequester the activity of the Gβγ dimer. It is not yet clear how the perception of auxins by plants is linked to Gα activity, particularly as the only functionally characterized GPCR-type membrane receptor in *Arabidopsis* (GRC1) is a sensor for cytokinins, not auxins (*5*). How Gα/Gβγ action might be tied to cell cycle control is also unknown, but it may be relevant that free Gβγ in animal cells activates mitogen-activated protein kinase (MAPK) signaling (*3*), and that activation of a specific MAPK cascade in plants was recently found to prevent transcription of genes induced by auxins (*6*).

Wang *et al.* (*2*) have used the same *Arabidopsis gpa1* mutants to study a very specific aspect of plant biology—regulation of the closure of stomatal apertures by the phytohormone abscisic acid (ABA). ABA stimulates loss of turgor in leaf guard cells resulting in closure of stomata, and also inhibits stomatal opening. Several modes of signal processing have been identified in this system, including the activities of protein kinases, protein phosphatases, and phospholipases, as well as changes in Ca^{2+} ion fluxes, phosphoinositides, and cytosolic pH, but the link between ABA and these biochemical responses is unclear. Analysis of the *gpa1* mutants revealed that ABA could no longer block stomatal opening because of a failure to inhibit inward-rectifying K^+ channels. Curiously, however, ABA still promoted stomatal closure in the *gpa1* mutants. This apparent anomaly was resolved when the authors discovered that cytosolic H^+ depletion induced by ABA was responsible for activation of the anion channel activity that underpins stomatal closure. Whatever links ABA perception to this pH shift is evidently not Gα-dependent, whereas Gα clearly is essential for connecting ABA perception to K^+ channel activation. Again, definition of the links upstream and downstream of the guard cell Gα protein will require further work.

These new results fit another piece into the puzzle of plant hormone signal processing, but they also serve to emphasize the huge gaps in our knowledge. It is striking that silencing of GPA1, the only prototypical Gα encoded in the *Arabidopsis* genome, creates such a mild phenotype. Either the heterotrimeric G-protein signaling module is of relatively modest importance in plants, or redundant signaling complexes exist that are able to compensate for its loss. The small number of Gα, Gβ, Gγ proteins, and GPCR receptors in plants might argue for the first interpretation. On the other hand, the existence in *Arabidopsis* of highly atypical Gα-type proteins (such as AtXLG1) (*7*) raises the possibility that the ancestral heterotrimeric G-protein transduction module may have evolved along different paths in plants and animals. In either case, we can anticipate that systematic gene silencing experiments in *Arabidopsis* and other plants, combined with microarray analysis of the resulting phenotypes, will be likely to reveal new plant-specific signal transduction networks. These will have evolved to meet the unique challenges faced by that large part of the biosphere that must deal with its daily environmental challenges without running away.

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