Natural Selection and Blending Inheritance

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ABSTRACT: Blending inheritance, if it existed, would allow a normal evolutionary response to natural selection.

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Darwin (1859) was ignorant of the true nature of inheritance, as he took frequent pains to acknowledge. Yet the mechanism of natural selection is intimately involved with the mechanism of inheritance. Although Darwin was later to propose a particulate theory of inheritance, namely pangenesis, it appears from various references that in general he implicitly subscribed to the prevalent idea of blending inheritance. In The Genetical Theory of Natural Selection, Fisher (1930) argued that the original formulation of the theory of natural selection was not merely incomplete or in factual error, but was internally inconsistent and therefore seriously flawed. According to Fisher, natural selection is impossible with blending inheritance, and thus would not occur under Darwin's implicit assumptions. It is my aim here to demonstrate that Darwin's theory was consistent and Fisher was incorrect; that although the hypothesis of blending inheritance is factually wrong, it is in no way incompatable with Darwinian evolution through natural selection.

Fisher showed that blending inheritance, under random mating, would reduce the genetic variance of any continuous trait by half in each generation. He argued that natural selection would be rendered ineffective by such dilution, since there would soon be very little variance on which selection could act, and because any progress made would be likewise successively halved. Fisher's main point is that blending inheritance, under random mating, would quickly reduce a population to a uniform genetic constitution. Very soon the only genetic variance on which natural selection could act would be that due to immediate or very recent mutation. Much depends, however, on the amount of mutational variance one is willing to posit.

Under the (factually incorrect) hypothesis of blending inheritance, the genetic constitution of each individual is exactly the mean of its two parents (the "midparent mean"), plus any deviation from that mean due to new mutation. Any genetic difference between siblings, then, can be due only to mutation arising in that generation. The key difficulty with blending inheritance is the rapid halving of the genetic variance inherited from previous generations. Since it can be shown that the variance of midparent means is half the total variance of the parental generation, the genetic variance is halved in each generation except for the input of new mutation. If the genetic variance of the parental generation is given by V_o, and the genetic variance of the offspring generation is given by V_1, this relationship is stated as follows:

$$V_1 = \frac{V_o}{2} + V_m, \qquad (1)$$

where V_m is the genetic variance due to new mutation.

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Evolutionary Theory 7: 41-43 (May, 1984)
The editors thank R. Lande and W. Wimsatt for help in evaluating this paper.

Similarly, in the absence of natural selection,

$$V_2 = V_m + \frac{V_1}{2} = V_m + \frac{V_m}{2} + \frac{V_o}{4} \qquad (2)$$

and ultimately, at generation k,

$$V_k = \frac{V_m}{1 + \frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \ldots}, \qquad (3)$$

where the infinite series converges on 2, and the genetic variance at equilibrium is

$$V_e = 2V_m . \qquad (4)$$

In other words, the equilibrium genetic variance is equal to twice the genetic variance of new mutation introduced in each generation. This relationship can also be derived directly from (1) by setting $V_e = V_1 = V_o$. A plausible amount of genetic variation requires much higher rate of mutation than one finds in reality, but this is consistent with Darwin's understanding of variation: he incorrectly attributed to spontaneous variation (i.e., to mutation) the observable fluctuations that we know now are due to recombination. Again, my objective is to show not that Darwin's facts were correct, but that his theories were consistent; in Darwin's formulation, spontaneous heritable variation was an observable fact, although he was unable to make the distinction between recombination and true mutation. (Nor is the distinction so clear as we would like to believe. It is seldom possible to distinguish between novelty arising by recombination and novelty arising by mutation in practice, and it is probably never possible with polygenic effects. The distinction between mutation and recombination is blurred in the evolutionarily important process of unequal crossing over). In fact, as I will show, the distinction scarcely matters as far as it affects the efficacy of natural selection in the short run. In the long run it does matter, but here, surprisingly enough, blending inheritance is the more efficacious.

With blending inheritance, the expected phenotype of the offspring is equal to the midparent mean (that is, to the average of the two parental phenotypes), providing that the additional assumption is made that mutational variation is symmetrical around this expectation. Thus the variation around the expected value would have a mean of zero and a variance of V_m, or half the total genetic variance. By comparison, with additive polygenic traits in randomly mating Mendelian populations the expected phenotype of the offspring is also equal to the midparent mean, and variation around this expected value is also symmetrical, with a variance of half the total genetic variance. The expected progress of the population mean in one generation of directional selection is the same in both cases.

Thus the genetic variance within sibships is half the total genetic variance both with blending inheritance and with additive polygenic inheritance, so there is no distinction between hypotheses in this respect. Likewise, the between-sibship variance is half the total variance both with polygenic inheritance and blending inheritance, given random mating in both instances.

For a given level of genetic variance, the initial response to natural selection under blending inheritance is the same as with additive polygenic inheritance. In both cases, of course, nongenetic phenotypic variation can reduce the heritability of a trait in proportion to its occurrence. Additive polygenic inheritance converges on the hypothetical regimen of blending inheritance as the number of independently segregating loci becomes infinite and the effect of each locus becomes infinitesimal.

For long-term evolutionary change, both additive polygenic inheritance and blending inheritance depend on the input of new mutation -- not merely genetic recombination. Without new mutation, additive polygenic variance is ultimately depleted by directional selection; the long-term rate of progress is dependent on the mutational input. For a given amount of genetic variation in an initial equlibrium population, which for blending inheritance requires a large mutation rate, blending inheritance would actually allow much greater rates of sustained evolutionary change than are observed with polygenic inheritance.

Evolution requires genetic variation, mutation, and differential reproduction. It does not require particulate inheritance. The principle of natural selection is sufficiently robust that it works quite well in populations with Mendelian biparental reproduction, in asexual populations with clonal rather than particulate inheritance, and in hypothetical schemes of biparental reproduction with blending inheritance.

Literature cited

Darwin, C. 1859. _On the origin of species by means of natural selection_. London: John Murray.

Fisher, R.A. 1930. _The Genetical Theory of Natural Selection_. pages 1-27. London: Oxford University Press.

Editorial comment:

Lande, in his favorable review, interprets Fisher differently. He also says that "King's conclusion ... that 'blending inheritance would actually allow much greater rates of sustained evolutionary change than are observed with polygenic inheritance' (assuming that the same amount of heritable variation is maintained in both schemes without selection) is valid only for (finite) populations under intense directional selection, such that most mutations in the selected direction are eventually fixed. With blending or particulate inheritance a population should be equally capable of tracking a slowly moving optimum phenotype." We do not, of course, know what King's response would have been.