since, when the bat was at rest, the membrane was so drawn up into itself that there appeared only very little tail membrane; at least, there was nothing to compare with the tail membranes of other insectivorous bats. (In noninsectivorous bats, such as the fruit eaters and the nectar and blood feeders, there is only a very short tail and almost no tail membrane.)

The early morning dive of the bats into the cave was observed and photographed by a different method. The camera was located on the surface near the edge and flashed at random with a focal distance setting of about 4 meters at $f/4.5$ and 1/60 of a second exposure, an electronic flash (Heiland with 1500 BCPS) being used.

One Kodachrome slide showed seven bats silhouetted against the early morning sky. The cover picture is an enlargement showing the position of the wings in the power dive into the cave. The wings made a characteristic fluttering sound, which we believe is caused by the air action as the bat exceeds his normal flying speed. A blur against the light of the sky shows the motion in the 1/60 second shutter time. If the bat is 10 cm in length, head to tail, the blur caused by motion during 1/60 of a second from this photo is 25 cm. The velocity of the diving bat is 1500 cm/sec, as estimated very roughly from the above-mentioned blur.

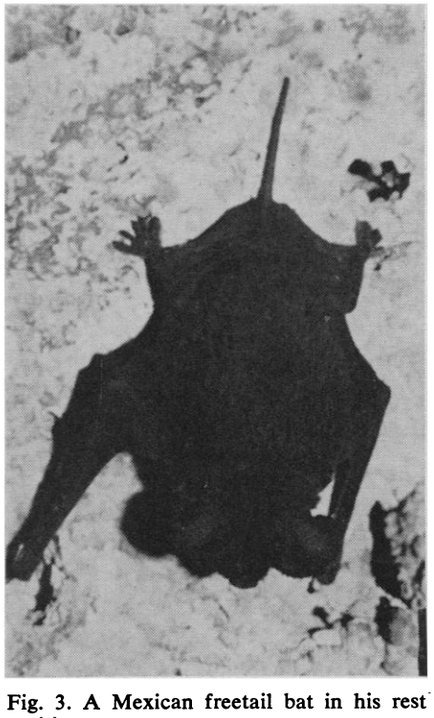

Fig. 3. A Mexican freetail bat in his rest position.

The photographic blur of the wings against the sky indicates that the bat does not flutter his wings in a normal manner, but uses them in a half-folded position as air brakes to limit his velocity during the dive.

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References

1. J. K. Baker and P. F. Spangle, *Southwest. Nat.* **7**, 76 (1962).
2. F. A. Webster and D. R. Griffin, *Animal Behavior* **10**, 332 (1962); F. Webster, *Proc. Int. Congr. Technol. Blindness* **I**, New York, 1963; J. J. G. McCue, *Nat. Geogr. Mag.* **119**, 571 (1961).

18 April 1966

Mating Speed in Male *Drosophila melanogaster*: A Psychogenetic Analysis

Abstract. *A diallel analysis of mating speed as measured by the copulation frequency of male* Drosophila melanogaster *revealed strong directional dominance for high frequency involving a minimum of five genes. The trait as measured is highly correlated with sexual drive and fitness. Consequences for artificial selection and the nature of the heterosis displayed by the crosses are discussed. High copulation frequency of the male is probably the result of unidirectional natural selection.*

Mating speed in *Drosophila melanogaster*, measured in both sexes simultaneously, has been subject to artificial selection by Manning (*1*), thus demonstrating that genetic variation exists for this trait. Parsons, following recent trends in behavioral biometrical genetics (*2*), has partitioned this variation and calculated heritabilities (*3*).

However, mating speed measured in both sexes at once relates to the behavioral interaction of a particular pair of genotypes only, and generalization to other possible genotypic combinations, such as would certainly arise in natural populations, is consequently dubious. This report is concerned, therefore, with mating speed in males only, measured against a broad range of female genotypes. Mating speed was taken as the number of successive copulations accomplished by a male during a 12-hour period, and not the time to first mating, as previously used. These variations allowed a more extensive observation of behavior and a simple and valid method of scoring to be devised.

In the first experiment each 36-hour-old male fly was placed in a tube containing six virgin females. The females were chosen one from each of six available inbred lines to provide a heterogeneous, but standard, test situation for the males. The tubes were set in a rack and observed every half minute during the first 30 minutes, and thereafter every 2 minutes, to detect further copulations. Observation was carried out at 25°C for 12 hours, after which time each female was placed, singly, in a fresh tube, and scored for the yield of progeny produced during 8 days. In this experiment four measures were therefore obtained for each male—time to first copulation, number of copulations, number of copulations resulting in fertilization, and the total number of progeny he produced. The sixty males tested were obtained from the same six inbred lines as the females and also from a sample of six F_1 crosses made from these lines, five males being taken from each of these twelve genotypes. The 12 male genotypes and their average scores on the four measures are given in Table 1.

Table 1 shows that there were few repeat matings between males and particular females, since the number of copulations that occurred resulted in almost as many individual fertilized females (mean discrepancy = 0.7).

The product-moment intercorrelations of measures, presented at the foot of Table 1, indicate that males which mate fast on the first occasion also copulate more often, more successfully, and leave more progeny. The four measures thus appear as aspects of a general characteristic of male mating behavior. The intercorrelations further suggest the number of copulations resulting in fertilization as a convenient method of measuring mating speed, since, with $r = 0.96$, the two measures are practically interchangeable. This proposal has the advantage that it avoids constant observation during the 12-hour period of mating. This method was used in the second experiment involving the genetic analysis of a diallel set of crosses.

The necessary subjects for the diallel analysis were provided by crossing the six inbred lines of the first experiment in all 36 possible ways, thus producing 36 families, six of which were the original lines and the remaining 30 the 15 F_1 crosses and their reciprocals. Five males from each family were tested, singly, each with six females, exactly as before, and the number of females fertilized during 12 hours was recorded. Individual scores, which could thus vary between 0 and 6, were averaged for each family and arranged in a 6×6 table. Two weeks later the diallel table was replicated with the outcome shown in Table 2.

Table 1. Mean scores for 12 male genotypes and intercorrelations*. (Each mean is based on five individual males.)

Genotype of males	(Item 1)* Time to first copulation (min)†	(Item 2)* Observed number of copulations	(Item 3)* Number of copulations resulting in fertilization (maximum 6)	(Item 4)* Number of offspring produced
Edinburgh (Ed)	9.2	4.6	4.0	147
6CL	34.6	1.6	1.0	33
Samarkand (S)	26.4	2.8	1.8	98
Wellington (W)	16.4	4.2	3.6	236
Oregon (Or)	18.2	2.8	2.4	158
Florida (F)	14.8	3.6	2.8	118
F × Ed	3.6	6.2	5.4	302
F × W	6.8	5.8	5.4	340
Or × W	5.6	5.2	5.0	270
6CL × Ed	5.6	5.0	4.6	234
6CL × S	7.6	3.2	1.4	63
Or × Ed	5.2	5.4	4.2	225

* Intercorrelations: Item 1 and item 2, -0.87 ($p < 0.001$); item 1 and item 3, -0.78 ($p < 0.01$); item 1 and item 4, -0.69 ($p < 0.02$); item 2 and item 3, 0.96 ($p < 0.001$); item 2 and item 4, 0.90 ($p < 0.001$); item 3 and item 4, 0.95 ($p < 0.001$). † Times greater than 40 minutes were recorded as 41 minutes. This practice (*3*) serves to normalize a very skewed distribution.

Table 2. Replicated diallel cross of mating speed in male *Drosophila melanogaster* (units = number of females fertilized out of six possible).

Lines of fathers of males tested	Lines of mothers of males tested						Statistics	
	6CL	Ed	Or	W	S	F	V_r*	W_r*
6CL	*1.4* *1.2*	3.6 2.6	2.2 2.6	3.2 3.8	2.6 3.4	3.0 3.2	0.759	0.547
Ed	4.0 3.2	*3.0* *3.8*	3.7 4.6	3.4 4.0	3.2 2.8	3.2 4.2	0.172	0.001
Or	2.3 1.6	3.4 4.6	*1.8* *0.8*	3.4 4.0	2.4 1.6	2.8 3.8	1.120	0.903
W	3.2 3.4	4.4 3.0	3.8 3.2	*3.0* *2.2*	2.4 3.6	3.6 4.2	0.218	0.020
S	2.4 3.2	3.6 4.0	2.0 2.2	2.4 4.6	*1.2* *1.2*	2.4 3.8	0.707	0.585
F	3.3 3.8	4.0 4.2	3.2 2.8	4.6 3.4	2.0 3.6	*2.8* *1.8*	0.524	0.382

* V_r is the variance within an array, and W_r is the covariance of the members of an array with the nonrecurrent inbred line. W_r and V_r were calculated from the diallel table averaged over both reciprocals (above and below the inbred lines, shown in *italics* in the diagonal) and replicates.

Table 3. Hayman's analysis of variance of the diallel table.

Item	Aspect of model tested	Degrees of freedom	Mean square	F-ratio
a	$D + H_1 - H_2 - F$	5	4.958	15.95*
b	H_2	15	1.481	4.77*
b_1	Directional dominance	1	16.684	54.10*
b_2	$H_1 - H_2$	5	0.047	
b_3	Residual dominance	9	0.589	1.90
c	Maternal effects	5	0.125	
d	Other reciprocal effects	10	0.156	
Replicate		1	0.408	1.05
Error	Environmental effect	35	0.391	
Total		71		

* $p < 0.001$. Pooled error mean square (including the nonsignificant c, d, and replicate items) 0.311 for 51 degrees of freedom was used for tests of significance and as an estimate of environmental effects (E).

Such a replicated diallel cross has the structure of a two-way analysis of variance with randomized blocks where rows and columns detect additive genetic effects, and rows × columns, the nonadditive effects of dominance and genic interaction. Although this approach may be useful (*4, 5*) in the present instance a more informative analysis follows the methods of Hayman (*6, 7*) and Jinks (*8*) and yields five parameters. These are: D, the additive genetic variation present; H_1 and H_2, the two dominance variation parameters which differ only in the presence of unequal gene frequencies; F, which indicates whether dominant or recessive alleles are more frequent; and E, the environmental variation (*9*). The significance of some of these parameters is shown by the Hayman analysis of variance (Table 3). The analysis shows significant additive (item a) and dominance (item b) variation for mating speed with the dominance strongly directional (b_1) for high mating speed, as indicated by the means in Table 2. Since $H_1 - H_2$ (b_2) is not significant, gene frequencies are on average equal and the five original parameters contract to three, D, H, and E. In this diallel there were no differences between reciprocal crosses due to maternal effects (c) or to other causes (d) as found previously (*3*), so that the diallel table could legitimately be averaged over reciprocals (above and below the diagonal in Table 2) and the $W_r \cdot V_r$ analysis of Jinks (*8*) could be used to test the adequacy of a simple additive-dominance model of the genetic variance and to estimate the relative magnitudes of D, H, and E.

The six pairs of V_r and W_r statistics obtained for each line or array in Table 2 were plotted in the form of a variance-covariance diagram (Fig. 1). These points representing the six inbred lines define a straight line of unit slope [b = 0.97 ± (S.E.) 0.05], and this absence of curvature indicates that there is no evidence of a failure of the assumptions underlying the simple model postulated above. In consequence, gene effects determining male mating speed are correctly represented by D, H, and E, there being no significant genic interaction or correlated gene distributions for these data.

The ordering of points along the line

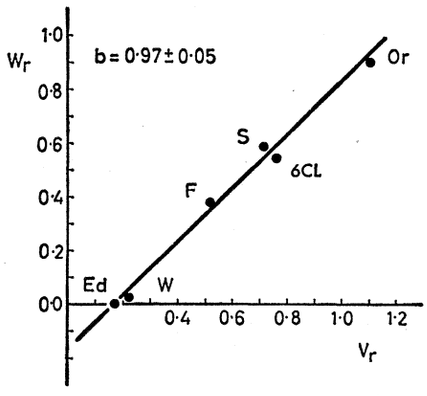

Fig. 1. Variance-covariance diagram for mating speed in male *Drosophila melanogaster*. The graph shows the regression of W_r on V_r for number of females fertilized for a replicated diallel cross of six inbred lines.

in a variance-covariance diagram indicates the proportion of dominant to recessive alleles carried by each line, Edinburgh carrying mostly dominant alleles and Oregon mostly recessives. The rank-order indicated correlates +0.87 ($p = 0.03$) with the mean mating speed of the lines, confirming that genes for high speed are dominant over those for low.

D, H, E, and a parameter for the square of average dominance $(\Sigma h)^2$ were estimated by a least-squares procedure (*6*) and gave estimates of D = 0.69, H = 1.31, E = 0.26, and $(\Sigma h)^2 = 6.56$.

These parameters are useful in attacking three important psychogenetic problems: how high and low selection lines may be established from a heterogeneous base population, the nature of the heterosis displayed by those crosses, and the biological importance of mating speed.

Advance under selection depends mainly on the "narrow" heritability, given by $\frac{1}{2}D/(\frac{1}{2}D + \frac{1}{4}H + E)$ and equaling 0.36 in these data, and on the number of gene blocks, given by $(\Sigma h)^2/H$ as 5.01. With only half the total genetic variance or "broad" heritability, given by $(\frac{1}{2}D + \frac{1}{4}H)/(\frac{1}{2}D + \frac{1}{4}H + E)$ as 0.71, being fixable even under ideal conditions, advance under selection is expected to be slow. Furthermore, since the dominance is for high mating speed, most advance should be in the low direction, and, indeed, Manning, by later selecting through one sex, on an individual basis, achieved a response for low mating speed only (*1*). With blocks of genes numbered at five—almost certainly an underestimate (*8*)—the complete homozygote will occur with a frequency of less than $(\frac{1}{4})^5$, that is, one in about 1000 individuals. Hence a large number of generations of selection would be required to achieve the maximum possible advance.

As regards heterosis, the level of dominance, given by $(H/D)^{\frac{1}{2}}$ and equaling 1.38, draws attention to the striking heterosis in these crosses suggestive of overdominance. However, a *small* amount of apparent overdominance could easily be produced by the dispersion of dominant and recessive genes among the parents making up these crosses and yet fail to produce significant curvature in the $W_r \cdot V_r$ diagram. It is clear though, from the $W_r \cdot V_r$ diagram, that genic interactions play no part in producing this heterosis.

Mather argues that the genetic architecture of inbred lines may be regarded as a vestigial form of that found in natural populations in spite of considerable natural selection during inbreeding (*10*). Consequently, the genetic architecture for genes controlling male mating speed in these lines has important implications relating to the biological importance of this trait. In natural populations of *Drosophila melanogaster*, where most gene combinations would necessarily be heterozygous, highly directionally dominant genes, either dispersed or slightly overdominant, would ensure a high proportion of fast mating males. Such architecture argues for a history of strong natural selection for maximum rather than for intermediate or for low expression of this trait (*10*). Independent evidence for the importance of this high mating speed as a component of fitness is provided by the high correlation with yield ($r = 0.90$) found in the first experiment. But the genetic evidence must be preferred, since it can be related to the long history of the organism in the wild state.

The genetic approach to individual differences in behavior is thus able to provide information, not only concerning laboratory experiments, but also the adaptive value of the behavior to the species. The approach adopted is quite general. It is not even necessary that the phenotype observed should have a very large genetic component, for natural selection may be expected to operate in a characteristic way when acting on even very small genetic differences. In such cases the analytical problem is largely one of stringent environmental control (*2*) in order to emphasize the genetic effects and make them detectable in an experiment of reasonable size.

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References and Notes

1. A. Manning, *Animal Behav.* **9**, 82 (1961); *ibid.* **11**, 116 (1963).
2. P. L. Broadhurst, in *Experiments in Personality*, H. J. Eysenck, Ed. (Routledge and Kegan Paul, London, 1960), vol. 1.
3. P. A. Parsons, *Genetica* **35**, 141 (1964).
4. J. L. Jinks and P. L. Broadhurst, *Heredity* **18**, 319 (1965).
5. S. Wearden, *ibid.* **19**, 669 (1964).
6. B. I. Hayman, *Biometrics* **10**, 235 (1954).
7. ———, *Genetics* **39**, 789 (1954).
8. J. L. Jinks, *Heredity* **9**, 223 (1954).
9. These parameters are defined as follows in terms of gene frequencies, u and v, and linear effects of individual gene blocks, d being the additive effect and h the dominant: $D = 4\Sigma uvd^2$; $H_1 = 4\Sigma uvh^2$; $H_2 = 16\Sigma u^2v^2h^2$; $F = 8\Sigma uv(u - v)dh$; and E is the environmental variation between the means of families sized five.
10. E. L. Breese and K. Mather, *Heredity* **14**, 375 (1960).
11. This report is based on a thesis in partial fulfillment of the requirements for the M.Sc. degree in applied genetics at the University of Birmingham during the tenure of a "British" Medical Research Council award for further training. Financial support was also received from a grant from the USPHS, MH-08712, from NIH. I thank Professors P. L. Broadhurst and J. L. Jinks for advice and encouragement during this investigation.

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Opposite Responding in Two Sense Modalities

Abstract. *Monkeys were trained to respond in one way to a pair of solid objects when discrimination was by touch; in the opposite way, when by vision. These opposite habits are formed independently and can be used concurrently. The finding suggests that the neural systems responsible for tactile and visual learning are separate, even with a single pair of objects.*

In a report primarily concerned with cross-modal transfer of a conditional discrimination task, Ettlinger and Blakemore (*1*) mentioned that four monkeys readily learned to make opposite responses to one pair of test objects when discrimination was in the light and dark. This incidental observation has an important bearing on the question of cross-modal effects in the monkey. We now report replication of the finding of concurrent and opposite responses in two modalities, using less ambiguous training procedures; we used