free. The seat can be rocked by the observer's pressing a pedal.

A hollow nonshiny stainless-steel sphere, 4 inches in diameter, mounted on an adjustable rod, is positioned so that only its near and visible surface can be touched by the infant. Touching the sphere activates a capacitance relay, the sensitivity of which is adjusted by a variable frequency oscillator. Control equipment in an adjacent room operates a cumulative recorder, counters, and stimulus-producing elements, namely, a continuousmovie projector (3) and a closed-loop tape system (4). Images are projected on the crib screen; auditory stimuli come from a speaker located directly behind the screen. Stimuli presented either way can be controlled by the infant's responses to the sphere, by a clock, or manually by the operator. The durations of the movie, the sound, and the experimental conditions are controlled by timers (5). A variable resistance-capitance relay is included to make the inter-response interval adjustable from 50 msec to 5 sec. As we have used the apparatus, responses which are spaced in accordance with a predetermined interval (typically, 0.2 second) appear on a cumulative recorder, while counters accumulate all responses spaced more than 17 msec apart.

The infant's behavior is monitored in the control room by closed-circuit television (6) and earphones. The television camera is mounted on the ceiling on the crib, while a microphone over the infant's head transmits his vocalizations both to the operator and to a tape recorder. An intercom system connects observer and operator. The infant's behavior can be photographed from the television screen.

Most 4- to 6-month-old infants will perform in the apparatus for at least 8 minutes without fussing, a period of time comparable to that used by other investigators studying conditioning in human infants (7). Some preliminary work with older children, 2 to 5 years of age, suggests that the experimental period for this group may be extended to 20 minutes or longer. If the infant fusses, the observer rocks him, but if the infant cries, he is removed at once.

Mothers assist in placing their infants in the crib and then go to the control room to observe their infants on the television screen.

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currently under investigation. Sample performances are shown in the cumulative records of Fig. 2. In both cases, touching the sphere produced a motion picture of brightly colored geometric paper figures moving over a black velvet drum for 1.5 seconds.

A great variety of visual and auditory stimuli can be used, programmed as either reinforcing or discriminative. The projected images may be of things or people, known or strange, and such stimulus properties as complexity and novelty can be varied systematically. The effect of auditory reinforcement, alone or coupled with visual reinforcement, can be analyzed, while other manipulanda can be introduced to study response differentiation.

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9 January 1962

## **On "Reflexive Selection"**

Abstract. Some natural populations show an extremely high degree of polymorphism, especially in color and pattern, which may be interpreted as "protective variation." Two possible genetic models, one based on frequency-stat (like thermostat) and one based on higher selection value of heterozygotes, have been proposed to account for the phenomenon.

Moment (1) discusses the massive diversity in color and pattern in natural populations of certain species, as exemplified by that of brittlestar, Ophiopholis aculeata. Out of hundreds of individuals collected it is not possible to find two exactly alike. This is a very interesting but not uncommon phenom-

Table 1. Distribution of the 3025 possible  $B_{10}$  is for pattern, each with frequency 1/10. genotypes if  $A_1, \ldots, A_{10}$  is for color and  $B_1$ ,

	10 Genotypes .01 $A_1A_1$	45 Genotypes .02 $A_1A_2$
.01 B <sub>1</sub> B <sub>1</sub>	100 Genotypes (total freq., .01)	450 Genotypes (total freq., .09)
.02 B <sub>1</sub> B <sub>2</sub>	450 Genotypes (total freq., .09)	2025 Genotypes (total freq., .81)

enon. In fact, I venture to say it would be a common phenomenon if every trait were as conspicuous as color or pattern.

Moment observes: "Massive diversity of this kind is usually dismissed as the result of the free play of meaningless mutation in the absence of selection on the assumption that the colors and patterns have a selection value of approximately zero." In this connection I wish to add that since publication of the statement of E. B. Ford in 1953, evidence has begun to accumulate indicating that even the most unsuspected "neutral" genes of long standing (for example, the ABO locus in man) may have selective effects, although the precise nature of these effects remains obscure. The recent thinking of most geneticists is that diversity of such a magnitude is maintained by some kind of balanced or stabilizing selection scheme, rather than by the free play of mutation in the absence of selection. (The latter case would lead to biological chaos.) Hence, I agree with Moment that we should view the diversity in terms of selection.

As to the scheme of selection, Moment suggests: "In the case of massive variation the possibility presents itself that it is the variation as such which is adaptive, giving a measure of protection against predators. . . . The term reflexive selection suggests itself because it is the variation per se which is adaptive, and the frequency of any one type is determined by a feedback relationship with all the other types." The suggestion is quite reasonable as far as it goes, but it seems to me that it does not go far enough. It does not say anything about the mode of inheritance of color and pattern, the system upon which selection operates. All I wish to do in this note is to add a few speculative remarks to complete the story and to stimulate experimental investigation on this subject.

The idea of feedback relationship suggested by Moment is probably not different from the familiar model based on the view that the selective value of a genotype (or phenotype) is determined by its frequency in the population. It is known that stable equilibrium may be achieved if a genotype enjoys selective advantage when it is rare and selective disadvantage when it is abundant. Let me illustrate. Consider a series of multiple alleles A<sub>1</sub>, A<sub>2</sub>, A<sub>3</sub>, . . . with frequencies  $p_1$ ,  $p_2$ ,  $p_3$ , . . . where the sum of the p's is unity. In the simplest case-where the selective value of A<sub>1</sub>A<sub>1</sub> is  $1 - cp_1^2$ , that of A<sub>1</sub>A<sub>2</sub> is  $1 - cp_1^2$  $cp_1p_2$ , and so on—the stable equilibrium condition under panmixia is reached when  $p_1 = p_2 = p_3 = \ldots$ . If there are ten alleles, each will have a frequency of 1/10 in the population. The genotypic array of the population under random mating will then be  $(.1 A_1 +$  $.1 A_2 + ... + .1 A_{10})^2 = .01 A_1 A_1 +$  $\ldots$  + .02 A<sub>1</sub>A<sub>2</sub> +  $\ldots$  There are ten homozygous genotypes with a total frequency of .10 and 45 heterozygous genotypes with a total frequency of .90. The "feedback" model described is, however, not the only one that can maintain such a diversity. If all homo-

maintain such a diversity. If all homozygotes have the same (constant) selection value and all heterozygotes also have the same, but a superior, selection value, the same stable equilibrium condition will be reached. More generally, if we take the selection value of all heterozygotes to be unity and that of homozygotes  $A_1A_1$  to be  $1 - s_1$ , and so on, then the equilibrium condition is  $s_1p_1 = s_2p_2 = s_3p_3 = \ldots$  In other words, the equilibrium frequency of allele  $A_1$  ( $i = 1, 2, \ldots, 10$ , say) is:

$$p_i = \left(\frac{1}{s_i}\right) \left| \sum \left(\frac{1}{s_i}\right) \right|$$

This equilibrium will maintain the same kind of massive diversity as the feedback model. The mere fact of diversity does not discriminate one model from the other. Moment says that it does not seem to be balancing selection where heterozygotes are superior (in selection value) to homozygotes. We really have no way of telling at this stage of our knowledge.

Whatever the actual selection scheme, the diversity in color and pattern may be accounted for by postulating multiple alleles controlling them. If  $A_1, \ldots, A_{10}$  is for color and  $B_1, \ldots, B_{10}$  is for pattern, each with frequency 1/10, the distribution of the 3025 possible genotypes would be as shown in Table 1. Under these circumstances, we would

e ten tion," if indeed such things exist. Until fregous like to add several brief comments. Al-.90. though it may be true, as Li suggests, d is, that semicryptic genetic variation is a very common phenomenon among animals, protective variation most certainly is not. My own observations and

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mals, protective variation most certainly is not. My own observations and surveys of the literature as well as correspondence received since the publication of my report in *Science* indicate that protective variation has a frequency among animal species of about the same order of magnitude as the frequency of mimicry.

hardly expect to find two individuals

exactly alike in a sample of a few hun-

dred. The nature of the selection scheme

is admittedly very difficult to ascertain

under experimental conditions, but I

hope some breeding work may be done

to see if essentially multiple alleles or

multiple loci are responsible for the

diversity in color and pattern reported

Reference and Note

 G. Moment, Science 136, 262 (1962).
 This paper is dedicated to Professor L. C. Dunn in recognition of his long and distinguished contribution to the science of genetics.

Li is entirely right in emphasizing the

need for further data concerning "pro-

tective variation" and "reflexive selec-

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by Moment (2).

One correspondent pointed out that the essential concept of protective variation is found in a little book on evolution by P. M. Sheppard (London, 1958). It is, I have found, mentioned there briefly in connection with variation in a European land snail, only to be quickly dismissed in favor of orthodox protective coloration. Happily, this author does suggest that the idea itself is worthy of investigation.

Several correspondents have asked why protective variation should be limited to massive variation. I see no reason why it should be. It is even conceivable that the melanistic phase of the eastern squirrel derives some advantage from this difference from the common form, but I have no evidence that this is so.

In connection with the evidence since 1953 that genetic polymorphism has a basis in selection, it should be remembered that in the best understood cases the "balancing selection" is due either to a fixed advantage of the heterozygote, as in sickle-cell anemia, or to a changing environment, as in *Adalia*. This is rather different from the kind of feedback implied by the term *reflexive* selection, where the selective value of a gene is either positive or negative depending on the relation between its frequency and the frequency of other genes.

The mathematical model offered for reflexive selection should be useful. It ought to be possible to test the applicability of the nonfeedback model because it assumes a stable diversity already in existence which does not change, while the proposed theory of protective variation assumes that any mutation producing a new pattern would enter the system with a selective advantage which would decline as the frequency of the responsible gene increased. Furthermore, the nonfeedback model assumes fixed selection values for homozygotes, lower than values for heterozygotes, while the proposed theory implies that the selection values of genes will fluctuate inversely with respect to frequency and regardless of whether the pattern in question is homozygous or heterozygous.

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## Radiation-Induced Chromosomal Aberrations and Lethals in Aspergillus nidulans

Abstract: The frequency of translocations induced in diploid conidia of Aspergillus nidulans by gamma rays was much higher than that of recessive mutants involving a single chromosome. More than half of the surviving nuclei contained viable translocations at radiation doses within the range normally employed for induction of mutants in microorganisms.

Uninucleate conidia from a diploid strain of the normally haploid ascomycete Aspergillus nidulans, in which each pair of the eight linkage groups was genetically marked, were irradiated with cobalt-60 gamma rays. The doses ranged from 30 to 50 kr and resulted in survival frequencies of approximately 10 percent to 1 percent. Normal appearing strains grown from the survivors were tested for translocations, recessive lethals, and recessive nutritional mutants. A method based on mitotic recombination was used for the detection of these mutations. It makes