where τ is lag, $R_1(0) = 2/T \int_0^{T/2} \mathrm{VEP}(t)^2\,dt$, and $R_2(0) = 2/T \int_{T/2}^{T} \mathrm{VEP}(t)^2\,dt$. For an ideally repeatable VEP, $\rho(0)$ will approach 1. For a random signal, $\rho(0)$ will be around 0. The other weighting factor is defined as $s = s_e/(s_e + s_o)$ where s_e and s_o are the sum of the even and odd power spectral components of VEP(t), respectively. Calculating the discrete power spectral components of a periodic signal (which has in fact a period of $T/2$) over an integration interval T has the effect that all components at odd multiples of the basic harmonic frequency ($\omega = 2\pi/T$) become zero. For an ideal VEP (no noise, $s_e \neq 0$, and $s_o = 0$), s will approach 1. For a noise signal ($s_e \sim s_o \neq 0$), s will be close to 0.5. Thus, the two weighting factors leave the RMS value of an ideal VEP unchanged, but reduce the contribution of noise to the RMS value of an experimental VEP.

12. The relative weighted RMS values (RWR's) for the three stimuli NP, DF, and SS are defined as
$$\mathrm{RWR(NP)} = 100 \times \mathrm{WR(NP)/WR(BW)}$$
$$\mathrm{RWR(DF)} = 100 \times \mathrm{WR(DF)/WR(BW)}$$
$$\mathrm{RWR(SS)} = 100 \times \mathrm{WR(SS)/WR(BW)}$$
13. Chi-square tests showed no significant differences between the three observed distributions of RWR values (for the stimuli NP, DF, and SS) and three normal distributions with the same mean values and standard deviations. Assuming normal distributions, the probability of a stereoblind subject to produce a RWR value equal to or greater than 12 percent in one of the test stimuli (NP or DF) was estimated as P[RWR(NP) $\geq$ 12 percent or RWR(DF) $\geq$ 12 percent] = .0025. The probability of a stereonormal subject producing a RWR value less than 12 percent in both test stimuli was estimated as P[RWR(NP) < 12 percent and RWR(DF) < 12 percent] = .0018.
14. D. Fender and B. Julesz, *J. Opt. Soc. Am.* **57**, 819 (1967).
15. A. M. Slater and J. M. Findlay, *J. Exp. Child Psychol.* **20**, 248 (1975).
16. O. Braddick, J. Atkinson, J. French, H. C. Howland, *Vision Res.* **19**, 1319 (1979); H. C. Howland, J. Atkinson, O. Braddick, J. French, *Science* **202**, 331 (1978); J. Gwiazda, S. Brill, I. Mohindra, R. Held, *Vision Res.* **18**, 1557 (1978); I. Mohindra, R. Held, J. Gwiazda, S. Brill, *Science* **202**, 329 (1978).
17. See also G. Westheimer and S. P. McKee, *J. Opt. Soc. Am.* **70** (No. 7), 772 (1980).
18. V. Dobson and D. Y. Teller, *Vision Res.* **18**, 1469 (1978); J. Atkinson, O. Braddick, J. French, *Invest. Ophthalmol. Visual Sci.* **18**, 210 (1979).
19. I. Mann, *The Development of the Human Eye* (British Medical Association, London, 1964).
20. P. I. Yakovlev and A. R. Lecours, in *Regional Development of the Brain in Early Life*, A. Minkowsky, Ed. (Blackwell, Oxford, 1967), pp. 3–70; K. Nakayama, *Jpn. J. Ophthalmol.* **11**, 132 (1968); T. L. Hickey, *Science* **198**, 836 (1977).
21. J. L. Conel, *The Postnatal Development of the Human Cerebral Cortex* (Harvard Univ. Press, Cambridge, Mass., 1939–1951), vols. 1–4. For a review of the development of binocularity in cats and monkeys, see J. A. Movshon and R. C. Van Sluyters [*Annu. Rev. Psychol.* **32**, 477 (1981)].
22. Although it was found in adults (*3*) that cyclopean checkerboards with alternating crossed and uncrossed binocular disparities elicit VEP's, they are smaller in amplitude than the VEP's elicited by the cyclopean checkerboards used in our study. For our stimuli, not only the disparity but also the amount of binocular correlation changes. Therefore, the question of whether the cyclopean checkerboard VEP's that we measured are attributable either to cortical binocularity or to the somewhat more complex process of stereopsis cannot be answered [this ambiguity of interpretation applies to all published work on infants as of now (*1*, *4*)]. Since we have now explored the range of infants' binocularity, it will be profitable to use alternating crossed-uncrossed binocular disparity stimuli, which have constant correlation and, therefore, have the potential to reveal the onset of stereopsis by itself.
23. M. S. Banks, R. N. Aslin, R. D. Letson, *Science* **190**, 675 (1975); A. Hohmann and O. D. Creutzfeldt, *Nature (London)* **254**, 613 (1975).
24. We thank Y. Lehareinger, V. Corti, and P. Lüthy for technical assistance and D. Lehmann and T. Darcey for their comments on the manuscript.

* Present address: Scheie Eye Institute, University of Pennsylvania, 51 North 39 Street, Philadelphia 19104.

3 November 1980; revised 15 April 1981

Mating Preferences Are Not Predictive of the Direction of Evolution in Experimental Populations of *Drosophila*

Abstract. *The general applicability of two models used in predicting evolutionary directions from asymmetry in reproductive isolation was tested in the laboratory. In mate preference tests with strains of* Drosophila melanogaster *whose ancestral and derived relationships were known, no correspondence was found between sexual isolation and direction of evolution.*

Several different models have been proposed for the origin of premating reproductive isolation during speciation (*1*, *2*). Examination of pre- and postmating isolation among a variety of closely related species and incipient species of *Drosophila* indicates that reproductive isolation between any two species or two populations of a species tends to be asymmetrical; that is, to favor one of the two species or populations. This asymmetry provides the basis for two opposing models for predicting the direction of evolution among related species of organisms. Kaneshiro (*3*) proposed that females from an ancestral population discriminate against males of the derived population because derived males have lost important courtship elements and that this is general enough to be considered a rule. Watanabe and Kawanishi (*4*) claimed the opposite, namely, that derived females do not mate with ancestral males and that courtship elements are gained, not lost, during evolution. The authors of the two models assume they know the correct phylogenetic relationships among the species they studied. However, since present-day investigators were not witness to the speciation events, we cannot be absolutely certain which species are ancestral and which are derived. My results in mating tests with populations whose ancestral or derived status with respect to each other is known show that neither the Kaneshiro model nor the Watanabe-Kawanishi model is invariably correct.

Since 1971, a heterogeneous base population of approximately 3000 *Drosophila melanogaster* has been maintained in a population cage at Arizona State University (*5*). From this base population, four derived strains of flies were selected for photopositive, photonegative, geopositive, and geonegative behavior in Hirsh-Hadler mazes (*5*). Three different experiments were carried out in June and July 1980 to determine whether mating preferences between the base and derived strains were consistent with either model. (i) In a series of multiple choice experiments, equal numbers of males and females from the ancestral strain and one derived strain (five pairs from each strain) were placed in an observation chamber for 1 hour. The joint isolation index (*6*) was calculated from the resulting data. (ii) In female choice tests, one female, either ancestral or derived, and two males, one from the same strain as the female and one from another strain, were observed for 1 hour. The female isolation index (*6*) is a measure of the proportion of matings with a male from the same strain as the female. (iii) In male choice experiments, one male and two females, one from the same strain as the male, were observed, and the male isolation index was calculated (*6*). The male and female isolation indices should allow partitioning the joint index into isolation arising from male and female preferences. Isolation indices are significant at $P = .05$ when Z values exceed 1.96 (*4*).

Multiple choice experiments resulted in two significant indices, one of which (that for the photonegative and base strains) reflected positive assortative mating (Table 1). A significant tendency toward heterogametic matings was shown by the photopositive and base strains. Thus the multiple choice experiments have not shown any mating preference patterns that might influence the direction of evolution.

Since females are assumed to choose

Table 1. For each multiple choice test, five pairs of flies from the ancestral (A) strain and five pairs of flies from a derived (D) strain were observed for 1 hour.

Derived strain	Matings observed in multiple choice tests					
	Repetitions	A♀ × A♂	A♀ × D♂	D♀ × A♂	D♀ × D♂	$I \pm$ S.E.
Geopositive	8	20	18	16	24	0.128 ± 0.105
Geonegative	8	18	20	16	18	0
Photopositive	7	17	11	13	28	−0.282 ± 0.096*
Photonegative	10	18	26	24	10	0.304 ± 0.100*

*$P < .05$.

0036-8075/81/0918-1405$01.00/0

between two males, it is theoretically possible to draw some inferences about female discrimination from female choice experiments. In this series six of eight indices are statistically significant, two showing that derived females mated excessively with ancestral (base) males, three that ancestral females mated more often with ancestral males, and one that derived females mated more often with derived males (Table 2). A significantly asymmetrical pattern of isolation in the direction predicted by Kaneshiro is observed for three of the four combinations of ancestral females with ancestral and derived males. Ancestral males were most often chosen in five of the six categories with significant indices. It is possible that ancestral males, coming from a heterogeneous, unselected strain, might simply be showing a greater mating propensity. Courtship latency and courtship duration are frequently used as measures of mating propensity, there being a strong correlation between short latencies, short durations, and mating success (*7*). Courtship latencies (time until initiation of courtship) and durations (time from initiation until copulation) were determined for males of the ancestral strain and four derived strains by pairing them individually with females from the Canton-S strain (Table 3). Males from the ancestral population are characterized by intermediate values for both measures, an indication that their comparatively greater mating success is due to factors other than or in addition to their general mating propensity.

Kaneshiro (*3*) and Watanabe and Kawanishi (*4*) utilized data from male choice tests to make inferences about female discrimination, since in this test situation one of the females may not be receptive to the male. In the male choice experiments in my study, three of the indices were statistically significant (Table 4). In one series, derived (geopositive) males mated excessively with derived females; in another, ancestral males were more successful with derived (geonegative) females; and in a third, derived (photonegative) males mated more often with ancestral females. Two of the three significant indices are in the direction predicted by Kaneshiro and the third is in the direction predicted by Watanabe and Kawanishi.

Female mating propensity, in addition to preference, may influence the outcome of the male choice test results. To measure female mating propensity, female mating speeds (from courtship initiation to copulation) were recorded for single females from all five populations paired with males from the Canton-S wild-type strain (Table 3). On the basis of mating speeds, females from the photopositive strain are the most receptive and photonegative females are the least receptive. The possibility must be considered that when significant isolation is observed, it is a function of the interaction of male and female mating propensities rather than discrimination. In the first category in which there is a significant isolation index in the male choice experiments, geopositive females mated with geopositive males more often than ancestral females mated with the derived males. While geopositive females are slightly (though not significantly) more

Table 2. For each female choice test, one female was placed in an 8-dram shell vial with one ancestral and one derived male.

Derived strain	Matings observed in female choice tests			
	Female	Ancestral male	Derived male	I_1 ± S.E.
Geopositive	Ancestral	60	48	0.111 ± 0.091
	Geopositive	70	32	−0.372 ± 0.078*
Geonegative	Ancestral	60	40	0.200 ± 0.089*
	Geonegative	54	58	0.036 ± 0.093
Photopositive	Ancestral	46	28	0.243 ± 0.101*
	Photopositive	46	14	−0.533 ± 0.088†
Photonegative	Ancestral	46	26	0.278 ± 0.098*
	Photonegative	34	54	0.227 ± 0.094*

*$P < .05$. †$P < .01$.

Table 3. Courtship latencies (in seconds) of males from the ancestral and derived strains paired with females from the Canton-S laboratory strain and courtship durations (in minutes) of individuals from ancestral derived strains when paired with flies from the Canton-S wild-type laboratory strain. Data were subjected to a Duncan multiple range test ($\alpha = .05$), and subset memberships are indicated by letters a, b, and c.

Strain	Mating propensity	*N*
	Courtship latencies	
Males		
Geonegative	52.51 ± 10.87[a,b]	84
Photonegative	65.95 ± 12.89[a,b]	70
Ancestral	72.46 ± 18.61[a,b]	68
Geopositive	79.20 ± 12.46[b]	88
Photopositive	125.04 ± 19.94[c]	82
	Courtship durations	
Males		
Geonegative	3.500 ± 0.251[a]	105
Ancestral	3.701 ± 0.281[a]	207
Geopositive	3.882 ± 0.310[a]	103
Photonegative	4.337 ± 0.540[a]	274
Photopositive	7.095 ± 1.399[a]	126
Females		
Photopositve	2.869 ± 0.173[a]	195
Geopositive	3.143 ± 0.142[a,b]	106
Geonegative	3.462 ± 0.401[a,b]	107
Ancestral	3.512 ± 0.286[b]	243
Photonegative	4.370 ± 0.340[c]	206

Table 4. For each male choice test, one male was placed in an 8-dram shell vial with one ancestral and one derived female.

Derived strain	Matings observed in male choice tests			
	Male	Ancestral female	Derived female	I_2 ± S.E.
Geopositive	Ancestral	51	47	0.041 ± 0.099
	Geopositive	26	70	0.458 ± 0.075†
Geonegative	Ancestral	33	59	−0.282 ± 0.088†
	Geonegative	56	44	−0.120 ± 0.094
Photopositive	Ancestral	50	40	0.111 ± 0.099
	Photopositive	40	30	−0.143 ± 0.118
Photonegative	Ancestral	48	39	0.103 ± 0.102
	Photonegative	56	32	−0.273 ± 0.091*

*$P < .05$. †$P < .01$.

receptive than ancestral females, it is doubtful that this increased receptivity is the cause of the isolation. The courtship latency and duration data indicate that geopositive and ancestral males have similar mating propensities, but in male choice experiments with ancestral males an almost equal number of matings occur with geopositive and ancestral females. The next significant index was found for ancestral males and geonegative females. Since geonegative females are no more receptive than ancestral females, the isolation observed cannot be attributed to differences in mating propensity between female types.

The absence of any correspondence between standard measures of mating propensity and the outcomes of the male and female choice experiments suggests the existence of courtship discrimination at some level in these populations. However, for the four derived strains I used, there is no apparent relation between this sexual discrimination and the direction of evolution. Furthermore, though an element of female preference is being measured by both female and male choice tests, the two types of tests give conflicting preference patterns in more than one instance. Inspection of the data shows that there is a closer correspondence between the results of multiple choice and female choice tests than between either of these and male choice tests. Caution should be exercised in interpreting results of male or female choice experiments for other reasons as well. What appear to be tendencies toward strong isolation, as in tests with the geotactic strains and the ancestral population, may in fact cancel each other out in multiple choice tests. No data exist to suggest which of the three experimental designs represents the closest approximation to breeding conditions of natural populations; but with the exception of those species in which males and females are distributed on different substrates, the multiple choice situation may be the most realistic.

While the strains in this study are not species, the pattern of the isolation described in this report has been found in these strains at two other time points during their history (*8*), and there is no reason to expect the trend to change. Mayr (*2*) proposed that selection may bring about behavioral changes before morphological changes during evolution, an idea that has been substantiated for the geotactic (*9*) and phototactic (*10*) strains used in this study. Multivariate analysis (*11*) of the mating behavior of these strains may provide insight into the question of gain or loss of courtship elements. Similar degrees of isolation have been found among other laboratory strains (*12*), suggesting that premating isolation may develop more rapidly than postmating isolation.

For the strains I have described, there appears to be no relation between mating preference and the direction of evolution. Thus the relationships proposed by Kaneshiro (*3*) and Watanabe and Kawanishi (*4*) are not general concomitants of the evolutionary process. However, a consistent relationship having predictive value might exist for certain species groups. Such relationships might depend on the ecological and evolutionary history of a particular group. Evolutionary events may occur differently for species that arise from a single female founder and that colonize an island, compared to species occupying mainland areas in large numbers (*13*). Sympatry and allopatry, which have been shown to impose asymmetrical character displacement for reproductive isolation, provide still another model for examining evolutionary directions (*14*).

THERESE ANN MARKOW
Department of Zoology,
Arizona State University,
Tempe 85281

References and Notes

1. H. J. Muller, *Biol. Rev.* **14**, 261 (1939); Th. Dobzhansky, *Am. Nat.* **74**, 312 (1940); H. Carson, *Stadler Symp.* **3**, 51 (1971); A. R. Templeton, *Genetics* **94**, 1011 (1980).
2. E. Mayr, *Animal Species and Evolution* (Belknap, Cambridge, Mass., 1963).
3. K. Kaneshiro, *Evolution* **30**, 740 (1976); *ibid.* **34**, 437 (1980).
4. T. Watanabe and M. Kawanishi, *Science* **205**, 906 (1976).
5. T. A. Markow, *Genetics* **79**, 527 (1975); S. L. King, thesis, Arizona State University (1977).
6. The joint isolation index, I, was calculated according to the formula
$$I = [(n_{11} + n_{22}) - (n_{12} + n_{21})]/n$$
where n_{11} is the observed number of matings between females of the first strain and males of the first strain, n_{12} is the number of matings between females of the first strain and males of the second strain, and n is the total number of observed matings [H. Stalker, *Genetics* **27**, 238 (1942)]. The standard error (S.E.) of I [C. Malogolowkin-Cohen, A. S. Simmons, H. Levene, *Evolution* **19**, 95 (1965)] is given by S.E. = $\sqrt{[(1 - I^2)/n]}$. Similarly, the female (I_1) and male (I_2) isolation indexes are given by
$$I_1 = (n_{11} - n_{12})/n$$
$$I_2 = (n_{22} - n_{21})/n$$
7. K. Connolly *et al.*, *Evolution* **23**, 548 (1969).
8. D. W. Pyle, *Behav. Genet.* **8**, 333 (1978); T. A. Markow *et al.*, *Genet. Res.* **35**, 59 (1980).
9. D. W. Pyle, *Am. Nat.* **110**, 181 (1976).
10. T. A. Markow, *Nature (London)* **258**, 712 (1975).
11. _____ and S. J. Hanson, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 430 (1981).
12. J. R. Powell, *Evolution* **32**, 465 (1978); L. Ehrman, *Am. Midl. Nat.* **82**, 272 (1969); F. R. Vandyken and W. Scharloo, *Behav. Genet.* **9**, 555 (1979).
13. A. R. Templeton, *Genetics* **94**, 1011 (1980).
14. M. Wasserman and R. Koepfer, *Evolution* **31**, 312 (1977); *ibid.* **34**, 1116 (1980).
I thank M. Oishi for technical assistance. Supported by NIH grant NS 15263.

15 April 1981

Spatial Localization After Strabismus Surgery: Evidence for Inflow

Abstract. *Strabismics pointed to targets (without sight of the hand) before and again after surgery that altered the position of the deviating eye in its orbit. Patients having this surgery for the first time were able to use proprioceptively derived information about the surgically altered eye position. In contrast, patients who had similar operations, but on muscles that had been operated on one or more times in the past, were apparently deprived of this information. The important afference may be supplied by the tendon organs.*

How do we know which way our eyes are pointing? Since the time of Helmholtz, the prevailing opinion has been that signals sent to the eye muscles from the brain (efferent, or outflow, signals) provide this information, whereas inflowing (proprioceptive, or afferent) signals are not used (*1*). Although it has been anatomically established that eye muscles contain spindle organs and tendon receptors, and although there is also physiological evidence demonstrating the properties of these receptors, their function remains unclear (*2*).

We have been testing eye-hand coordination in patients undergoing extraocular muscle surgery for strabismus. The results from those patients undergoing surgery for the first time are not consistent with the outflow model and suggest that these patients are using inflow information that apprises them of the changed position of the eye in its orbit. The results from a second group of patients who had repeated surgery on the same eye muscles suggest that the tendons are important structures in supplying this afference.

We required patients to point with an unseen hand to a small light in totally dark surroundings (created by a light-proof box that fit over the head and neck of the supine patient). It contained three light-emitting diodes (LED's) at arm's length, one placed in the median plane, one 10° to the left, and one 10° to the

0036-8075/81/0918-1407$01.00/0