

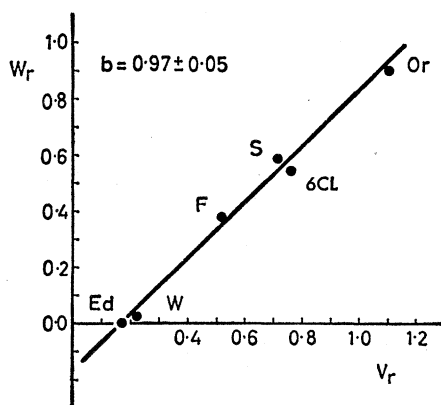


Fig. 1. Variance-covariance diagram for mating speed in male *Drosophila melanogaster*. The graph shows the regression of W_r on V_r for number of females fertilized for a replicated diallel cross of six inbred lines.

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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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: $D = 4\Sigma uv d^2$; $H_1 = 4\Sigma uv h^2$; $H_2 = 16\Sigma u^2 v^2 h^2$; $F = 8\Sigma uv(u - v)dh$; 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 Blake-more (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

Table 1. Sequence of training and numbers of trials required. Monkey 3a failed to learn the second tactile task in 680 trials, making 61 percent correct responses in the last 100 trials. C, cylinder; S, sphere; P, pyramid.

Monkey	Trials (No.)					Tactile and visual: errors in 80 trials in light and dark
	Tactile			Visual		
	C vs. S	Cone vs. P	P vs. cone	P. vs. cone	Cone vs. P	
1	90	0		20		3
2	210		0		40	4
3	80		40		20	5
3a	130		680 +			
4	170	50		60		1

different test objects and a group of naive monkeys.

Our subjects, four adolescent rhesus monkeys, were trained in standard apparatus with standard procedures for visual and tactile object discrimination learning (2). On all tasks 40 trials were given daily, 5 days a week, until each animal made 20 or fewer errors in 200 consecutive trials (Table 1).

All animals were first taught in the dark to perform a simple discrimination task (cylinder and sphere) merely in order to adapt them to tactile training. All were then required to discriminate in the dark between cone and pyramid; two were rewarded for choosing the cone; the other two, for choosing the pyramid. The animals then learned to make the opposite discrimination in the light: that is, those trained to select the cone in the dark were trained to select the pyramid in the light, and vice versa. Finally, all were given 80 trials of pseudo-random alternation between light and dark, with rewards as during training.

We can evaluate the results (Table 1) in two ways: First, we can compare learning scores for the reversed discrimination in a *different* sense modality with learning scores for a reversed discrimination in the *same* modality. These animals required more trials (ratio, 1.6:1) to learn the reversed discrimination by vision than were required for original tactile learning. In contrast, another group of eight animals required more trials (ratio, 75:1) to learn the reversed discrimination by touch than the original discrimination by touch, again with the cone and pyramid (3). Secondly, we can note that the performance of all four animals was 90-percent correct or better when retention of both habits was tested during 80 trials in the light and dark.

Our results imply that tactile and visual learning proceed independently in the monkey, as was shown earlier in two classes of experiment: First, work

was done on cross-modal transfer of training, when learning in a single sense modality may or may not lead to improved learning of the *same* (not *opposite*) discrimination in a second modality; such experiments have generally failed to produce evidence of significant cross-modal effects (4). Secondly, work was done on concurrent learning in two sense modalities, when sensory inflow through two sense modalities is made available during learning, but tests are subsequently made with the inflow restricted to a single modality; results were inconclusive (5).

Our findings show, first, that transfer of training did not take place between sense modalities in our monkeys, since the reversed discrimination was learned almost as readily by vision as the origi-

nal was learned by touch. Secondly, during training in the light, our monkeys failed to make use of the tactile information available to them as a result of their grasping the objects that were selected on the basis of vision; when subsequently tested on 40 trials in the dark, they responded in accordance with the original tactile training and not in accordance with their subsequent visual (and tactile) experience (6). Therefore, from two lines of evidence we conclude that tactile and visual learning take place in independent functional systems.

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6. Errors made by all animals during the 80 tactile and visual test trials were made in the dark on tactile trials. This observation may reflect either simple forgetting of the first-learned task or direct interference (of a minimal kind) between tactile and visual learning.
7. We thank G. D. Dawson for facilities and encouragement and the Medical Research Council for financial support.

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Carotid Body Chemoceptors: Physiological Role in Buffering Fall in Blood Pressure during Sleep

Abstract. *In cats whose aortic nerves were severed subsequent deafferentation of the carotid body chemoceptors (the carotid sinus baroreceptors remaining intact) did not change arterial pressure during wakefulness or light sleep, but the falls in pressure during deep sleep were markedly exaggerated. Subsequent baroreceptive denervation did not modify the hypotensive effect.*

Regarding circulatory changes accompanying the wakefulness-sleep cycle of the cat, we reported earlier (1) that the falls in blood pressure that occur during deep sleep (with a desynchronized electroencephalogram and bursts of rapid eye movements) are much greater after bilateral sino-aortic deafferentation: in several deafferented cats arterial pressure fell so low that episodes of transient cerebral ischemia occurred. Since in these experiments both baro- and chemoceptive fibers from the sino-aortic areas were interrupted, we could not decide whether it was abolition of baroreceptive or of chemoceptive reflexes that caused such striking exaggeration of the hypotensive effect of

deep sleep. The respective roles of the two types of receptors in controlling circulation during sleep could only be assessed by selective interruption of one type of afferent fibers while the other was left largely intact. We now report such experiments.

In all cats systolic and diastolic pressures were recorded throughout the wakefulness-sleep cycle from a permanently cannulated femoral artery; electroencephalogram, cervical electromyogram, and eye movements were also monitored (1). A first group of three cats were subjected to sino-aortic denervation in three stages, each stage being followed by a recording session. The first stage consisted in bilateral section