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C. H. Waddington

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NOTES AND COMMENTS

THE "BALDWIN EFFECT," "GENETIC ASSIMILATION" AND "HOMEOSTASIS"

C. H. WADDINGTON

Edinburgh, Scotland

When preparing my article on "Genetic Assimilation of an Acquired Character,"¹ I debated with myself whether to include a discussion of the old train of thought usually referred to as "organic selection," but in the interests of brevity decided not to. However, the immediately preceding article by Simpson on "The Baldwin Effect"² dealt with just this subject, and it would now perhaps be useful to indicate the way in which the idea which I was putting forward differs from those which he recapitulated.

Simpson describes the Baldwin Effect as taking place in three stages, which put very shortly are: (1) Individual organisms interact with the environment in such a way as to produce non-hereditary adaptations; (2) Genetic factors producing similar traits occur in the population; (3) These factors increase in frequency under natural selection. The gap in the argument is between steps (1) and (2). Is there supposed to be any connection between the developmental adaptations and the genes with similar effect, and if so, what? Simpson (p. 115) says that either there is no particular connection, in which case the theory signifies very little, or the connection must be by way of a neo-Lamarckian causal connection. Huxley (*Evolution: The Modern Synthesis*, 1942, p. 304) seems to put the point originally made by Baldwin and Lloyd Morgan more clearly when he writes that the adaptive modifications operate "by holding the strain in an environment where mutations tending in the same direction will be selected." Thus according to both Simpson and Huxley, the theory of "organic selection" still leaves the actual nature of the adaptive changes produced to the operation of random mutations or Lamarckism.

The theory which I put forward in 1942, in an article which Simpson seems to have overlooked³ (*Nature*, Vol. 150, p. 563), and which

provided the basis for the experiments described in my *Evolution* paper, attempted to go considerably further. I argued that natural selection for the ability to produce an adaptive phenotype would change the genotypes in such a way as to encourage the appearance of genetically controlled variants mimicking the adaptive type. The initial non-hereditary response therefore does not merely allow the organism to persist in a new environment and become adapted to it; it enables natural selection to set the stage in such a way that the useful genetic effect is likely to occur.

Simpson comes to the conclusion that the Baldwin effect, in the sense he describes it, has probably played a rather small role in evolution. The genetic assimilation mechanism, however, must be a factor in all natural selection, since the properties with which that process is concerned are always phenotypic; properties, that is, which are the products of genotypes interacting with environments. By speaking of mutations as "random," which is true enough at the level of the gene as a protein-DNA complex, we obscure the fact that the effect of a mutation, as far as natural selection is concerned, is conditioned by the way it modifies the reaction with the environment of a genotype which has already been selected on the basis of its response to that environment. This is not neo-Lamarckism, but it is a point which has been unduly neglected by neo-Darwinism.

The idea of the "canalization" or "buffering" of development (Waddington, 1939, 1940), which underlies the theory of genetic assimilation, is also closely related to the concept of homeostasis, which has recently been introduced in genetical theory. This word has been used in two senses, which should be distinguished. Lerner (1950) has applied it in connection with the tendency of the gene frequencies in a population, after disturbance by artificial selection, to return, under the influence of natural selection, to an equilibrium state. This may be called "homeostasis of gene ratios" or "genetic homeostasis." The aspect of natural selection concerned in maintaining it is what I have called "normalising selection" (Waddington, 1953). Dobzhansky and Wallace (1953) use the term in quite a different connection; an organism is said to be homeostatic when it "adjusts itself to recurrent environmental changes in such a

¹ *Evolution*, Vol. VII, No. 2, p. 118.

² *Ibid.*, p. 110.

³ Schmalhausen in his "Factors of Evolution," 1947, meant, I think, either nearly or quite the same thing, but seems to confuse the "normalising" action of selection, which keeps a population uniform, with its "stabilising" action, which renders development relatively independent of environmental variations.

way that its function continues unimpaired." This might perhaps be called "developmental homeostasis." But the word homeostasis is perhaps an unfortunate one, since it seems to imply a stationary state, whereas development essentially involves change in time. It is for this reason that I have preferred the words canalization or buffering, which refer to an equilibrium sequence of states rather than to one unchanging equilibrium state. For the aspect of natural selection concerned with setting up such buffered developmental systems, I have recently (1953) used the term "stabilising selection," which was introduced by Schmalhausen (1949) who, however, does not clearly distinguish it from normalising selection. But again this is perhaps not a very satisfactory expression, since the stabilisation of development would seem to

imply that change had been brought to a standstill. Probably the best expression would be "canalizing selection," derived from the word used in the original discussion of the concept.

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COMMENTS ON THE ORIGIN OF SEX AND OF MEIOSIS

EDWARD O. DODSON

Dept. of Biology, Univ. of Notre Dame

Boyden's (1953) paper on comparative evolution was most stimulating. His discussion of the origin of sexual reproduction is noteworthy for the emphasis upon the thesis that parthenogenesis is a modified form of sexual reproduction. He envisions the origin of sexual reproduction in terms of the origin of meiosis, but no theory is presented as to how or why meiosis originated beyond that it must have been a far simpler transformation than the previous development of mitosis. It is the purpose of the present note to add some further thoughts upon these problems.

As Boyden points out, terms like haploid and diploid have no meaning in relation to organisms at the pre-mitotic level of organization. The ability of bacteria to reproduce by simple fission, without any orderly alignment and segregation of the chromatin, indicates that the relatively few kinds of genes which they possess are probably all duplicated several times and scattered at random through the cell, so that both daughter cells are almost certain to contain genes of every kind. These might be called *multigenes*. But once the mitotic mechanism was established, haploidy must have been the norm for mitotically reproducing organisms. This is indicated by the lack of logical meaning of diploidy for an asexual organism (polyploidy would seem more reasonable for organisms derived from precursors with multigenes); by the frequency of odd numbers of chromosomes among asexually reproducing algae and Protozoa; and by certain facts relative to sexual re-

production in the algae, to be recounted below.

It is difficult to visualize why successful asexual organisms should ever have united pairwise to reproduce sexually. Because gametes of many algae appear to be simply small sized spores, the hunger theory of sex has been proposed, according to which the gametes are so small that, individually, they lack the minimum nutritive requirements for successful development; and these subminimal cells pool their resources by means of two-by-two fusions. The theory would be more satisfying were it not that the first divisions of a zygote are the two meiotic divisions, producing a group of four zoospores which successfully develop to maturity, in spite of their small initial size. Coulter (1914) examined and rejected this theory nearly forty years ago, but in its stead he was only able to suggest that sexuality was associated with metabolic products of a waning metabolism, somehow associated with the reduction divisions. He arrayed an impressive argument, but the key substances remained hypothetical. So we are left with no satisfactory explanation of the origin of sex, but once it did originate, great selective value made it nearly universal. Its selective value lies chiefly in the rapid re-shuffling of character combinations, which submits a maximum number of phenotypes to the test of natural selection in a brief time. Thus new adaptive combinations are more likely to be hit upon than with asexual reproduction.

The origin of meiosis is perhaps a simpler problem than the origin of sex. We have clues