



# Transport and sorting in the Golgi complex: multiple mechanisms sort diverse cargo

Gaëlle Boncompain<sup>1</sup> and Aubrey V Weigel<sup>2</sup>

At the center of the secretory pathway, the Golgi complex ensures correct processing and sorting of cargos toward their final destination. Cargos are diverse in topology, function and destination. A remarkable feature of the Golgi complex is its ability to sort and process these diverse cargos destined for secretion, the cell surface, the lysosome, or retained within the secretory pathway. Just as these cargos are diverse so also are their sorting requirements and thus, their trafficking route. There is no one-size-fits-all sorting scheme in the Golgi. We propose a coexistence of models to reconcile these diverse needs. We review examples of differential sorting mediated by proteins and lipids. Additionally, we highlight recent technological developments that have potential to uncover new modes of transport.

## Addresses

<sup>1</sup>Institut Curie, PSL Research University, CNRS UMR144, F-75005 Paris, France

<sup>2</sup>Howard Hughes Medical Institute, Janelia Research Campus, Ashburn, VA 20147, USA

Corresponding author: Boncompain, Gaëlle ([gaelle.boncompain@curie.fr](mailto:gaelle.boncompain@curie.fr))

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## Introduction

The secretory pathway is an essential process for eukaryotic cells. It is responsible for the synthesis, processing and delivery of a diverse collection of proteins to their final destination. The journey begins in the endoplasmic reticulum (ER) where proteins are synthesized and translocated. Cargo proteins are then transported to the Golgi complex, a polarized organelle composed of stacked cisternae, where cargo is eventually, processed and sorted. Finally, cargo is exported to its destination compartment, such as the plasma membrane or lysosomes, while resident Golgi proteins remain.

The mechanisms for cargo transport through the Golgi complex have been the subject of a long-lasting debate

[1]. Many reviews have addressed the details of these different models [2–4]. The most popular models include cisternal maturation [5], vesicular transport between stable compartments [6] and the rapid partitioning model [7]. Each of these models possesses strengths and weaknesses, and on their own does not fully accommodate all of the data present in the literature. Consequently, this has left the field ambivalent, making it arduous to declare one single model as the end-all method of transport across this organelle.

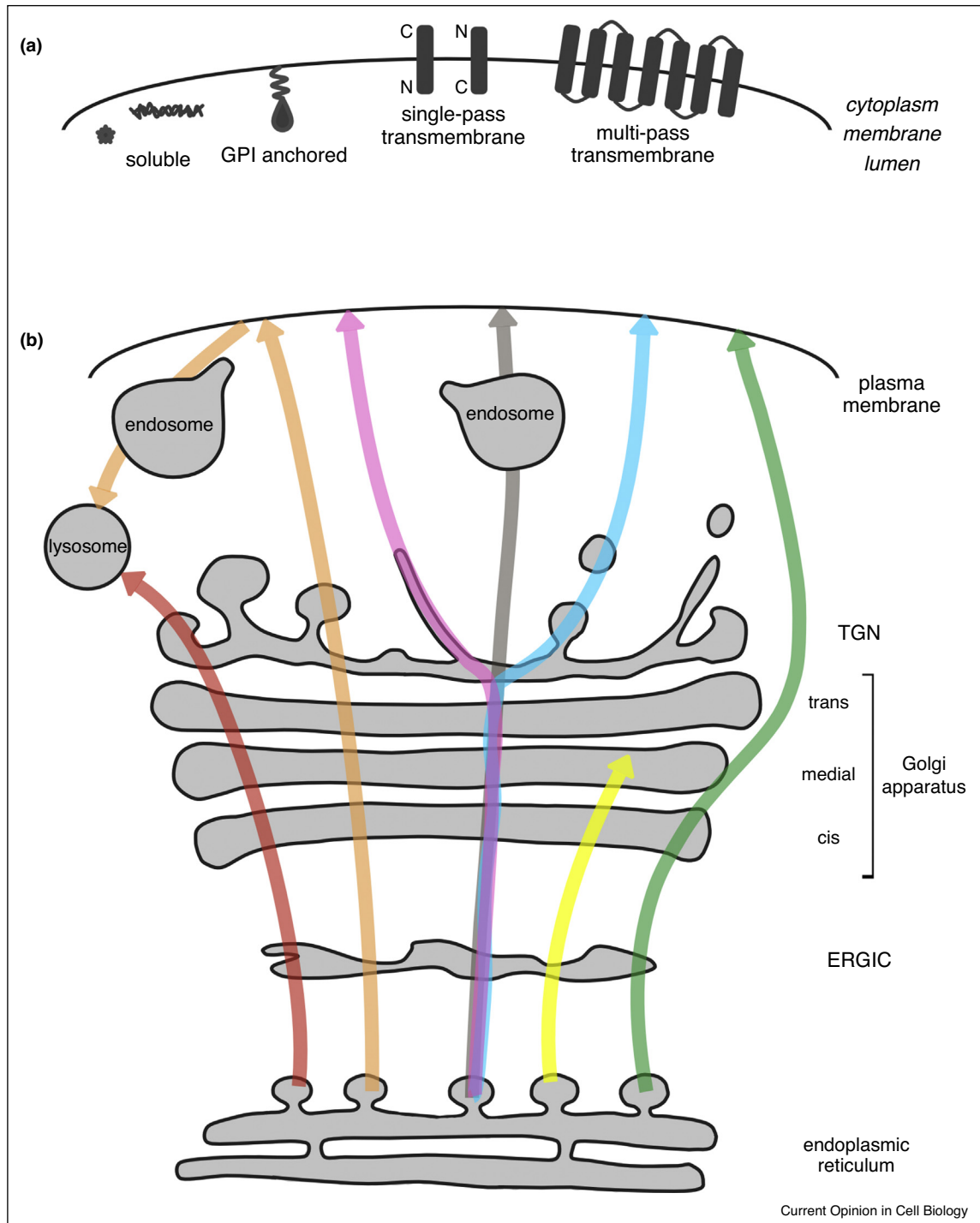
Cargo proteins vary considerably in size, membrane association, destination and modifications, thus, each has its own specialized sorting and trafficking requirements. The Golgi complex is a dynamic organelle and has to handle the diversity of secretory cargos and to ensure their correct sorting and targeting all while maintaining its own identity. Cargos are sorted and segregated to be excluded from or packaged into transport intermediates.

While there are likely not as many different sorting rules as there are cargo, we suggest that different sorting rules may apply to different classes of cargo. In this minireview, we discuss mechanisms of anterograde transport of cargos through the Golgi apparatus in mammalian, non-polarized cells. We propose that different sorting mechanisms coincide to ensure trafficking of diverse cargos and discuss the regulatory roles of both proteins and lipids. In addition, we highlight emerging technologies that may illuminate previously unappreciated differences in Golgi complex dependent sorting and trafficking.

## Diversity of cargos

The variety of cargos that transit the secretory system is vast. In mammalian cells, about 30% of newly synthesized proteins enter the secretory pathway. There is substantial heterogeneity in size, topology and function. A secretory cargo can be a soluble protein, a transmembrane protein or even anchored to a lipid within the membrane (Figure 1a). Soluble cargo can range from less than 10 kDa, such as some cytokines, all the way up to 100s of kDa (Human monomeric type I Collagen is ~400 kDa in its trimeric form). Similarly, transmembrane proteins vary greatly in size and shape. On one end of the spectrum is a simple, single-pass transmembrane protein. While at the other end lies a multi-pass protein, that assembles several subunits together, such is the case for many ion and ligand gated channels. Mixed into this assortment of secretory cargos is lipid anchored proteins, which includes prenylated proteins, fatty acylated proteins and

Figure 1



Diversity of the secretory pathway. **(a)** Cargos entering the secretory pathway are diverse, displaying a large variation in size and topology. By definition, at least part of the protein is contained within the lumen of the secretory compartments. This includes small soluble proteins such as cytokines, large soluble proteins such as collagens, GPI-anchored proteins, transmembrane proteins bearing either one or several transmembrane domains. **(b)** The secretory pathway is not composed of a single route from the endoplasmic reticulum to the plasma membrane, but rather the intersection of several routes. The destination compartments of cargos are diverse with cargos addressed to the plasma membrane, to the endolysosomal compartments or retained within Golgi apparatus. Consequently, their route through the Golgi is similarly diverse.

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