

## Exploring the inner geography of the plasma membrane

The plasma membrane is thought to be the major site where a cell perceives signals from its environment and neighbouring cells. It is also the site that has to organize the carbohydrate-rich surface of a cell, may it be the glycocalyx of animal cells or the cell wall of plant and fungal cells. This task requires intricate topological patterning of the plasma membrane, which, however, remains to be elucidated. In plant cells, where a cellulosic cell wall is built through the plasma membrane, the functional relevance of this patterning is obvious, which does not mean that it is understood. The spatial cues for this patterning must originate from the cytoplasmic interior. Even before they were actually discovered microscopically by Ledbetter and Porter in 1963, cortical microtubules were predicted to guide cellulose deposition (P. B. Green, *Science* 138: 1404–1405, 1962). During subsequent years, an intimate link between the orientation of these cortical microtubules and the texture of the cell wall could be demonstrated and was explained by a movement of cellulose-synthesizing enzyme complexes residing in the plasma membrane along microtubules. Although later disputed, this so called monorail model had been recently rehabilitated by live imaging of cellulose synthase subunits along microtubular tracks (A. R. Paredez et al., *Science* 312: 1491–1495, 2006). However, there remain many open questions. For instance, the directionality of cellulose texture, although generally correlated with microtubule orientation, can be uncoupled from microtubules under certain conditions, at least for short time periods. And the actual link between the cellulose-synthesizing complexes and cortical microtubules has remained enigmatic. These questions require a closer exploration of the inner face of the plasma membrane. Two contributions to the present issue consider what happens at the inner surface of the plasma membrane.

### *Sneaking at the cellulose synthase complex from inside*

The structure of the cellulose synthase complex is an important, but still unresolved topic in plant biology. Freeze

fracture images from algal and plant membranes indicate hexagonal structures of about 30 nm in diameter. When these complexes interact with microtubules, they must protrude into the cytoplasm. A. Bowling and R. Brown (pp. 115–127) investigated this by isolating membrane patches from tobacco BY-2 protoplasts. Upon partial extraction of membrane lipids, they were able to visualize the cellulose microfibrils through the plasma membrane and their association with the cellulose synthase complexes. By a combination of electron microscopy with Markham rotational analysis, they can show that the cytoplasmic part of the cellulose synthase complex is much larger than hitherto expected. Viewed from the cytoplasmic side, these complexes are found to be around 50 nm in diameter and hexagonal in structure. Thus, the hexagonal patterns previously visualized by freeze fracture represent only a small portion of the entire complex.

### *Do microtubules leave imprints in the plasma membrane?*

The partial uncoupling of microtubules and cellulose texture has stimulated an everlasting debate what actually guides the directional synthesis of cellulose. This debate has stimulated the work by B. Pickard (pp. 7–29). The author proposes a “plasmalemmal reticulum” as structural base for the topological patterning of the plasma membrane cooperatively with microtubules, but independently of them. This reticulum adheres to the cell wall through adhesion sites that are morphologically and molecularly similar to the adhesion sites known from animal cells and it is discussed as plant version of the lipid rafts. The geometry of the plasmalemmal reticulum changes during cell expansion from meshwork arrays in isodiametric cells to anisotropic patterns in elongating cells, thus mirroring the reorganization of cortical microtubules. Although the molecular base of this dynamic network is still to be identified, the plasmalemmal reticulum might be the cellular manifestation of the long known feedback of cellulose texture on the plant cytoskeleton.

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