

it deals with reproductive adaptations both at the subcellular and at the population and life history level. The majority of the papers emphasize empirical data on individual species. This is obviously a swing back from recent trends toward theoretical generalization based on assumption.

There are good papers in all four sections. The following are examples representing, perhaps, my personal bias. K. B. Clark *et al.* document a fascinating phenomenon in the reproduction of *Elysia* (an ascoglossan opisthobranch) that generates a number of unanswered questions concerning life history strategies. Studies of this sort should be encouraged. Turner and Lawrence provide, as expected, valuable information on the relationship of egg volume to organic composition and successfully refute some of the theoretical models. Strathmann and Branscomb present a new concept of larval settling behavior and recruitment. Their conclusion that "wide dispersal of larvae and spatial variation in the attributes of favorable sites combine to limit the effectiveness of cues available to settling larvae" is amenable to testing, and they have provided preliminary evidence on barnacle settling. Woodin's paper outlines an elegant theoretical argument backed by specific examples of a number of factors that must be considered in analyzing and interpreting recruitment patterns (temporal and spatial). This is an excellent review for studies of population ecology and benthic communities. Woodin is also careful to point out examples where her generalizations concerning recruitment can be negated by other types of selective pressures. R. B. Clark presents an extremely interesting review of the control of polychaete gametogenesis and of spawning, described in a most lucid style. He focuses on proximate rather than ultimate effects of the environment. His review is valuable to anyone working with invertebrate life histories in that it includes a thorough reassessment of the terms and concepts used, and dispels much confusion surrounding the terms. Woollacott discusses in detail the effect of the environment on ascidian reproduction, concentrating on organismal responses at the cellular and biochemical levels. Switzer-Dunlap and Hadfield furnish important quantitative data on life history parameters of aplysiid opisthobranchs. Their data indicate some interesting correlations among adult size, growth rate, fecundity, and age of onset of sexual maturity. Hines's paper on barnacle reproduction presents an inter-

esting and intelligent interpretation of results. I feel this is another excellent contribution to the population ecology of benthic communities.

On the other hand, I find myself not entirely in agreement with the interpretation or conclusions in a number of papers. For example, Spight's assumption that related species tend to have similar life history features can easily be refuted by examples provided in this volume (in the papers by K. B. Clark *et al.* and R. B. Clark).

In summary, this is a valuable book. It contains rich resources of information, although more than two years old. Invertebrate zoologists and marine biologists of all types should benefit greatly from it.

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## Gene Regulation

**The Operon.** Papers from a meeting, Cold Spring Harbor, N.Y., July 1976. JEFFREY H. MILLER and WILLIAM S. REZNIKOFF, Eds. Cold Spring Harbor Laboratory, Cold Spring Harbor, N.Y., 1978. x, 450 pp., illus. \$42. Cold Spring Harbor Monograph Series.

What is the mechanism by which certain genes are expressed while other genes in the same cell are not? This question lies at the heart of the problem of cellular differentiation and has occupied geneticists and molecular biologists for decades. On the basis of their studies of *Escherichia coli* and its bacteriophage lambda, François Jacob and Jacques Monod formulated in 1961 the operon concept for the regulation of gene expression. A contiguous block of related genes (the operon) is coordinately regulated by an adjacent site (the operator) where a repressor acts to prevent operon expression. The activity of the repressor, in turn, is regulated by a small-molecule signal from the environment. Subsequent work by others showed that the operator is DNA physically continuous with the genes and that the repressor is a protein whose binding to the operator blocks initiation of transcription by preventing RNA polymerase from binding to the promoter site located very near the operator site. Although these studies were done with bacterial genes, it was supposed that a similar mechanism might regulate genes in other organisms, including eukaryotes.

*The Operon* is a collection of reviews of what we understand, as of 1976, of regulation of gene expression in enteric bacteria (*E. coli* and *Salmonella typhimurium*) and some of their viruses. The first half of the book presents a detailed analysis of the *lac* operon, confirming the basic proposal outlined by Jacob and Monod. Current research described in the book emphasizes the physical chemistry of the interaction between the controlling proteins and the controlling site. One can read about topics ranging from the isolation and mapping of over 1000 mutations in the *lac* repressor gene, to the nucleotide sequence of the *lac* promoter-operator complex, and on to the rate of dissociation of repressor from operator. Nucleotide sequence analysis has revealed the exact relation between the operator and promoter sites and the beginning of the gene itself. One gets the impression that the only piece missing from the picture is the determination via x-ray crystallography of the three-dimensional fit of the repressor onto the operator.

In the second half of the book, however, one learns that the world is not all one and the same. There are marvelous variations on the operon theme. In each of the six other systems reviewed (*trp*, *gal*,  $\lambda$ , *hut*, *ara*, and flagellar phase variation) the regulatory sites are controlled in a manner different from the *lac* site. In some cases transcription does not occur unless a regulatory site is coupled with an activator protein, which in turn is activated by a small molecule from the environment. Some operons are controlled by two or even three regulatory proteins acting in concert to turn the genes on or off in appropriate fashion. Although regulatory mechanisms of these types were not part of the original definition of the operon, they are clearly logical extensions of the operon concept.

Two quite different types of gene control are also discussed in the book. In one aspect of regulation of the *trp* operon, continued transcription through the operon is governed not by a regulatory protein but by the ability of ribosomes to translate the initial leader RNA. An adequate supply of tryptophan, and hence charged tryptophanyl-transfer RNA, allows translation, which by a not-yet-understood mechanism leads to termination of transcription before the *trp* structural genes. As in other operons, expression of the genes is regulated by the environment, but by a radically different mechanism that appears to be widespread among amino acid biosynthetic operons. In another case, that of switching from

one flagellar protein to another, a gene is apparently coupled and uncoupled from its regulatory site by reversible recombination.

It is clear from these last two examples that gene expression is regulated by a variety of mechanisms. It seems likely to me that there are mechanisms not yet conceived that are at work in nature. To those who claim that we know all about how gene expression is regulated in bacteria, I would point out that only a dozen cases have been analyzed in sufficient depth to reveal the basis of their regulatory mechanisms. Nearly all these cases are in enteric bacteria. What mechanisms are used, for example, to control genes for nucleotide biosynthesis or fatty acid metabolism in *E. coli* or to control genes in other bacteria? Each case studied so far has provided new insights, and unimagined mechanisms surely await discovery. The analyses described in *The Operon* provide an excellent guide for further biochemical and genetic studies of gene expression, both in prokaryotes and in eukaryotes. Particularly valuable are the chapters by Beckwith and his colleagues discussing the genetic analysis of operons with transpositions, deletions, and gene fusions.

Two aspects of the subject are not dealt with in the book. First, many well-studied operons are mentioned only in passing, if at all. The volume would be a much better source book if other operons, such as *mal*, *bio*, *ilv*, *glp*, *thr*, *his*, *arg*, *deo*, *bgl*, and *rha*, had been at least briefly described. Second, the book lacks a discussion of the common theme of operons and variations on it, such as I have briefly attempted in this review. The reader achieves an overall view of strategies of regulation only by making his or her own synthesis. It is particularly unfortunate that some excellent reviews of operon control are not cited in the book. For example, a review on autogenous regulation by Goldberger (*Science* **183**, 810 [1974]) should have been mentioned in connection with  $\lambda$  and *hut*, whose repressors are self-regulating. A consideration of several operon regulatory strategies by Savageau (*Biochemical Systems Analysis*, Addison-Wesley, 1976) is also not mentioned. Editors of collections of this type should provide overviews to aid readers unfamiliar with the field, readers for whom these collections are particularly valuable.

How widespread are operons? They have been described only in bacteria and their viruses. Clusters of related genes controlled by an adjacent site have not, to my knowledge, been unequivocally

demonstrated in eukaryotes. Yet the basic element of the operon, a gene with an adjacent controlling site, appears to be universal. Of the several mechanisms of regulation described for bacteria, which most closely resembles that utilized by eukaryotes? There are indications, for example from immunoglobulin synthesis and from yeast mating-type interconversion, that the recombination mechanism operating in flagellar phase variation may be one strategy adopted by eukaryotes. Whether repressors and activators are present in eukaryotes should be known in the near future.

This volume, like the concept of the operon, should be a valuable aid to investigators of gene expression both in prokaryotes and in eukaryotes in that it demonstrates the power of coupling genetic and biochemical approaches to solving basic biological problems.

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## Theories of Memory

**Perspectives on Memory Research.** Essays in Honor of Uppsala University's 500th Anniversary. Papers from a conference, Uppsala, June 1977. LARS-GÖRAN NILSSON, Ed. Erlbaum, Hillsdale, N.J., 1979 (distributor, Halsted [Wiley], New York). xiv, 400 pp., illus. \$24.95.

This volume comprises 16 papers on the psychology of memory that were presented at a conference held in commemoration of Uppsala University's 500th anniversary. Although one or two of the contributors make occasional reference to "the past 500 years," the birth of Uppsala University did not coincide with any major development in the psychology of memory. If there were to be any commemorative dates, after one marking the publication about 100 years ago of the first major experimental study of memory, there would be one marking a fundamental shift that occurred about 20 years ago from a pretheoretical orientation based on a simple associationism to an orientation incorporating more complex, information-processing concepts. Thus, whereas in the 1950's the rememberer was seen as a passive associator of stimuli and responses, in the 1960's he or she became a more complicated processor of information. The radical nature of this conceptual reorientation is illustrated by comparing the subject index of the present book with

that of the leading textbook of the 1950's, McGeoch and Irion's *The Psychology of Human Learning*: the books share fewer than 2 percent of even their first-level entries.

In both the preface and his introductory chapter, Nilsson ponders the new levels of complexity that these last 20 years have brought and argues that the field has become "far too diverging . . . leading everywhere and possibly nowhere" and that there "seems to be a strong need for some overall perspective." He sees the main purpose of this volume as providing a start toward meeting this need.

Measured against this criterion, it is unlikely that the book will achieve any perceptible success. In most cases the contributors have written with a broader sweep than they usually do, but they have nonetheless fallen a long way short of clarifying the relations among their theories. Nilsson's valiant attempts to identify global theoretical perspectives add up to no more than one person's grouping of an extraordinarily diverse set of chapters.

The metatheory of humans as information processors has given rise to a proliferation of new procedures and findings that have called for more complex theories, which in turn have resulted in more procedures and findings. This spiraling complexity is illustrated in the present volume in four chapters (by George Mandler, Fergus Craik and Larry Jacoby, Donald Norman, and Gunnar Johansson) in which the authors update their earlier theorizing, as well as in a chapter by Alan Allport on production systems and in one by Bennet Murdock describing a new model based on principles of correlation and convolution. Although some people see this tendency for researchers to develop their own, personal theories as a sign of health, others, like Nilsson, are troubled and want theorizing constrained in some way.

It is one thing to argue that theorizing needs pruning to sustain vigorous growth but quite another to know how the pruning should be done. Some understanding of the problem can be gained from, conveniently enough, a consideration of the remaining chapters.

Of most direct relevance is a provocative and entertaining chapter by Endel Tulving. Although not entirely pessimistic—he raises the possibility that research endeavors may be just now reaching critical mass—Tulving questions whether the vast amount of research done over the last 20 years adds up to much real progress. He offers a set of