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The Golgi apparatus – still causing problems after all these years!

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The Golgi apparatus lies at the very heart of the secretory pathway, which is composed a series of organelles involved in the production, processing, storage and secretion of a hugely diverse range of complex carbohydrates, proteins and lipids. The Golgi is unique in that not only can it receive, package and send material (cargo) to and from organelles such as the endoplasmic reticulum (ER), the vacuolar and endosomal system and the cell surface (exocytosis and endocytosis), but it also has considerable biosynthetic capability. It is therefore not surprising that huge efforts have been directed at elucidating its structure, molecular dynamics and modes of action in a range of cell types in different kingdoms. By the very nature of the different experimental approaches pursued by different laboratories, this has resulted in a very considerable controversy about the nature and mechanics of the various secretory organelles. Questions such as, what is the mode of transport of cargo across the stack – are vesicles really involved in transport between the ER and Golgi – is the Golgi a static organelle or is it ephemeral in nature, increasing in size or even in number when needed and disappearing when cells stop secreting – have stimulated robust debate amongst the cell biological community.

In this issue of CMLS we have put together a collection of papers reviewing some of the latest thoughts on the Golgi apparatus in mammals, plants and yeast and including results from application of some of the latest techniques such as photobleaching and electron microscope (EM) tomography. These point to some of the controversial issues surrounding Golgi structure and function and highlight areas where we still have much further work to do.

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Murshid and Presley discuss the recent data on transport between the ER and Golgi and the role of COPII coat proteins in membrane cargo concentration and of COPII vesicles in transport to the Golgi via vesicular-tubular clusters in mammalian cells. The necessity of a vesicle vector in transport between the ER and Golgi in mammals (see paper by Polishchuk and Miranov) as well as in some plant cell types due to the close proximity of the Golgi to the ER is questioned (see paper by Ward and Brandizzi). The role of the cytoskeleton in these transport routes is also considered.

Polishchuk and Miranov explore in detail the morphology of the mammalian Golgi stack and the new data that have arisen via green fluorescent protein expression and photobleaching studies (see Ward and Brandizzi) combined with analysis of new EM data. Here the controversial concept of tubules rather than vesicles for transport between the ER and Golgi is considered along with the problems associated with COPI vesicles as cargo carriers. The dynamic nature of the Golgi apparatus is discussed with the concept of the size of the Golgi being related to the need for exporting cargo at any given time. This hypothesis, combined with the ability of the mammalian ER to produce functional mini-Golgi stacks adjacent to ER exit sites in the presence of microtubule depolymerising agents (Murshid and Presley), and the apparent ability of the plant Golgi to increase in number when the secretory pathway is stimulated by GFP expression of membrane proteins (Saint-Jore-Dupas et al.) may lead one to postulate that the Golgi is indeed a transient rather than a stable organelle.

At first glance the plant Golgi (Saint-Jore-Dupas et al.) appears to be a very different structure from the mammalian ribbonlike organelle and maybe more similar to the Golgi in some yeasts such as *Pichia pastoris,* which have distinct cisternal stacks (Nakano). However, the plant Golgi apparatus consisting of upwards of a hundred or more individual cisternal stacks is surprisingly

motile, and in many cells travels over the cortical ER network driven by the actin/myosin cytoskeleton. Thus, how cargo is transferred from the ER to the Golgi is still a matter for debate. The authors also consider the various mechanisms by which transferases are targeted to and are held in the Golgi stack along with vacuolar sorting receptors, as well as the role of the plant Golgi as a major factory for the production of non-cellulosic cell wall material.

The power of fluorescent protein technology combined with FRAP (fluorescent recovery after photobleaching) in analysing protein transport in the secretory pathway is addressed by Ward and Brandizzi. By photobleaching specific regions of the Golgi apparatus or ER, transport of new protein into the bleached area can be measured. Any recovery of fluorescence, however, not only reveals transport into the bleached region but also indicates a corresponding transport of equivalent molecules out of the region. Thus, for example, it has been shown that Golgi transferases continually cycle between the Golgi and ER in mammalian cells and likely in plant cells. Thus, the concept of retention of such enzymes within the Golgi by some form of oligomerisation now seems unlikely. Whether the development of photoactivatable fluorescent proteins will be able to shed more light on Golgi function remains to be tested.

Finally, Nakano considers the yeast Golgi complex in comparison with its mammalian and plant counterparts. With these organisms we can address the question of why or why not to stack. In *Saccharomyces cerevisiae* the Golgi can function perfectly adequately as a series of dispersed cisternae, each having equivalent function of *cis*, *medial* or *trans* cisternae of a stacked Golgi. The power of genetic screening has revealed new proteins such as Emp46p and Emp47p, which function as receptors for packaging cargo into COPII vesicles, and the development of high-resolution real-time imaging systems may permit us to at last resolve putative COPII and COPI vesicles in yeast cells. A final thought here addresses the apparent fundamental differences in the nature of the Golgi among the yeasts, mammals and plants. Do the different morphologies and patterns of Golgi distribution in different cells reflect fundamental differences in the organelle or do they just reflect the exceedingly pleiomorphic nature of a structure that is ever changing, ever dynamic but operates under the guidance of a basic fundamental set of rules governing cargo and membrane transport out of and back to the ER?