the wavelength is proportional to the angles of incidence and diffraction of the light (instead, it is proportional to the sum of the sines of these angles); Dollond is stated to be the inventor of the achromatic lens instead of its first commercial maker. But these are minor points in a balanced coverage of a very large subject.

To me the most interesting chapter is that dealing with instruments used in acoustics, which was an active field of research in the second half of the century. The illustrations suggest a number of lecture demonstrations that can still be used today. Examples are the sonometer, standing waves around the rim of a glass vessel, and Lissajous's method of compounding two simple harmonic motions at right angles to each other (although I suggest the use of a laser beam instead of an Argand lamp as a light source!). Turner has included photographs of a number of pieces of apparatus by the German-French acoustician and manufacturer Rudolph Koenig. Readers should look carefully at the Koenig devices for what we now call Fourier synthesis and analysis and marvel just how much excellent physics could be done in the era before the invention of the oscilloscope and other electronic devices.

American physicists from older colleges and universities who go through their own apparatus collections with Turner's book in hand will quickly appreciate that only British and Continental apparatus is illustrated. This is reasonable; Turner is senior assistant curator of the Museum of the History of Science at Oxford. Though American manufacturers are given only a passing reference, much of the simpler apparatus used in the United States was produced by manufacturers such as Pike of New York, Queen of Philadelphia (which also imported a good deal of apparatus), Ritchie of Boston, and Daniel Davis, Jr., of Boston. The omission of Davis leaves a gap, as Davis's electromagnetic apparatus was both widely sold and important in the understanding and demonstration of magnetism and the interaction of electric currents with the magnetic field.

This is a large-format, handsomely printed and bound book that invites the reader to browse a little, or a lot, but always to come back. It must be considered the definitive introduction to the study of 19th-century scientific apparatus.

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The Status of the Neutral Theory

The Neutral Theory of Molecular Evolution. MOTOO KIMURA. Cambridge University Press, New York, 1983. xvi, 367 pp., illus. $69.50.

The neutral allele theory of molecular evolution was proposed by a number of people in the late 1960's to explain the pattern of variation in the amino acid sequences observed in proteins. Motoo Kimura was among the first to embrace neutrality and has been the main architect of the theory in its present form. The theory asserts that "most" of the observed sequence variation in DNA and proteins both within and between species is due to the random fixation of nearly neutral alleles by genetic drift. Before neutrality, natural selection was routinely invoked to account for most of this variation. The neutral theory, even more than the observations of the variation itself, has had an emormous impact on population genetics, molecular biology, and our ideas about evolution. With the publication of a large number of DNA sequences over the past few years, acceptance of the neutral theory seems to have increased considerably. This theory is now invoked as routinely as selection was a few years back. The publication of this book is very timely, giving us a chance to review the theory in light of the old and new data and to judge the ability of the theory to account for evolutionary patterns at the molecular level.

The original arguments in support of the neutral theory included the constancy of the rate of evolution of proteins (the "molecular clock"), the almost random frequency of the amino acids found in proteins, and the apparent problems that genetic loads would pose if selection were solely responsible for the variation. Sixteen years later, Kimura uses these same arguments in a more developed fashion plus a number of new ones. In brief summary, Kimura uses the following observations as support for neutrality: (i) the approximate constancy of the rate of evolution of specific proteins or stretches of DNA; (ii) that those parts of protein or DNA molecules that are judged to be of less functional significance evolve more rapidly (so, for example, the third position of a codon evolves faster than the second); (iii) that substitutions that do occur tend to be conservative, causing little apparent disruption in the secondary or tertiary structure of the molecule; (iv) that codon usage in translated DNA tends to match the most abundant transfer RNA species available; and (v) that the frequencies of alleles in natural populations are similar to those predicted by the neutral theory. The basic arguments against selection are that selection is incompatible with all the observations listed above and that selection must entail enormous genetic loads to produce the patterns seen in the data. There are many other, less important arguments, but these capture the core of Kimura's justification for the theory.

Is Kimura's current defense of the neutral theory convincing? Not totally, perhaps not even in the greater part. Within Kimura's argument for the constancy of evolutionary rates, we learn that they are not, in fact, constant. The variance of the rates appears to be two to three times larger than expected under neutrality (Kimura calls those who worry about this "picayunish"). Even this variance may turn out to be an underestimate because of the technical difficulties of assigning mutations to remote branches of evolutionary trees. In addition, the rates of evolution are dependent on clock time, rather than on generation time, as required by the neutral theory. Kimura recognizes this as a serious problem. Since his original claim that the rate of mutation is proportional to the generation time has not been supported by subsequent data, Kimura now assumes that the generation time of a species is inversely proportional to the square root of its population size. Needless to say, there is no supporting evidence for this relationship either. The correlation between the perceived functional importance of a portion of a molecule and its rate of evolution is certainly in accord with neutrality and provides the most appealing argument for the theory. The codon usage story is the least appealing argument. Kimura argues that the fact that codon usage matches the most abundant transfer RNA is an example of stabilizing selection of nearly neutral alleles. However, he goes on to say that each species has its own characteristic frequency of usage of redundant codons. If the abundances of different tRNA's vary from species to species (for whatever reason), and if the codon usage changes to match the tRNA's, then it would seem that selection, rather than drift, is causing the codon usage to track the tRNA's. This problem of codon usage may well be the battleground on which neutrality receives its severest test.

It is not enough to argue that the neutral theory is compatible with the observations; it must also be shown that selection is incompatible. This is the weakest part of the book. Kimura's arguments against selection are the same arguments that have failed to convince anyone for the past 15 years. The main problem is that Kimura's standard model of selection assumes that a species has an infinite reservoir of unique advantageous mutants that have been slowly leaking into the population by mutation for the past few hundred million years in the face of a static environment. However, if selection is operating in response to a constantly changing environment, then even the most naïve of models yields evolutionary rates that are independent of both the population size and the mutation rate. This is because mutations to advantageous alleles do recur in large populations. Kimura, of course, knows this. Had he taken models of natural selection more seriously, he might have shaken population genetics out of the silly notion that these mechanisms of molecular evolution can be distinguished by facile arguments. As it is, his treatment will undoubtedly perpetuate an already undistinguished literature.

Although the book tries to present a summary of the relevant data from molecular biology, there are some very telling omissions. Conspicuously missing are essentially all the studies examining the evolution of protein function. No mention is made, for example, of the fascinating work of George Somero or Dennis Powers on the adaptations of enzymes to temperature and pressure in fish, or of any of the large number of papers on hemoglobin adaptations. As for the neutral theory itself, Kimura gives a very complete description of the mathematical theory as developed by himself and others at Mishima but gives very little space to the contributions of W. J. Ewens, J. F. C. Kingman, G. Watterson, F. Stewart, and others who have in many ways pushed the theory to its most sophisticated level.

Throughout one gets the sense that Kimura is using the book as a vehicle to establish for himself a niche in the history of science. He carefully tells us about his original conception of the neutral theory in 1967 and his announcement of the theory to the Genetic Club of Fukuoka in November 1967, thus attempting to establish clear priority for the idea. He spends an entire chapter, entitled "The overdevelopment of the synthetic theory and the proposal of the neutral theory," belittling the contributions of many of the participants of the synthesis. For example, he writes, "Dobzhansky's main contribution to the science of population genetics . . . is his finding with A. H. Sturtevant that chromosome polymorphisms involving inversion are abundant in some species of *Drosophila*" and "Despite the various attempts to glorify the synthetic theory of evolution, actually very little progress was made at this time." Such judgments may or may not be valid, but one is unaccustomed to hearing them from a scientist who is setting the stage for the historic importance of his own theory.

The neutral theory is a great achievement. It provides a simple (and elegant) explanation for a large number of the observations of molecular evolution. By presenting the theory from such a strong position of advocacy, Kimura does little to help the scientific community judge its merit. His aggressive stance toward those who have published criticisms is particularly distasteful because it is still unclear that the neutral theory is in better accord with the facts than are theories based on the action of natural selection.

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Sex Determination

Evolution of Sex Determining Mechanisms. JAMES J. BULL. Benjamin/Cummings Advanced Book Program, Menlo Park, Calif., 1983. xx, 316 pp., illus. $19.95. Evolution Series.

The near ubiquity of separate sexes in vertebrates, especially the mammals and birds, with which humans are most familiar, predisposes even biologists to assume that sex determination is a rather uniform process among higher animals; the question of sex determination in higher plants escapes attention. Bull's book provides a recent summary of what is known about sex determination in animals and plants and reminds us of the great diversity of mechanisms that have actually been observed.

The book is divided into two parts, the longer first section being concerned with sex determination as such and the shorter second part dealing with the evolution of sex chromosomes. In the first part, Bull is concerned not with the origin of sex or with the evolution of parthenogenesis but instead explores the conditions under which a change from one of these mechanisms to another might occur, a subject on which he has made numerous contributions. Using his "combinatorialist perspective," he places the known mechanisms among those that are theoretically possible, a perspective reminiscent of the method of multiple working hypotheses advocated by T. C. Chamberlin and useful in encouraging an open mind and broadening inquiry.

A survey of the literature confirms that male heterogamety and female heterogamety are two of the most common forms of sex determination in higher animals. In some taxonomic groups, such as birds and mammals, one or the other of these seems uniformly to occur; in other groups, such as salamandrid salamanders and chironomid midges, individual species vary. Bull develops the argument that transition between male and female heterogamety occurs through intermediate stages with multiple sex factors. Under a variety of plausible conditions, paths of equilibria connect the extremes of male and female heterogamety. The mathematical development of this hypothesis is not presented, but references and a discussion of the assumptions and conditions for the analysis are provided. The absence of detailed mathematical treatment permits the ideas to follow more readily for a larger group of readers. Two of the three appendixes to chapters, however, do provide more detailed treatments that have not been published elsewhere, one for sex ratio evolution under systems of paternal genome loss, the other for evolution of genes with sex-specific fitnesses as a function of linkage to sex factors.

Similar treatments are provided for other possible transitions: to haplo-diploidy (arrhenotoky), in which males hatch from unfertilized and females from fertilized eggs; to paternal genome loss, in which males arise from fertilized eggs but transmit only the maternal genome. In these systems, a male transmits to progeny only its mother's genome, which doubles the genetic identity of mothers with their grandchildren. Arrhenotoky has an additional advantage: a single female can produce sons by laying unfertilized eggs; with their sperm, she can found a colony with both sexes present. This advantage is absent when the paternal genome is lost.

Particularly interesting to this reviewer was the summary of data on environ-