

SHORT COMMUNICATIONS

Wing-Folding in *Drosophila*

Asymmetries in any organism are of interest for the light that they may throw upon human brain asymmetries (M. C. Corballis & M. J. Morgan, *Behav. Brain Sciences*, 1, 261-269, 1978) particularly since no adequate example has ever been described of an asymmetry being inherited according to a simple Mendelian mechanism. Purnell & Thompson (*Hereditas*, 31, 40-45, 1973) concluded that it was possible to select for wing-folding in a wild strain of *Drosophila melanogaster*, at least for a number of generations, for either of the two possible phenotypes (right wing over left wing, R/L, or left wing over right wing, L/R).

It is clearly of little use to try selecting for one of two phenotypes if those phenotypes are themselves unstable in time. Purnell & Thompson tested for consistency of wing-folding by examining 20 individuals on 10 separate occasions and finding that 'each individual fly did show a strong tendency to close the same wing first each time'; detailed statistics were not however given. As a preliminary to an attempt to replicate the selection experiment of Purnell & Thompson we looked at the consistency of wing-folding, and, having found no evidence of consistency, did not continue with the experiment proper.

Specimens of *Drosophila melanogaster* (white-eyed and wild-type) were obtained from a commercial animal suppliers (T. Gerrard, Sussex), and kept in bottles containing 'Blue Formula 4.24' culture medium. Virgin flies were collected within 16 h of eclosion and the flies etherized. Flies were kept individually in 50 × 12 mm culture tubes. Wing-folding was assessed with the unanaesthetized flies placed in their individual culture tubes on the stage of a low-power binocular microscope, lighting being laterally from above, and at an almost glancing angle. Each fly was assessed in this way on at least five separate occasions at intervals of at least 24 h. Some of the flies were then assessed whilst etherized, ether vapour being injected into the culture tube through the cotton wool plug by means of a hypodermic syringe. After assessment air was injected into the tube in order to dispel the ether vapour.

One hundred and forty individual flies were examined. Ninety-seven survived sufficiently long to be assessed on five distinct occasions whilst unanaesthetized. Table 1 shows that the vast majority (92/97) showed some inconsistency in wing-folding, and that the distribution was indistinguishable from a binomial distribution with $p(L/R) = 0.5$. Forty flies were tested while etherized, and of these 33 survived for five successive assessments. The

table shows that the majority of flies (27/33) were inconsistent and that the distribution was indistinguishable from a binomial with $p(L/R) = 0.5$.

The 33 flies tested whilst etherized had also been tested earlier whilst unanaesthetized; the correlation between the number of times a fly folded L/R whilst unanaesthetized and the number of times the same fly folded L/R whilst etherized was only 0.187, which is not significantly different from chance ($n = 33$).

Thirty-seven flies were also assessed for wing-folding whilst unanaesthetized and then immediately etherized and re-assessed. Only 22 (59.5%) flies showed the same pattern of wing-folding as they had done two or three minutes earlier when unanaesthetized ($\chi^2 = 1.32, 1 \text{ df}$, NS).

There is thus no evidence from the present analysis for consistency of wing-folding in *D. melanogaster*, and so this report is consonant with the report of Perelle et al. (*Anim. Behav.*, 27, 622-623, 1979) of a lack of lateral consistency in other behaviours in *Drosophila*. Given a lack of consistency it is difficult to see how selection for wing-folding type could be effective. A possible explanation of the apparent selection found by Purnell & Thompson is that their statistical analysis may be in error. Consider their Table 2: for L/R bias there is a correlation of 0.962, significant at the 0.01 level, between generation number and proportion of L/R flies. However, the decision to analyse only generations 0-4 out of the 15 possible generations is clearly ad hoc. It is therefore artificially selecting only one out of 12 possible consecutive groups of five from fifteen (e.g. 1-5, 2-6, etc.). Moreover it is apparent that the decision to analyse five successive generations was also ad hoc, for in the R/L analysis, eight successive generations were analysed. Under such conditions the significance level quoted is seriously over-estimated since contrasts are a posteriori rather than a priori. This problem is compounded by the impossibility of re-constructing the data set in order to re-analyse it, since there is no indication of the number of flies assessed in order to plot each of the points on their Fig. 1. The hypothesized selection for R/L bias is of the order of 8% over 8 generations, i.e. 1% per generation. To detect such a difference between one generation and the next would require at least 1000 progeny per generation in order to produce a statistically significant difference between successive generations. This conclusion is supported by the failure of Ehrman et al. (*Genet. Res.*, 32, 231-238, 1978) to replicate the selection experiment.

Table 1. The Number of Times out of Five Trials that Each Fly was Observed to Fold Its Wings Left Over Right. (Expected Values under a Chance (Binomial) Hypothesis are shown beneath the Observed Values)

	No. of L/R foldings out of 5					
	0	1	2	3	4	5
Unanaesthetized flies ($N = 97$)						
Observed	2	17	27	35	13	3
Expected	3.0	15.1	30.3	30.3	15.1	3.0
$\chi^2 = 1.96$ (NS)						
Etherized flies ($N = 33$)						
Observed	3	4	9	9	5	3
Expected	1.0	5.1	10.3	10.3	5.1	1.0
$\chi^2 = 0.51$ (NS)						

Wing-folding laterality in *Drosophila* is neither consistent nor heritable.

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I. C. McMANUS

Department of Psychology,
Bedford College,
Regent's Park,
London N.W.1, and

Department of Psychiatry,
St. Mary's Hospital,
Harrow Road,
London, W9 3RL.

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Heritability and the Paradox of Genetic Variation: A Reply to McManus

Successful selection for an asymmetrical bias is difficult, but not impossible (e.g. Reeve 1960; Beardmore 1965). There are many reasons for this, the most important probably being that in bilaterally organized systems, the requisite genetic variation for a breakdown, or specialization, of symmetry is not present in large amounts. Only in unusual instances can one identify polygenic segregation that influences the expression of symmetry. Seven years ago, Purnell & Thompson (1973) reported such an instance.

In our study, both the left over right and the right over left selection lines for wing-folding in *Drosophila melanogaster* responded to selection; but, after a 6-10% bias had been achieved, the accumulated response was lost in each line. While the lines were responding, the sexes alternated in high asymmetry values each generation, a pattern typical of sex-linkage. We pointed out, however, that this example was an unusual one when we repeated these experiments in the context of a more general study of laterality (Ehrman et al. 1978). In analysing wing-folding, maze behaviour and courtship patterns, we found that some individuals can be left or right dominant, but most individuals are ambidextrous. Changes in the population would not be expected, since each experimental group, as a whole, showed no lateral preference and laterality does not appear to be a factor in courtship success. Thus, genetic variation for laterality, if present, must be slight. The present critique (McManus 1981) adds little of substance to our own discussion of our experiments.

The experiment reported by McManus (1981) is, however, valuable in another way. It illustrates the experimental pitfalls of what one might call the 'variation paradox' in quantitative genetics. Consistency requires variation.

This can probably best be explained in the following way. 'Heritability' is defined, in one sense, as the proportion of phenotypic variation that is due to genetic segregation ($h^2 = V_G/(V_G + V_E)$), where V_G is the genetic component of variation and V_E is all other sources, including random accident or behavioural intention (Falconer 1960). Consistency in left or right bias is expected to be traceable to genetic differences among individuals in some morphological or physiological trait expressing itself in terms of wing-folding.

Consistency of expression cannot be expected if the only variation is random and environmental in origin, and heritability is zero. For the same reasons, one cannot expect a response to selection if genetic variability is absent. Standard laboratory strains, such as those used by McManus, are typically homogeneous in genetic background, owing to unavoidable inbreeding and natural selection within the confines of the laboratory environment. Even selection on a highly plastic trait, such as bristle number, will fail if proper precautions are not taken to ensure that there is a wide range of segregating polygenic variation. Quantitative geneticists do this by using newly-caught wild-type strains or by inter-mating a number of such strains before beginning selection. This normal precaution was not taken by McManus. It is, therefore, not surprising that his search for phenotypic consistency failed, given the fact that after surveying a broad sample of genetic backgrounds we concluded that modifiers of symmetry were rare, if they exist, in a population (Purnell & Thompson 1973; Ehrman et al. 1978).

The second criticism was aimed at our choice of statistical analysis. A selection response is a pattern that has many pieces of information embedded in it (Falconer 1960). As I pointed out above, the first few generations of both selection lines consistently had two things in common: a positive increase in the phenotype being selected, and the alternating expression typical of sex-linkage. In both lines, when a certain degree of change had been reached, both of these were lost. This is precisely what would be expected if natural selection were acting to counter artificial selection and maintain symmetry in a homeostatic balance. As with the description of plateaued responses, accelerated responses, and many other components of a selection pattern, we simply used the regression analysis to compare these similar segments.

There are other points of misunderstanding, such as the statement that we failed to provide information about the number of individuals used to plot selection responses, though this is given in the methods section (Purnell & Thompson 1973, page 402). The main point remains one of experimental design. Evolution of a behavioural character requires that significant genetic variation is segregating and that random environmental effects can be controlled. In the case of asymmetrical bias, it is clear that genetic variation is rare. Yet any examples should help us better understand the complexities of the genetic basis of such behavioural flexibility.

JAMES N. THOMPSON, JR.

Department of Zoology,
University of Oklahoma,
Norman,
Oklahoma 73019,
U.S.A.

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