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Review

Membrane remodelling in bacteria

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ABSTRACT

In bacteria the ability to remodel membrane underpins basic cell processes such as growth, and more sophisticated adaptations like inter-cell crosstalk, organelle specialisation, and pathogenesis. Here, selected examples of membrane remodelling in bacteria are presented and the diverse mechanisms for inducing membrane fission, fusion, and curvature discussed. Compared to eukaryotes, relatively few curvature-inducing proteins have been characterised so far. Whilst it is likely that many such proteins remain to be discovered, it also reflects the importance of alternative membrane remodelling strategies in bacteria where passive mechanisms for generating curvature are utilised.

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1. Introduction

Lipid bilayers are indispensable to living systems acting as physical barriers that both separate the inside of the cell from the external milieu, and provide scope for compartmentalisation and specialisation. They must be sufficiently rigid to maintain the integrity of the cell boundary and architecture of organelles, yet plastic to allow for continual remodelling and shape revision. Proteins integrated within the lipid bilayer or attached to its periphery provide a means for exquisite tuning of bilayer consistency and curvature, and ultimately for the evolution of diverse functions. In eukaryotes, classic examples include SNARES (Jahn and Scheller, 2006), dynamin (Praefcke and McMahon, 2004), and BAR-domain containing proteins (Mim and Unger, 2012) all of which have distinct mechanisms for fusing, cutting, and sensing membrane curvature.

Whilst bacteria do not have the same organelle complexity as eukaryotes, they still have extensive membrane reservoirs undergoing continual morphological differentiation, and face many of the same mechanical challenges for membrane remodelling. In comparison to eukaryotes, the number of known bacterial proteins dedicated to membrane remodelling is surprisingly low. Is this because important families are yet to be discovered or does it reflect a more fundamental difference in the way bacteria approach membrane manipulation? In this review we differentiate between membrane remodelling that requires the active involvement of curvature-inducing proteins (CIPs) often by scaffolding and/or wedging (McMahon and Gallop, 2005), and passive remodelling which occurs in their absence (CIP-free) via mechanisms such as protein crowding (Stachowiak et al., 2012), asymmetric lipid enrichment (McMahon and Gallop, 2005), or membrane blebbing (Schwechheimer and Kuehn, 2015). CIP and passive membrane remodelling processes are not mutually exclusive and will work in concert within a cellular context. In eukaryotes, CIPs are prevalent in many membrane shaping processes, and in this review we assess whether the same phenomenon holds for bacteria.

Sophisticated life cycles, unexpected complex social behaviors, and increasingly diverse morphological specialisations are being discovered in bacteria. As this review describes, these are often critically dependent on membrane remodelling events (Fig. 1) with regions of high local curvature observed at both the cytoplasmic membrane (CM) and outer membrane (OM) (Fig. 2). The mechanics of how such curvature is introduced is relatively well understood in some systems such as cell cytokinesis. However, in many systems almost nothing is known. For example, is *Myxococcus xanthus* inter-cellular communication and OM exchange a CIP-free membrane remodelling process (Ducret et al., 2013; Pathak et al., 2012)? And might MamY in *Magnetospirillum magneticum* be a *bona fide* BAR-domain involved in magnetosome CM curvature (Mim and Unger, 2012)? In such cases are there conserved families of proteins driving these membrane remodelling processes or has each species evolved its own unique toolkit? Are CIPs required? These are the kinds of questions that this review aims to

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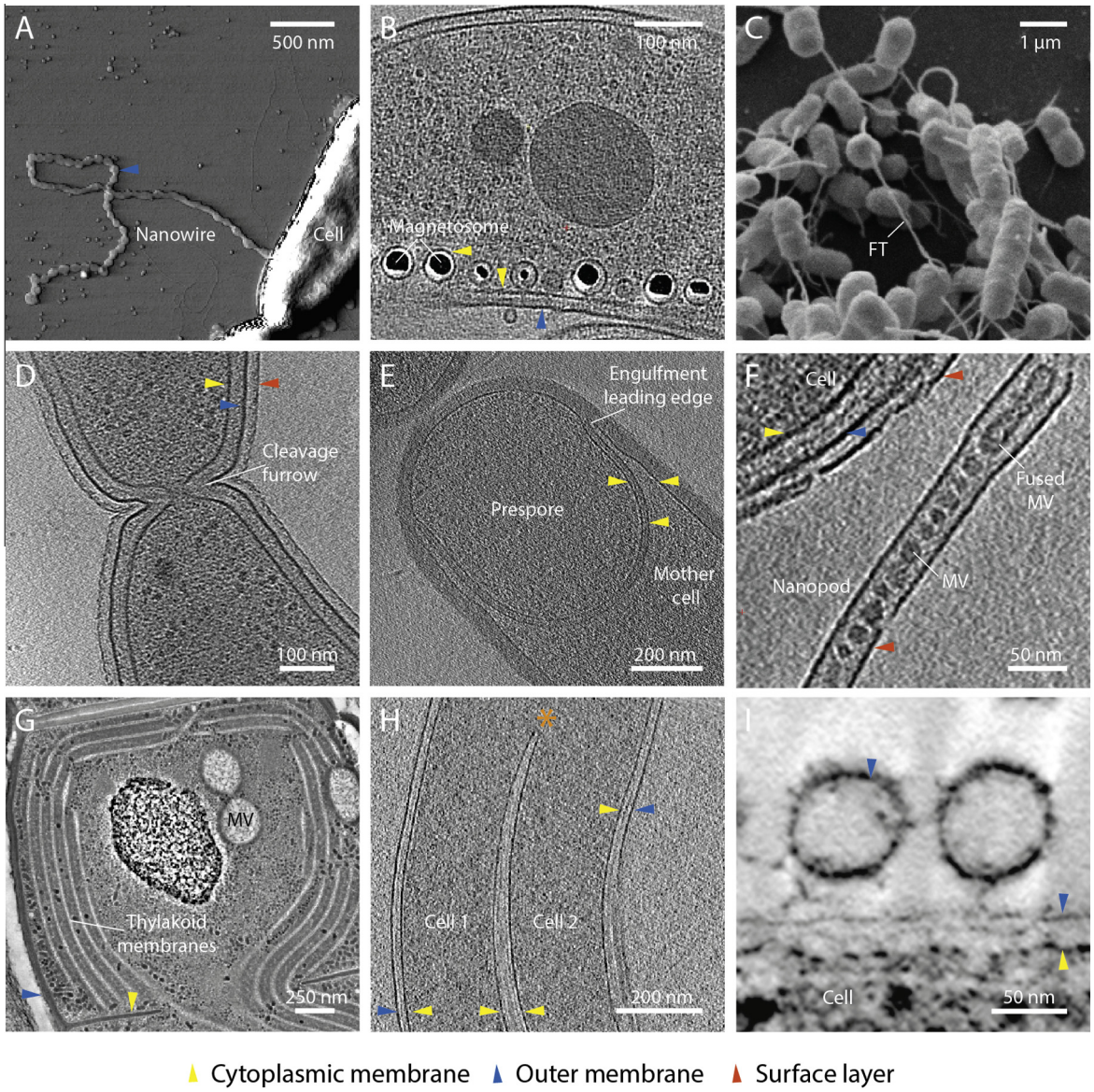

Fig. 1. Selected examples of high membrane curvature and remodelling in bacteria. (A) Atomic force microscopy image of a *Shewanella oniedensis* MR-1 cell with an OM extension that forms a nanowire (Pirbadian et al., 2014). Image courtesy of Sahand Pirbadian and Mohamed El-Naggar. (B) Electron cryo tomogram (ECT) of *Magnetospirillum magneticum* AMB-1 shows that magnetosomes are invaginations of the CM (Komeili et al., 2006). Image courtesy of Arash Komeili and Grant Jensen. (C) Scanning electron micrograph showing cross-feeding between *Escherichia coli* and *Acinetobacter baylyi* connected by nanotubular membrane structures (Pande et al., 2015). FT – feeding tube. Image courtesy of Christian Kost. (D) ECT showing a late stage dividing *Caulobacter crescentus* cell with invaginated cytokinetic cleavage furrow. Image courtesy of Tanmay Bharat and Jan Löwe. (E) ECT of sporulating *Bacillus subtilis*. The prespore is in late stage engulfment by the mother cell (Tocheva et al., 2013). Image courtesy of Elitza Tocheva and Grant Jensen. (F) ECT of a *Delftia* sp. Cs1-4 nanopod (Shetty et al., 2011). MV – membrane vesicle. Image courtesy of Elitza Tocheva, Grant Jensen and William Hickey. (G) Thin-section micrograph of a high-pressure frozen, freeze-substituted *Microcoleus* sp. cell showing CM vesicles (MV) and extensive thylakoid membrane network (Scheuring et al., 2014). Image courtesy of Dana Charuvi, Reinat Nevo and Ziv Reich. (H) ECT of two *Borrelia garinii* cells with fused cell envelopes (Kudryashev et al., 2011). Asterisk shows merging of cytoplasmic cylinders and a region of high IM curvature. Image courtesy of Misha Kudryashev and Friedrich Frischknecht. (I) Micrograph of high pressure frozen, freeze substituted *Myxococcus xanthus* biofilms depicting OM vesicles tethered to cell surface (Palsdottir et al., 2009; Remis et al., 2014). Image courtesy of Manfred Auer.

investigate and what makes this emergent field of membrane remodelling in bacteria important.

2. CIP-mediated membrane remodelling in bacteria

This section focuses on those examples where active membrane remodelling occurs in bacteria through recruitment of CIPs that bind and directly drive rearrangements in bilayer shape. The aim is to focus specifically on the mechanism by which membrane remodelling is induced and to understand how this feeds through to function.

2.1. Bacterial dynamin-like proteins

2.1.1. The dynamin family and their discovery in bacteria

Dynamin family members (DFMs) are ancient GTPase domain containing CIPs that mediate fission, fusion and active reshaping of membrane. In eukaryotes, they are fundamental in diverse basic cellular processes such as endocytosis, mitochondrial maintenance and viral resistance. The hallmark feature of DFMs is their ability to couple oligomerisation, usually through assembly of a helical scaffold, to induction of high curvature in lipid bilayers (Praefcke and McMahon, 2004). This destabilises the bilayer and promotes membrane fission or fusion probably via a hemi-fission intermediate.

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