

The operon model and scientific explanation

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There are multiple accounts of scientific explanation on offer in philosophy of science, which variously locate explanatory power in fundamental processes, general laws, counterfactual dependencies, detailed causal mechanisms, unifying principles, simplified minimal models and more besides. Jacob and Monod's operon model of gene regulation (1961) has, at one time or another, been used as an example in support of many of these accounts. How can one scientific case justifiably support such diverse views of explanation? This paper takes an historical approach to the question, which illuminates changing relations between philosophy and science. The results motivate, for our current context, a pluralist stance toward scientific explanation.

Across the different philosophical accounts, the operon model itself is a constant. Based on many years of experiments in *Escherichia coli*, the model schematically represents relations between genetic and biochemical entities (structural genes, regulatory genes, DNA sequences, proteins, small molecules). These components and relations comprise a genetic regulatory switch, on 'or off' depending on the presence or absence of small molecules in a cell's environment. Briefly: a repressor protein specifically binds a region of DNA (a regulatory gene) located near a protein-encoding DNA sequence (one or more structural genes). The bound repressor prevents transcription of the nearby structural genes. A specific small molecule, however, can also bind the repressor, thereby preventing its binding to the regulatory gene. If this small molecule is present, then transcription of the structural genes proceeds. The structural genes encode enzymes needed to metabolize nutrients associated with the inducing small molecules, completing the regulatory circuit.

All agree on the basics of this simple model. Similarly uncontroversial is the claim that the operon model explains (in some sense of the term) regulation of gene expression. But further analysis of this claim runs the full gamut of philosophical views on biological explanation. The operon model has been interpreted as an instance of DN explanation (Schaffner 1969), a step toward reduction of biological phenomena to physical and chemical laws (Schaffner 1974, Kimbrough 1979), an "interfield theory" linking genetics and biochemistry (Darden and Maull 1977), an example of anti-reductionism for Mendelian and molecular genetics (Kitcher 1984), an illustration of highly abstract models of gene regulatory networks (Richardson 1996), one of a heterogeneous collection of theories or mechanisms required to "cover the domain" in the absence of biological laws (Beatty 1997), an example of mechanistic explanation supporting interventionism over causal process theories (Woodward 2002, Craver 2007), an example of an abstract model that contradicts the basic mechanistic view (Levy and Bechtel 2013), and an example satisfying general principles of biological organization (Bich et al 2015). This compendium of uses suggests that the operon model is a mirror in which philosophers see what they want to see, illustrating explanation by more fundamental laws, by description of causal mechanisms, by abstraction, or by general principles, depending on who is looking. How can one scientific case justifiably support such a range of views about explanation? What does this one-many relationship tell us about the relation between science and philosophy, and the status of any one philosophical account of explanation?

The most incisive way to answer these questions, I propose, is to take a historical approach. Considered as a trajectory through conceptual space over time, the uses of the operon model reflect not only the philosophical preoccupations of particular intellectual contexts (reduction, laws of nature, mechanisms,

computational modeling) but also features of the relation between science and philosophy. This approach yields several interesting results. For one, it indicates that rejection of the traditional association of explanation and theory-reduction was the upshot of careful critical reflection. No other explanatory accounts of the operon have been decisively rebutted in this way. The historical approach also highlights a key shift in relations between science and philosophy. As philosophers of biology were reaching an anti-reductionist consensus in the 1980s, biologists were extolling the virtues of reductionist approaches. That is, what came to be the prevailing philosophical view tacked against dominant scientific ideas of the time. This oppositional tendency is no longer in evidence by the turn of the millennium. Recent uses of the operon model are closely aligned with the prevailing views of particular fields of biology.

These two points lead to a third, which is the main focus of this paper. The traditional reductionist account excepted (for reasons noted above), the operon model supports diverse accounts of scientific explanation: causal mechanisms, interventionism, multilevel systems models, and more. Supporters of each can make a good case for their favored account of explanation. The operon model can be construed as a basic mechanism of gene regulation, grounded in experimental successes of molecular biology.

Its relations include specific causal processes and a wide variety of difference-making relations, which afford fine-grained prediction and control over systems to which it applies. The model can also be construed as an abstract circuit, a regulatory genetic motif, or a multilevel systems model. Each of these accounts focuses on a single aspect of the operon model, identifying it as the source of explanatory power. Each can appeal to norms and standards of explanation in particular fields of life science: molecular biology, biomedicine, or systems biology. Taken together, these diverse philosophical uses of the operon model support pluralism about scientific explanation.

Moreover, the operon model's interpretive inclusivity is, in our current intellectual environment, an explanatory virtue. It is a familiar point that science is increasingly interdisciplinary perhaps unavoidably, with increasing specialization and accelerating technological change. So, going forward, more and more significant scientific explanations will require contributions from multiple fields and disciplines. In such a context, a model supporting different styles of explanation is a valuable resource - a versatile point of contact between fields with diverse explanatory aims and commitments. The view of the operon model that emerges from considering its philosophical uses in historical perspective, is well-suited to our current interdisciplinary context. Monism about scientific explanation is an artifact of a limited, ahistorical approach. This is, at least, what the operon case suggests.