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Classic Spotlight: Dynamics of the Bacterial Cytoplasm

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The bacterial cytoplasm is complex and crowded with macromolecules, providing an environment very different from the dilute solutions used in traditional *in vitro* biochemistry (1). The ability of different molecules to diffuse within this complex environment must influence almost every aspect of bacterial biochemistry, yet the sheer complexity of the cytoplasm makes prediction of diffusion rates extremely uncertain.

Until 1999, no information was available on molecular diffusion kinetics in the bacterial cytoplasm. Diffusion kinetics can be quantified by fluorescence recovery after photobleaching (FRAP) and other fluorescence-based techniques such as fluorescence correlation spectroscopy (FCS) and single-particle tracking (SPT), but the methods traditionally applied to eukaryotic cells were technically challenging in bacteria due to their much smaller cell size and the impracticability of microinjection of fluorescent tracer molecules. Then, in a groundbreaking paper in the *Journal of Bacteriology*, Elowitz et al. reported the first direct measurements of protein diffusion in the cytoplasm of *Escherichia coli* (2). These authors solved the microinjection problem by using as their fluorescent tracer green fluorescent protein (GFP) endogenously expressed, and they were able to perform accurate FRAP measurements by a combination of state-of-the-art microscopy, careful data analysis, and the simple but ingenious trick of making the *E. coli* cells longer by treatment with the septation inhibitor cephalixin (2).

The GFP diffusion coefficient ($7.7 \mu\text{m}^2 \text{s}^{-1}$) reported by Elowitz et al. (2) became a standard reference point for modeling the dynamics of the bacterial cytoplasm (see, e.g., reference 3). Furthermore, by showing that a short tag of 6 histidine residues significantly slowed diffusion, Elowitz et al. demonstrated an influence of electrostatic interactions on protein mobility. Their results have been used to aid in quantitative understanding of specific

dynamic processes from chemotactic signal transduction (4, 5) to chromosome segregation (6) and the spatial organization of translation (7).

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