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HALDANE AND WADDINGTON: EVOLUTIONARY GENETICS AND EPIGENETICS

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As a disciple of J B S Haldane, I grew up in the classical theory of population genetics, the neo-Darwinian theory, as it came to be called later on. It has been customary to see evolution by gradual steps in terms of Mendelian genetics, especially in terms of natural selection which, as Haldane showed, results in altered gene frequencies in due course. However, in later years, Haldane himself pointed out the limits of the classical theory which proved inadequate to account for the evolutionary process that has already occurred. This set the stage for Waddington's proposal of the concept of epigenetic landscape, a metaphor for how genetic regulation modulates development. Waddington found that one effect of mutation (which could modulate the epigenetic landscape) was to affect how cells differentiated. He also showed how mutation could affect the landscape, and used this metaphor in his discussions on evolution which mainly occurred through mutations that affected developmental anatomy. It had been suggested that epigenetic inheritance in the germ line might introduce the possibility that environmental influences which induce phenotypic changes could become heritable. There are now many well documented examples of transgenerational effects, presumed to have an epigenetic basis. It is well established that DNA methylation is involved in genomic imprinting, but the biological reasons for the existence of imprinting remain uncertain. An important challenge for the future is to understand the specificity of genomic re-programming when the germ cells and fertilized egg are formed.

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