Opinion

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# Enzyme Activity in *Escherichia coli*

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## Opinion

*Escherichia coli* (E. coli) are bacteria that can be found in people's and animals' intestines, as well as the environment. *Escherichia coli* is a large and diverse bacterial group. Although the majority of *Escherichia coli* strains are harmless, others can cause illness. Some *Escherichia coli* strains can cause diarrhoea, while others can cause urinary tract infections, respiratory illness, pneumonia, and other illnesses.

*Escherichia coli* and other facultative anaerobes make up about 0.1 percent of the gut microbiota, and fecal–oral transmission is the main way pathogenic strains of the bacterium cause disease. Cells can only survive outside the body for a short period of time, making them potential indicator organisms for testing environmental samples for faecal contamination. However, a growing body of research has focused on environmentally persistent *Escherichia coli*, which can survive and grow outside of a host for many days.

The bacterium can be easily and cheaply grown and cultured in a laboratory setting, and it has been extensively researched for over 60 years. *Escherichia coli* is a chemoheterotroph, which means that its chemically defined medium must include a carbon and energy source. *Escherichia coli* is the most widely studied prokaryotic model organism and an important species in biotechnology and microbiology, where it has served as the host organism for the majority of recombinant DNA work. It can take as little as 20 minutes to reproduce under ideal conditions.

Microbes that thrive in ever-changing environments constantly adapt their proteins through a variety of mechanisms ranging from slower transcriptional regulation to rapid modulation of protein activity via interaction with other proteins or small molecules. While most non-covalent regulatory interactions with proteins are transient, covalent post-translational modifications (PTMs) can achieve long-term activity modulation that persists even after the initial stimulus is removed. Reversible serine/threonine/tyrosine (S/T/Y) phosphorylation, which is catalysed by hundreds of kinases and phosphatases, is one of the most common PTMs, affecting up to 75% of all yeast or human proteins. Although S/T/Y phosphorylation and PTMs in general, are less common in prokaryotes and typically occur at a lower stoichiometry of modification, recent phosphoproteomic studies identified over 2000 phosphorylation sites (phosphosites) on approximately 20% of *Escherichia coli* proteins.

Thus, phosphoregulation may be common in bacteria, despite the fact that only a few S/T- and Y-kinases and phosphatases are known, and their in vivo substrates and regulators are unknown. The presence of a phosphosite alone provides little evidence for function, which is usually inferred indirectly from phosphosite conservation, co-occurrence with other modifications, and correlation of the degree of protein phosphorylation with physiological variables like metabolic flux. Actual function elucidation necessitates time-consuming in vitro phosphorylation of individual proteins, followed by stability, activity, or interaction assays. As a result, less than 5% of the yeast phosphosites detected have a known function, and even fewer in *Escherichia coli*. On a larger scale, genetic phosphosite perturbation has been combined with phenotypic assays, the most recent of which revealed growth phenotypes for 42 percent of the 474 phospho-deficient yeast mutants under at least one of the 102 conditions tested. The largest *Escherichia coli* study to date mutated 134 PTM sites on enzymes at predicted regulatory hotspots, including 48 phosphosites from a 2008 phosphoproteomics study.

According to the prioritisation, 88 percent of these acetylation and phosphorylation mutations had an effect on fitness in at least one of the seven tested conditions. Meanwhile, the number of mapped *Escherichia coli* phosphosites has increased more than 20-fold, leaving the physiological role of the other 2000 reported sites unknown.

To assess the functionality of S/T/Y phosphosites in bacteria more broadly, we focus on *Escherichia coli* central metabolism, where 70% of enzymes have recently been shown to be phosphorylated. We changed 52 reported phosphosites on 23 central enzymes to a non-phosphorylatable amino acid or a phosphorylatable residue. Despite the fact that neither enzymes nor sites were prioritised, 58 percent of the phosphosites studied here caused a growth phenotype when perturbed in at least one of two tested

conditions. This high proportion of phenotypic consequences is surprising given that a similarly unbiased yeast screen required testing over a hundred conditions to identify phenotypes in 42 percent of the mutants. Even in the absence of a phenotype, determining the metabolic profiles of our phosphomutants provided additional evidence of functionality. Overall, we present evidence of functionality for 44 of the 52 investigated phosphosites, implying that regulatory phosphorylation plays a significant role in *Escherichia coli* metabolism. We show how single phosphosites modulate enzymatic activity and regulate metabolic fluxes in glycolysis, methylglyoxal bypass, acetate metabolism, and the split between the pentose phosphate (PP) and Entner–Doudoroff (ED) pathways by combining in vitro and in vivo experiments for selected cases.