BREEDING ANALYSIS OF NATURAL UNITS
IN BEHAVIOR GENETICS

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On receiving my assignment for this refresher course, my self-appointed task became an examination of the term behavior, and consideration of the kind of knowledge genetic analysis has to contribute to the understanding of behavior and behavior analysis has to contribute to understanding in biology.

At a reception following a conference two summers ago, Joshua Lederberg asked me "How do you define behavior?" It's a disconcerting experience at any time to be caught off guard harboring an unanalyzed premise. It's doubly so when it happens on one's first encounter with a Nobel laureate. A survey of textbook and dictionary definitions proves very unsatisfactory and suggests a possible reason for his question. In one form or another, most definitions hinge upon response to stimulation. As Skinner (1938) has so appropriately pointed out, while response to stimulation certainly does occur, so does behavior occur in the absence of antecedent events that bear an easily demonstrable stimulating relation to a given behavior.

BEHAVIOR

In the physical sciences, ever since J. W. Gibbs, a system has been defined as that part of the universe chosen for consideration. In the behavioral sciences we can define behavior as whatever an organism does or, by analogy to physical science, that part of what an organism does that we choose for consideration.

The study of behavior employs the descriptive methods of the naturalist, classificatory taxonomic methods such as are used by the medical diagnostician and the biological systematist, and the analytic experimental methods of the laboratory scientist. In Ernst Mayr's words "it is the basic task of the systematist to break up the almost unlimited and confusing diversity of individuals in nature into easily recognizable groups, to work out the significant characters of these units, and to find constant differences between similar ones" (1942, p. 9). Similarly, the student of behavior must select out of the continuous stream of activity that is behavior, those units which are suitable for study and which can be classified.

The importance of a "suitable" choice of descriptive features and taxonomic categories will be appreciated when it is realized that the units of behavior chosen and the criteria by which they are recognized will strongly influence the future course of research with respect to both the kinds of analyses performed and the kinds of interpretations made. It is convenient, therefore, to consider the study of behavior as consisting of three distinguishable phases: description, taxonomy, and analysis.

Description. To be part of science, non-introspective observations must be formulated in terms that will place them in the public domain. An adequate description of a behavior presents a statement of its differentiating properties and of its relations to other events, so that other observers can identify it.

Descriptions of behavior may refer to either means or ends—what Hinde (1959) has called "physical description" and "description in terms of consequences." Ideally, physical descriptions would be made in terms of the means by which a behavior is executed, and thus would refer to the intensity, duration, and pattern of the physical activities of the body. In practice, though, to avoid cumbersome detail, only the grosser aspects of behavior are usually described, e.g. the startle reaction, the amount of time spent in crouching by a bird, the rate of intromission in sexual

behavior, etc. Descriptions in terms of consequences, made by reference to the goals of behavior, do not always include an account of the particular means by which those goals are sought. This type of description groups into broad categories (such as reproductive behavior, homing, maze-learning) all those performances that achieve the same end state.

The two types of description, however, are not always alternative. In some cases, for example, description in terms of muscular contractions is undesirable because of the unwieldy complexity of the data that result. In other situations, description by consequence is equally undesirable. "Sometimes—as in the threat and courtship posture of birds, which involve both a relatively stereotyped motor pattern and an orientation with respect to the environment—both must be used" (Hinde, 1959, p. 571).

Taxonomy. An ideal behavioral taxonomy would provide a theoretical system under which classes of behavior could be arranged in some meaningful and consistent way. The classes in the taxonomy would be defined in terms of the behaviors they include. In such a system the subjects of classification are behaviors, and the subjects of taxonomy are classifications (King and Nichols, 1960; Simpson, 1961). As yet, no taxonomic system has been devised which attempts to do for behavior what the Linnaean system attempted for species.

Analysis. Analysis breaks behavior down into components that can be related to antecedent and contemporary events, as well as to the physical properties of the organism. The responses of any behaving organism can be represented as points in a four dimensional space whose axes may be labeled: response, time, stimulus, and individuals. The experimental analysis of behavior may be thought of as the study of relations among variations along these four dimensions, because behavior shows: (1) temporal variation or differences in response over time; (2) stimulus-response covariation or changes in response as a function of changes in stimulation; and

(3) individual variation or response characteristics dependent upon the particular organism observed.

Terms like conditioning, learning, maturation, fatigue, adaptation, sensitization, etc., refer to those aspects of behavior in which, for a given individual observed under constant stimulus conditions, a response changes over time. Tropisms, taxes, kineses, preferences, and all of the phychophysical relations refer to those aspects of behavior in which, for a given individual observed over a given time interval, the response changes as a function of changes in stimulation. Mental tests and psychometric methods refer to techniques for the measurement and analysis of individual differences in response; for all behavior, under a given set of stimulus conditions over a given time interval and in a specified population, the characteristics of the response will depend upon the particular individual observed. The three major methodologies employed in the experimental analysis of behavior are conditioning, psychophysics, and psychometrics (after Hirsch, 1962).

LEVELS OF ORGANIZATION AND DIMENSIONS
OF ANALYSIS

The most characteristic feature of all biological material is "organization," by which I mean that when two or more things are put together something new appears, the qualities of which are not always additive or expressible in terms of the qualities of the constituents. Electrons and nuclei combine to form atoms, atoms to molecules, molecules to amino acids, amino acids to proteins, proteins and nucleic acids to nucleoproteins, etc. Chemical and colloidal structures are integrated into the specialized organelles, different organelles are integrated into cells, cell populations into tissues, different tissues into organs and systems of organs, these into multicellular organisms, bisexual organisms into Mendelian populations, and the last finally into ecological communities.

These levels of organization are properties of nature, some of which are obvious

and readily observable as in the case of an individual organism, while others, as in the case of the chemical constituents of the hereditary material, have only been discerned as the result of decades of research.

The strategy of the scientist's approach to the study of behavior involves the use of dimensions of analysis. Stimulus conditions are manipulated as independent variables and response measures are observed as dependent variables. The methods of research, however, must not be confused with the objects studied. Upon the presentation of radiant energy of different wavelengths, properly instructed human subjects respond with different hue names (Graham and Ratoosh, 1962). The data which are collected in this way can be used to test: (1) genetic theories about the inheritance of genes controlling the development of color vision; (2) physiological theories about the nature and functioning of the color receptor apparatus (Fuller and Thompson, 1960); or (3) behavioral theories about psychophysical relations. Certainly, dimensional analysis is a powerful tool which can yield much reliable information about behavior. The interpretation of that information, however, requires both an understanding of biological organization and an appreciation of the levels of organization for which the information from a particular analysis may be relevant.

BIOLOGICAL STRUCTURE AND GENETIC ANALYSIS

In the discussion that helped set Maurice Wilkins on the road leading to the Watson-Crick model, the physicist Erwin Schrödinger points out how "It is well-nigh unthinkable that . . . laws and regularities should happen to apply immediately to the behavior of systems which do not exhibit the structure on which those laws and regularities are based" (1946, p. 3).

We now possess considerable information about the master plan of most organisms and about the genotypic structure of bisexual species populations. The many implications that this knowledge has for the study of behavior are just beginning to be

appreciated. In the first half of this century, it was learned that organisms have properties that are as fundamental to behavioral science and biology as thermodynamic properties are to physical science. Mutation, recombination, and meiosis are properties of organisms that generate an endless succession of unique genotypes, upon which natural selection and genetic drift exert the influences that mold the populations these genotypes comprise.

Morphologically, the fundamental units of life may be chromosomes. Each chromosome, we know, is linearly subdivided into local units of function called genes. The image of beads on a string, such as we see in an abacus or a lady's necklace, provides a sufficiently precise physical analogy for this discussion.

Since the chromosomes come in pairs, the genes also come in pairs. The genotype is the name for the set of all gene pairs on the total number of chromosome pairs in the karyotype of a species. By means of breeding analysis, each pair of genes, in principle at least, is distinguishable from every other pair; and the allelic alternatives are frequently, but not always, distinguishable from one another. The alleles of a gene pair are chosen from a set of alternative forms which seems to have no fixed number. For some genes, only two alternative forms have been distinguished, for others many have been recognized. A familiar example of multiple alternatives is the ABO blood system in man.

In a geometry that facilitates generalization, I shall represent each gene by a dimension in a multidimensional coordinate space, where the permissible values along each dimension are the allelic alternatives of the gene it represents. Each chromosome contains hundreds, possibly thousands, of genes. Hence the haploid chromosome complement of the gametes, called the genome, can be represented by a point in an n-dimensional space, where the letter n represents the total number of genes and is fairly large, say anywhere from 10,000 to 50,000 in man. Since the genotype results from the union of two independently formed gametic genomes, it can

be represented by a point which is the intersection of two n-dimensional genome spaces. Therefore, genotypically an individual is a single point in a hyperspace that defines the sample space of possible genotypes for a species.

Since the dimensions in the hyperspace are independently variable and their number is very large, the probability of any two genotypes having all the same coordinates and therefore occupying the same point in a sample space is infinitesimally small.

The population is the effective breeding unit of the species. It consists of all those members of a species that comprise a geographically and temporally continuous group, and among whom reproduction is possible. The members of a population can be represented by a distribution of points in the hyperspace of genotypes. The set of genotypes from one generation is replaced by a set of different genotypes the following generation. Consideration of the nature of the genotype has shown that, although a population consists of sets of substitutable and replenishable points, each point is unique and non-replicable. Therefore, the population can be represented over the generations by a cloud of ever-shifting points. We now realize that an understanding of the structure of heterogenic, biparental populations with the manifold multivalued dimensions of allelic variation that comprise their gene pools is of fundamental importance in the study of behavior. Since the lawful relations which make up the content of science are an expression of the structure of the events studied, the more intimate our knowledge of that structure becomes the clearer will be our ideas about what relations are possible.

Behavior has been defined as whatever an organism does that we choose to consider. Furthermore, the activities of an organism are lawful events—the lawful functioning in a specific environmental context of a biological system with a specific structure.

Szent-Györgyi and his associates isolated actin and myosin from muscle tissue. When they recombined these two chemicals in

the presence of adenosinetriphosphate and certain ions, the threads of the highly viscous actomyosin contracted before their eyes. "To see them contract for the first time and to have reproduced *in vitro* one of the oldest signs of life, motion, was perhaps the most thrilling moment of my life" said Szent-Györgyi (1963). He was observing the emergence of one element of behavior when the proper constellation of constituents had been arranged.

If we put organisms into the appropriate conditions, much about their behavior can be predicted from knowledge of their phylogeny, their genotype, and their ontogeny —most *Drosophila* seem to be negatively geotactic; by selective breeding, however, we have produced genotypes which show a predominantly positive geotaxis. The important point of the discussion by Schrödinger, cited above, is that lawful relations derived from one system cannot be expected to apply immediately to other systems of different structure. Genetics explains the simultaneous existence, within a species, of both similarities and differences in structure among individuals.

While it is true that we have some knowledge about the master plan of most organisms, it is also true that with respect to understanding how behavior occurs we have barely started to map the functional anatomy of any organism. Obtaining such a map is a very difficult task because the usual methods of physiology and biochemistry involve insult to the very systems under observation. An operated or drugged animal is a different organism from the one whose behavior we wish to understand.

Only the breeding techniques of genetics —selection, inbreeding, hybridization, and test-crossing—permit analysis of both the structure and the functioning of biological systems without insulting the integrity of the behaving organism to be observed. Genetic methods, however, involve the study of populations over several generations. Selection has been defined as the non-random differential reproduction of genotypes. This method, and the others, permit us to control the composition of populations. By selectively breeding among in-

dividuals rank-ordered on one or more dimensions of analysis, it is possible to effect drastic reorganizations at many levels of biological organization. Breeding methods, in fact, accomplish an elegant dissection of the total organism under study and a subsequent re-assembly of its component parts into an array of alternative organizations. Never before has the student of behavior had available a technique powerful enough to influence without insult every cell in the body of the behaving organism.

In Benson Ginsburg's well chosen words "Just as the parsing of a sentence gives us only a certain kind of understanding about it, so the analysis of some aspects of an organism into gene-controlled reactions tells a limited story, but it is a story that adds immeasurably to our understanding of living systems in their behavioral, as well as morphological and physiological, capacities" (1958). It is in this way that we can discover the natural units of biological organization. They are natural in the same sense that Ginsburg describes phenylketonuria in man as a natural entity. It is an abnormal allelic alternative to a gene-controlled link in a metabolic chain that has been produced by evolutionary selection pressure. Tyrosinosis and alkaptonuria are also genetic alternatives to the normal. They involve adjacent links in the same chain. Through these genetic deviations from what natural selection has produced as the norm, the chain and its links are being identified. A phenotype on which evolutionary selection could have acted as well as its substituent genotypes—especially those genotypes showing deviations from the norm, as in the examples just reviewed —constitutes what some of us mean by a natural analyzable entity. If such a phenotype and its genetic-metabolic correlates can be studied in a broad comparative series of taxonomically related organisms, its evolutionary history may also be elucidated. Several laboratories have been attempting to do this with the audiogenic seizure syndrome.

There are presently available to us two well known series of studies which illustrate how genetic analysis yields informa-

tion that can be obtained in no other way. The studies of the effects of domestication in the rat, which Richter reviewed, show that in the domesticated animals activity as measured in a revolving drum was mainly dependent upon gonadal secretion, whereas in the wild animals it was mainly dependent upon adrenal secretion. Apparently, the selective influences of domestication reorganized the endocrine balance, increasing gonadal output relative to adrenal output.

About a decade ago a team of psychologists and a biochemist began studying the chemical basis of learning (Rosenzweig et al., 1960). When they compared two reproductively isolated strains of rats, they found that the two strains differed behaviorally in their maze performance, and chemically in their cholinesterase concentration. They reported their finding of a correlation between the expression of these two traits, and then embarked upon an ambitious research program exploring many ramifications of this empirical relationship. Years later when the appropriate breeding controls were instituted, the chemical-behavior correlation broke down in the progeny of hybrids between the two strains.

It has taken a very long time for it to be appreciated that there is no surgical or biochemical substitute for proper breeding analysis. In genetic terms, the correlation between two traits can represent either the pleiotropic effects of an integrated genetic system or the accidental combination of two or more independent genetic systems. It is only the breeding of F_1 hybrids and their subsequent F_2 and backcross test crosses which affords us the chance, not the certainty, of distinguishing between these two alternative possibilities.

Quite recently I was consulted about a physiological study that was looking for a chemical-behavior correlation. When I pointed out that, even though a different behavior and a different biochemical were involved, the problem was analogous to the cholinesterase-maze–performance fiasco and must therefore remain inconclusive without appropriate breeding controls, my ad-

vice was met with the remonstration "But we haven't enough time or facilities for genetic experiments; we hadn't planned to study the *genetics* of this problem!"

Perhaps the phrase "the genetics of this problem" brings out a fundamental and widespread misconception. Its prevalence may be one of the reasons it has been so difficult for both behaviorists and biologists to talk sense about the relations between heredity and behavior. Many discussions of heredity and behavior have run afoul of the nature-nurture issue. They have been formulated in a causal frame of reference and, therefore, may have been misleading. It is a fallacy to ask the nature-nurture question for any behavior. The best we can do is to consider heritability, a concept which refers to the correlation between genotypic diversity and individual differences in behavior. Moreover, this correlation has no fixed value; for every behavior it must be measured in specific populations under specific conditions, because it varies with both.

At a conference the summer before last, when I objected to the phrase "the *genetics of* behavior," I was overwhelmed by Benson Ginsburg who was supported by Ernst Caspari and apparently by almost everyone else there. Those of you who followed the advance notices of this refresher course may have noticed that its title changed from "Genetics of behavior" in the summer or autumn issues of *Science* magazine to "Behavior genetics" in its recent issues. So it is clear that we teachers of this refresher course are, at best, only one step ahead of its students.

It might once have been useful to think in the causal frame of reference and it probably helped to establish genetics. Genetics is now well established and has a beautifully articulated body of knowledge. Furthermore, the broad features of the relations between heredity and behavior are rapidly becoming clear. What must next be more widely appreciated is that it is not a specialty to be relegated to a conceptual corner. As Sewall Wright observed some time ago, it is a fallacy to speak of physiological effects and genetic effects as

though they were two different classes of phenomena, because genes are the ultimate physiological agents.

Breeding experiments are the only methods we have available for varying the balance and composition of physiological systems. It is in this way that we can articulate and discover those properties and interactions which are neither immediately obvious nor easily revealed by surgical and biochemical methods alone.

Behavior Analysis and Biology

In closing, I should like to call to the attention of geneticists in particular and biologists in general that behavior might provide a most sensitive measure of organismic diversity. To quote an observation by Fuller and Thompson (1960) that I have cited many times ". . . two individuals of superficially similar phenotypes may be quite different genotypically and respond in completely different fashion when treated alike." As both Dobzhansky and Mayr might say: Fuller and Thompson's observation is incomprehensible to typological thinking and self-evident to population thinking.

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