STUDIES ON THE BAR SERIES OF DROSOPHILA III. THE FACET RELATIONS IN DORSAL AND VENTRAL LOBES OF THE EYE

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INTRODUCTION

THE relative growth of parts of many organisms has been shown to conform to the simple power function

$$y = bx^k$$

where y and x represent the parts measured, and b and k are constants. When y and x are plotted on a logarithmic scale a straight line is obtained. The many applications of this equation to growth data have been fully reviewed by HUXLEY (1932). More recently, HERSH (1934) and ROBB (1935a, 1935b) have extended the application of the relative growth function from the purely ontogenetic sphere to the phylogenetic, through investigations on the evolutionary relative growth of parts in the Titanotheres and the horse, respectively.

The first attempt to apply the relative growth function to data on the relative sizes of parts in Drosophila was made by HERSH (1928). The well known lobing of the compound eye in Bar-eyed flies makes possible a quantitative determination of the relative sizes of the two lobes expressed in terms of facet number. In a series of investigations on Bar raised at different temperatures (HERSH 1928) and on different Bar stocks raised at the same temperature (HERSH 1931), HERSH concludes that the relative growth function adequately expresses the observed relations between facet number in the dorsal and ventral lobes of the eye.

In my own investigations on facet number in Bar (MARGOLIS 1935), separate records of facet number in the two lobes of the eye were kept in so far as possible. These data, together with others gathered subsequently onan unrelated Bar stock obtained from DR. A. L. BARON, serve as the material for the present analysis of the facet relations in dorsal and ventral lobes of the eye. My own results differ from those of HERSH in several respects, particularly with reference to the applicability of the relative growth function. At the same time, the data suggest a possible basis for the observed differences and are accordingly presented.

EXPERIMENTAL

Stocks

The data on facet number are taken from two unrelated but genetically homogeneous Bar stocks. The stock designated as A is the one used in

my earlier experiments on the effect of the gene vestigial on facet number in Bar. The details concerning inbreeding, genetic homogeneity, culture methods, facet number for the whole eye, etc., have been presented elsewhere (MARGOLIS 1935). The stock designated as B is the one obtained from Dr. A. L. BARON. This stock had previously been rendered isogenic with a wild Oregon stock used by Dr. POWSNER in his experiments on the duration of various developmental periods at different temperatures (POWSNER 1935). The general method of rendering the two stocks isogenic through the use of chromosomes with dominant markers and crossover suppressors has already been outlined (BARON 1935). Before using stock B in my own experiments, the stock was inbred with a vestigial stock by pair brother-sister matings for fifteen generations. This vestigial stock had previously been backcrossed to POWSNER'S wild stock for 34 generations. This latter procedure was carried out in order to continue my earlier experiments on Bar and vestigial. The method insures a high degree of genetic uniformity in both the Bar and vestigial stocks and, at the same time, a close relationship to the wild stock of POWSNER. Since this latter stock has shown such excellent viability, fertility, and genetic homogeneity, a number of workers in our laboratory are using it as a standard wild-type with which the developmental effects of various mutant characters may be compared. The actual degree of genetic uniformity obtained in stock B by the above procedure, as measured by the parent-offspring correlation, will be discussed later.

Methods

The experimental methods employed in securing the data for stock A have been described elsewhere (MARGOLIS 1935). A series of seven experiments were conducted using several temperatures in each experiment, and extending over a period of a year and a half.

The data on facet counts in stock B were taken from a series of experiments dealing with a preliminary localization of the temperature-effective period for facet determination in this stock, and from other experiments dealing with the effect of reduced atmospheric pressures on facet number. None of the data on stock B have been published previously and are presented here strictly from the point of view of determining the relation between dorsal and ventral lobes of the eye in respect to facet number. The experiments on the effect of reduced atmospheric pressures proved negative and will be considered elsewhere as one aspect of the effects of various environmental agencies on facet number in Bar. The facts relating to culture methods, temperature control, and general uniformity of environmental factors are the same for stock B as for stock A.

Facet counts

In making the facet counts on both stocks, separate records of facet number in the two lobes were kept where possible. In the case of Bar there is always some indication of lobing of the eye; but in the larger eyes, especially at low temperatures, there is a tendency for the two lobes to merge, making accurate discrimination between lobes difficult. I found it extremely difficult to distinguish accurately between lobes at temperatures below 22°C, so that the data below this temperature are far too meager for analysis and are not given. At all temperatures, personal error in distinguishing between lobes was minimized by recording the lobes separately only in cases where clear definition was possible. A comparison of the total eye size of flies in which dorsal and ventral lobes were clearly distinguishable with the total eye size of the population as a whole, at each temperature, indicates that the former is truly a random sample of the latter. This fact is easily verified by comparing table 1 of this paper with table 3 in the paper previously cited (MARGOLIS 1935).

Data on facet number in dorsal and ventral lobes

Throughout this paper the mean facet number in the dorsal lobe at any temperature will be designated as D, and correspondingly the ventral lobe facet number as V. In table 1 are given the values of D and V, respectively, for different temperatures, together with their standard deviations. The column headed D/V gives the ratio of D to V and the column headed r, the correlation between lobes.

A number of interesting facts are apparent in the data. In those cases where experiments at a given temperature are repeated one or more times the values of D and V, in general, are similar within the limits of sampling error. The ratio, D/V, differs for the two sexes scattering narrowly around a value of 1.15 for the males and 1.0 for the females. For either sex the ratio is relatively constant over the temperature range. The values of the correlation coefficients (r) present the most interesting feature of the table. There is, in general, a fairly systematic decrease in the value of r with increase in temperature. At the same time, however, where experiments at a given temperature are duplicated there are in some cases significant differences in the values of r for any one temperature. This is especially noticeable in the case of the four experiments at 28°. This temperature was used as a control temperature throughout the series of experiments, and although the mean facet numbers display an insignificant scattering in the different experiments there are significant differences in r. This indicates an inadequate control of some factor or factors which influence variation in facet number in the two lobes, but which do not perceptibly shift the

TABLE 1

Statistics on facet number in dorsal and ventral lobes of stock A.

EXP.	SEX	T	D	σ_D	V	σ_V	D/V	r	n
IV	♂	22°	57.9±1.7	7.90	50.0±1.5	6.85	1.16	0.600±0.136	22
	♀	22°	51.2±1.3	6.60	51.6±1.3	6.60	0.99	0.279±0.181	26
V	♂	22°	58.6±2.3	9.20	52.0±2.0	8.10	1.13	0.902±0.047	16
	♀	22°	52.9±1.3	5.05	53.6±1.2	4.90	0.97	0.881±0.056	16
VII	♂	22°	58.2±2.1	8.85	48.0±2.1	8.85	1.21	0.690±0.124	18
	♀	22°	50.3±1.5	7.20	52.6±1.6	7.89	0.96	0.701±0.104	24
VII	♂	24°	45.4±1.3	7.26	37.9±1.1	6.39	1.20	0.515±0.129	32
	♀	24°	40.1±0.8	5.76	40.4±0.9	6.45	0.99	0.612±0.089	50
I	♂	25°	40.7±1.1	4.88	34.4±1.0	4.62	1.18	0.677±0.120	20
	♀	25°	38.6±1.0	5.34	35.7±0.8	4.29	1.08	0.555±0.131	28
VII	♂	25.8°	36.9±0.8	5.40	31.6±0.8	5.25	1.17	0.556±0.105	43
	♀	25.8°	35.5±1.1	5.31	34.7±1.2	5.49	1.02	0.680±0.114	22
II	♂	27°	31.3±0.8	4.40	27.2±0.6	3.52	1.15	0.448±0.145	30
	♀	27°	28.7±0.7	3.90	29.9±0.8	4.82	0.96	0.628±0.106	33
III	♂	27°	31.3±0.4	4.00	27.9±0.4	4.20	1.12	0.427±0.077	112
	♀	27°	28.6±0.4	3.92	29.1±0.5	4.26	0.98	0.398±0.090	88
II	♂	28°	27.3±0.6	4.18	24.3±0.5	3.54	1.12	0.634±0.081	53
	♀	28°	22.4±0.7	4.10	23.3±0.6	3.74	0.96	0.147±0.157	39
III	♂	28°	26.3±0.7	4.24	22.8±0.5	2.96	1.15	0.488±0.121	40
	♀	28°	26.4±0.7	4.08	22.3±0.6	3.40	1.18	0.404±0.146	33
IV	♂	28°	25.7±0.6	3.60	23.6±0.6	3.18	1.09	0.382±0.149	33
	♀	28°	25.4±0.8	4.48	25.0±0.7	3.68	1.02	0.224±0.173	30
VI	♂	28°	27.1±0.7	4.14	25.3±0.4	2.52	1.07	0.161±0.170	33
	♀	28°	23.7±0.8	3.78	25.8±0.2	3.66	0.92	0.164±0.203	23
I	♀	29°	22.6±0.8	3.24	19.8±0.6	2.44	1.14	0.063±0.249	16
III	♂	29°	22.0±0.5	3.40	20.2±0.4	2.46	1.09	−0.092±0.143	48
	♀	29°	20.9±0.5	3.06	19.0±0.4	2.38	1.10	−0.076±0.166	36
II	♂	30°	22.0±0.7	2.58	20.1±0.5	1.85	1.09	0.522±0.195	14
	♀	30°	19.8±0.6	2.24	18.7±0.4	1.68	1.06	0.017±0.250	16
III	♂	30.4°	17.3±0.5	2.35	14.8±0.6	2.87	1.17	0.225±0.194	24
	♀	30.4°	17.0±0.3	1.93	15.9±0.4	2.34	1.07	0.356±0.152	33
I	♀	31°	17.6±0.3	1.03	15.8±0.4	1.73	1.11	−0.231±0.231	17

mean value for the population. As will be seen later, this feature in the data appears also in stock B. There is, as one should expect, a close approximation in the values of r for the two sexes. The few exceptions to this fact will be considered in connection with the data in table 2.

The biometric constants for facet number on stock B are contained in

TABLE 2

Statistics on facet number in dorsal and ventral lobes of stock B.

EXP.	SEX	T	D	σ_D	V	σ_V	D/V	r	n
IIb	♂	22°	69.1±1.1	6.49	42.2±0.8	4.71	1.64	0.535±0.121	35
	♀	22°	48.3±0.9	5.85	42.9±0.8	4.91	1.13	0.252±0.146	41
IIc	♂	22°	79.7±1.3	6.45	49.6±0.9	4.50	1.61	−0.237±0.193	24
	♀	22°	49.0±0.9	4.08	44.1±1.3	5.81	1.11	0.332±0.199	20
IId	♂	22°	77.6±1.6	6.30	50.2±1.6	6.05	1.55	0.188±0.250	15
	♀	22°	47.8±0.8	4.56	43.2±1.2	6.77	1.11	0.221±0.165	33
IIa	♂	28°	43.4±0.6	5.72	26.2±0.3	3.31	1.66	0.192±0.092	110
	♀	28°	27.7±0.3	3.36	22.8±0.3	2.90	1.22	0.455±0.072	122
IIIa	♂	28°	44.4±0.8	6.38	27.8±0.5	3.80	1.60	0.391±0.106	64
	♀	28°	28.5±0.5	3.01	23.8±0.5	3.01	1.20	−0.190±0.145	44
IIIb	♂	28°	41.4±0.6	4.50	26.1±0.3	2.40	1.59	0.200±0.133	52
	♀	28°	29.6±0.6	3.79	23.2±0.5	3.08	1.28	0.250±0.154	37
IIIc	♂	28°	42.4±0.8	5.74	26.4±0.4	2.67	1.61	0.190±0.130	55
	♀	28°	29.9±0.5	3.08	23.0±0.5	3.17	1.30	0.251±0.159	35
IIId	♂	28°	41.2±0.9	5.87	25.3±0.4	2.70	1.63	0.156±0.143	46
	♀	28°	30.3±0.6	3.12	22.4±0.5	2.74	1.35	0.252±0.184	26
IIIe	♂	28°	45.2±1.0	6.92	26.5±0.5	3.48	1.71	0.350±0.125	49
	♀	28°	30.4±0.7	4.02	23.3±0.5	2.87	1.30	−0.048±0.166	36
IIIf	♂	28°	43.6±1.0	5.54	25.9±0.6	2.98	1.68	0.082±0.187	28
	♀	28°	30.6±0.8	3.88	23.0±0.5	2.63	1.33	0.141±0.192	26
IIIg	♂	28°	43.4±0.9	6.10	26.7±0.5	3.20	1.63	0.512±0.104	50
	♀	28°	32.8±0.7	3.72	25.0±0.8	4.52	1.31	0.276±0.168	30
IIIh	♂	28°	41.0±0.8	5.14	24.7±0.4	2.58	1.66	0.114±0.147	45
	♀	28°	30.8±0.6	3.70	22.5±0.5	3.18	1.37	−0.189±0.163	35
IIIi	♂	28°	46.0±0.9	4.26	25.6±0.7	3.14	1.80	0.107±0.206	23
	♀	28°	31.6±0.6	2.50	22.8±0.5	2.20	1.39	0.115±0.233	18
Ia	♂	28°	42.7±0.7	5.71	27.6±0.5	3.54	1.55	0.314±0.108	58
	♀	28°	29.0±0.6	3.00	24.0±0.6	2.90	1.21	0.188±0.182	28

table 2, and are arranged in the same manner as table 1. Only two temperatures are represented in the various experiments. Although data at other temperatures are desirable, these data in themselves clearly bring out certain features of the facet relations in dorsal and ventral lobes. In so far as duplication of means is concerned the experiments are entirely satisfactory with the exception of experiment IIb at 22°. The scattering in values of D and V at 28° does not appear to be significant statistically although there is a slight trend when the male and female values for different experiments are compared. This indicates some slight variation in experimental conditions from one experiment to another, too small to be detected in the sampling errors of the means in populations of this size.

The values of D/V differ for the sexes, although they appear to be relatively constant for the two temperatures in the males. There is some indication that D/V is lower at 22° than at 28° for the females. The correlation between lobes is, in general, small and in most individual experiments not statistically significant. Viewing the data as a whole there is no doubt that a small but significant positive correlation between lobes exists. The basis for this correlation may rest upon some residual genetic variability, upon some inadequately controlled environmental variable, or finally upon some sort of developmental interdependence between the two lobes. If development of facets is independent in the two lobes, then in a genetically homogeneous stock raised under uniform environmental conditions the correlation between lobes should be 0. In this event, the presence or absence of a significant correlation may be used as a test for the uniformity of all factors which determine facet number in any experiment.

An experiment was designed to test the degree to which genetic heterogeneity in stock B might account for the observed correlation between lobes. A parent-offspring correlation for facet number was carried out at 28°. In both the parents and the offspring separate records of dorsal and ventral lobes in left and right eyes were kept. Table 3 contains the data on the parent-offspring, left-right, and dorso-ventral correlations in stock B. The slight discrepancy in numbers of individuals on which each correlation coefficient is based is due to the previously mentioned fact that clear discrimination of lobes is not always possible, coupled with the fact that in some cases one or the other eye cannot be counted due to mechanical injuries of one sort or another.

The values of r for parent-offspring and for dorso-ventral lobes are very similar in both males and females. The small differences which appear are probably sampling errors. The left-right correlations, on the other hand, are much larger and differ significantly from the other correlation coefficients. This latter fact confirms my view that in Bar some form of developmental dependence exists between the two eyes (MARGOLIS 1935).

Since the parent-offspring correlation serves as a quantitative measure of the degree of genetic heterogeneity in a population, one may conclude that in this experiment genetic heterogeneity, in itself, is sufficient to account for the observed correlation between dorsal and ventral lobes. Environmental variations, if present, will increase the correlation. The same is true for any sort of developmental interdependence, as demonstrated by the left-right correlations.

The fact that residual genetic heterogeneity adequately accounts for the dorso-ventral correlation is further supported by the values of r at 28° in table 2. The great majority of these values in both sexes closely approximate the values of the parent-offspring correlations in table 3. The few exceptions which show high positive correlation may be due to some inadequately controlled environmental variable which escaped attention during the experiments.

TABLE 3

Parent-offspring, left-right, and dorso-ventral correlations in stock B taken from the same set of data.

MALES

r(parent-offspring)	$=0.188\pm0.060$; n = 256
r(left-right)	$=0.483\pm0.050$; n = 235
r(dorso-ventral)	$=0.273\pm0.061$; n = 228

FEMALES

r(parent-offspring)	$=0.246\pm0.069$; n = 182
r(left-right)	$=0.560\pm0.056$; n = 150
r(dorso-ventral)	$=0.196\pm0.074$; n = 170.

Attention has already been directed to those cases in table 1 where a significant difference in r between males and females is observed. A few similar cases are present in table 2. It is perhaps noteworthy that, with a single exception (table 2, exp. IIa), wherever a large difference in r exists, the males show the higher value. Formally, at least, this fact can be explained by assuming the presence of sex-linked recessive modifiers of facet number which are not uniformly distributed in the population. The presence of sex-linked modifiers of Bar is known from the experiments of HERSH (1929). Such modifiers would affect the facet number in the males, but might be masked in the females through the effects of more uniformly distributed dominant alleles. An alternative explanation in terms of differential effects of environmental variables on the two sexes is tenable but appears less probable.

The systematic trend in r for stock A (table 1) is interesting in the light of the explanation offered here for the correlation observed between lobes. One should expect to find the values of r scattering about some central value representative of the parent-offspring correlation, if the interpreta-

tion given for stock B applies equally to stock A. The parent-offspring correlation for stock A at 28° was found to be 0.17 ± 0.067 for the males, and 0.25 ± 0.065 for the females. At 28°, with the exception of males in experiment II, the values of r do not depart widely from the values for the parent-offspring correlation. It is obvious that at all temperatures below 28° the values of r are much higher than one is led to expect from the parent-offspring correlation. This raises an important question as to whether a routine determination of a parent-offspring correlation with reference to any quantitative character under a single set of conditions, for example a single temperature, is sufficient for establishing the degree of uniformity of genetic factors affecting that character. From our knowledge of the effects of environmental agencies on development in general, it appears probable that parent-offspring correlations will differ under different sets of conditions. An experimental investigation of this point is highly desirable and will be undertaken. The trend in r with temperature in table 1 may be due to the presence of eye modifiers not uniformly distributed in the population. The effects of these modifiers may be progressively obscured as temperature increases, through the more efficient operation of processes initiated by other genes which are more uniformly distributed. This explanation is, of course, purely formal but can be tested by investigating the parent-offspring and dorso-ventral correlations over a range of temperatures.

THEORETICAL

HERSH (1928) has investigated the inter-lobe correlation for a number of combinations of *B*, *BB*, and wild type over a range of temperatures. For comparison with my own results the data on *B* are most relevant. The correlation between lobes is moderately high at most temperatures and shows no systematic trend with temperature. The stock used in those experiments is the low selected forked Bar stock, obtained from ZELENY in 1921, and used by HERSH in other investigations (HERSH 1924 and 1927). No measure of genetic uniformity in the stock is available since no parent-offspring correlation is given. In view of the rigorous selection for low facet number in this stock, a high degree of uniformity may be assumed. However, a comparison of the facet temperature relation in 1924 with that in 1927 (compare table 3, HERSH 1927 with table 1, HERSH 1924) indicates that some germinal modification had taken place during the years following selection and inbreeding. This is indicated by the relatively higher count at all comparable temperatures in 1927. I have found in my own stocks a marked tendency toward accumulation of high modifiers following close inbreeding for many generations. This progressively accumulated genetic diversification is, perhaps, sufficient to account for the inter-lobe correlation.

Moreover, the use of a 3 to 4 day egg-laying period introduces an environmental variable which operates differentially on the flies in any one culture. Those flies developing from the early laid eggs are exposed to optimum conditions, whereas the flies from later eggs show effects of progressive depletion of food supply as evidenced by a decrease in facet number and general body size (LUCE 1931, MARGOLIS 1935). Data to be published elsewhere demonstrate clearly that poor culture conditions increase the inter-lobe correlations. PEARL (1906) observed a small but similar increase in size correlations in Chilomonas due to poor culture conditions. It is, of course, impossible to establish the degree to which the various factors mentioned contribute to the inter-lobe correlations observed, unless the genetic and environmental factors are controlled separately.

An interesting point of difference in HERSH'S 1928 data and my own, is in the relation of the facet ratio between lobes (D/V) to temperature. As illustrated in table 1 for stock A, D/V is constant for all temperatures, for both sexes. HERSH, on the other hand, finds that when log D is plotted against log V for each temperature a straight line is obtained. This, of course, means that $\frac{\log D}{\log V}$ is constant over the range of temperatures. From this fact HERSH concludes that the rate of formation of facets in the dorsal and ventral lobes is logarithmic in character. This analysis, however, tells us nothing concerning the rate of formation of facets in the individual under any specified set of conditions, but gives us the relation of facet number to temperature for dorsal and ventral lobes, respectively. This can be illustrated more clearly in the following manner. HERSH (1930) has shown that the facet-temperature relation for various combinations in the Bar series is exponential in character, conforming to the expression

$$y = ae^{rt}$$

where y is the number of facets, t the temperature, a and r constants, and e the base of the system of natural logarithms. This expression gives an excellent fit to the data. If now, both the dorsal and ventral lobes are exponential functions of temperature such that

$$D = ae^{rt} \quad (1)$$

$$V = a^1e^{r^1t} \quad (2)$$

then solving (1) and (2) in terms of t and eliminating t and e from the equations, D is related to V as a power function of the form

$$y = bx^k \quad (3)$$

where $y = D$, $x = V$, and b and k can be evaluated in terms of the constants

a, a^1, r, and r^1 in equations (1) and (2). This is, in fact, implicit in plotting log D against log V for different temperatures as carried out by HERSH. In plotting the data as indicated above it is temperature and not time which is implicit, so that no growth relation may be assumed.

Since, in my own data (table 1), it is $\frac{D}{V}$ rather than $\frac{\log D}{\log V}$ which is constant, some explanation for the difference is desirable. Considering again equations (1) and (2), in the special case where the constants r and r^1 are equal, the constant k in equation (3) which is equal to r/r^1 becomes equal to 1 so that the relation between D and V over the temperature range is rectilinear. It appears then that D and V in both HERSH's and my own data are related to temperature in the same manner but that HERSH's results conform to the more general relation of which my own represent a special case, for example when r and r^1 are equal.

In a further investigation of the facet relations in the dorsal and ventral lobes, HERSH (1931) has fitted the relative growth function to data on a series of Bar stocks differing from each other in respect to various mutant markers in different regions of the X chromosome. The experiment was conducted at 25° C. In applying the relative growth function to these data, HERSH points out that there is the assumption that increasing facet numbers in the two lobes represent progressive growth levels. Fifteen stocks were tested, some giving an excellent fit to the calculated curves, others a questionable fit, and still others rather wide departures. This statement is based merely on visual inspection of the curves rather than on any tests of goodness of fit.

The manner in which the facet numbers in dorsal and ventral lobes were calculated requires some consideration. In making these calculations for any one series, the facet data were seriated on the basis of total facet number instead of treating facet number in dorsal and ventral lobes as independent variates. The latter procedure is the one used in determining regression, and involves no assumptions concerning the relations of the variates. In his 1928 paper HERSH states that regression for those data was sensibly linear. If regression is likewise linear for the 1931 data, it is clear that the relative growth function cannot satisfactorily be fitted to data seriated with reference to either dorsal or ventral lobes treated as independent variates. It is of some interest, then, to determine the consequences of seriation of data on the basis of total eye size. Expressed in general terms the problem may be stated as follows: given two variables, D and V, such that $D+V=T$, assuming normal distributions for D and V, respectively, and o correlation, what will be the relation between D and V calculated from data seriated with reference to T?

This problem was attacked by building up a series of theoretically con-

structed correlation tables for D and V using the normal distribution, and assuming 0 correlation. Different relative magnitudes of the standard deviations and means were used for the two distributions. Analysis of these tables showed that for data seriated with reference to T there is a well defined relation between D and V despite the absence of any correlation. When the standard deviations for D and V differ, the relation is sigmoid; when the standard deviations are equal, the relation is rectilinear. The values of the means, however, do not affect the form of the relation.

It was of further interest to test the application of these conclusions to a set of data which approximated the conditions specified in the analysis, namely, normality of distribution of the variates and 0 correlation. For this purpose the data on facet number for the females of stock B, from experiments IIIa, IIIc, IIId, IIIe, IIIf, IIIh, and IIIi, were used (table 2). The data from the different experiments were then grouped together and biometric constants for dorsal and ventral lobes calculated. The values for the constants are as follows:

$$D = 30.10 \pm 0.237; \sigma_D = 3.484$$
$$V = 23.08 \pm 0.197; \sigma_V = 2.900$$
$$r = -0.0092 \pm 0.0680$$
$$N = 215$$

The data were then seriated with reference to total eye size and values of D and V calculated for each class. These values of D and V are plotted in figure 1, and are represented by open circles. The solid circles in figure 1 represent the values of D and V calculated from the same data, but seriated with reference to D. The latter represents graphically the regression of V on D calculated in the usual way. The curve in figure 1 represents a theoretially calculated curve using the means and standard deviations of dorsal and ventral lobes respectively and assuming normality of distribution of the variates as well as o correlation. The horizontal line represents the theoretical regression of V on D. The sigmoid character of the curve calculated from data seriated with respect to total facet number is clearly apparent. Were it not obvious that this is a consequence of the mathematical treatment of the data, one might be led to assume some functional relation between facet numbers in the two lobes. The absence of any such relation is, however, clearly indicated by the analysis of the data seriated with reference to either dorsal or ventral lobes, and by the absence of correlation between lobes. Considering the nature of the assumptions involved in the calculation of the theoretical curve, a remarkably good fit is obtained. The first point, for example, is based on only one individual. The whole question of the form of distribution of facet number in Bar will

be treated elsewhere, although the present data indicate an excellent approximation to normality.

One must conclude, at least for the data at 28°, that facet number in Bar is independently determined in the two lobes. The factors which lead

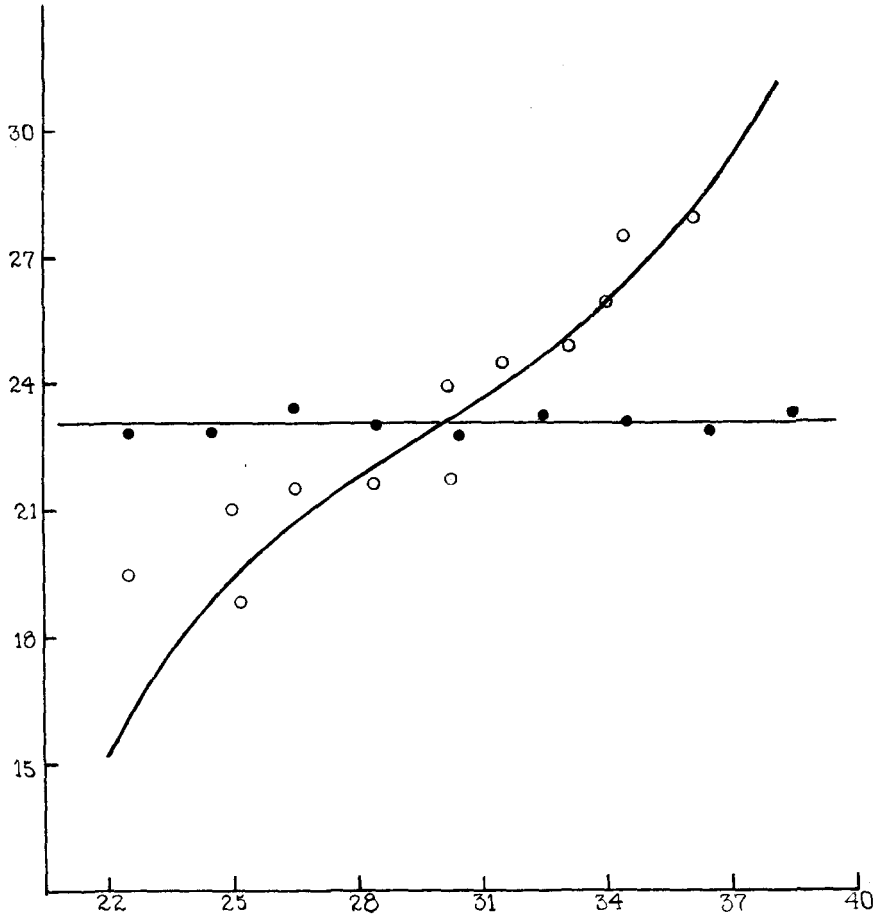

FIGURE 1. Ordinates—ventral facet number; abscissae—dorsal facet number. Solid circles represent data seriated with reference to facet number in dorsal lobe. Open circles represent data seriated with reference to total facet number. See text for calculation of curves.

to the impression of some degree of interdependence as evidenced by correlation between lobes have already been discussed at some length but may be summarized briefly.

1. Genetic heterogeneity in the population leads to a correlation between lobes since, although the lobes may vary independently of each other, the two lobes are covariant with respect to the genotype.

2. Environmental fluctuation operates in a similar manner. Facet num-

ber in either lobe varies with such factors as temperature, culture conditions, etc., so that variability in any one of these factors leads to concomitant variation in both lobes, in this way bringing about a correlation between lobes.

If this interpretation of the facet relations in the two lobes is correct, then we have a very simple method for testing the uniformity of both genetic and environmental factors in any experiment. Zero correlation should indicate uniformity of all factors affecting facet number. In this respect, the determination of inter-lobe correlations serves the same purpose as the left-right correlations for bristle number as used by PLUNKETT (1926) and subsequently by CHILD (1935). In the case of facet number, the left-right correlations are misleading since my data indicate some degree of developmental interdependence.

The question arises concerning the factors determining the lobing of the eye. DIETRICH (1907) has called attention to the fact that lobing is by no means uncommon among the Diptera. Moreover, this lobing is some times accompanied by differences in size of facets as well as histological pattern of the ommatidia in the two lobes. These facts are of interest since in Drosophila, superficially at least, there is no indication of lobing in the wild type eye, so that the Bar gene would seem to have introduced the lobing effect as a new feature. Recent unpublished observations of C. W. ROBERTSON of this laboratory, however, indicate that the ommatidia of the wild type eye are divisible histologically into two groups based upon the arrangement of the retinulae cells within each group. It appears then that the lobing in Bar is foreshadowed in the wild type, although the latter gives no superficial indication of this fact.

The apparent independence of facet number in the two lobes may be explained by at least two simple hypotheses. (1) The facet number in each lobe may be determined in a separate center. (2) Facet number may be determined as a whole, but an independent set of factors may operate to determine the lobing. If the factors determining the lobing operate independently of those determining facet number, then no correlation between lobes is to be expected. There appears at present to be no way of distinguishing definitely between these possibilities.

The observations and analysis of data on dorsal and ventral lobes of the eye in Bar-eyed Drosophila presented here show definitely that a number of factors may operate to produce an apparent relation between facet numbers in the two lobes where, in fact, no demonstrable functional relation exists. It is impossible to specify the manner in which each of these factors affects the end result, without experiments directed specifically toward that end. It is, however, clear that these factors should be evaluated in any analysis of the problem.

SUMMARY

Data on facet number in the dorsal and ventral lobes of the compound eye of Bar-eyed Drosophila are presented. Two unrelated but approximately genetically homogeneous stocks were used in the experiments. In stock A, the value of the correlation between lobes increases with decrease in temperature. This is interpreted as due to some residual genetic heterogeneity. In stock B, a series of experiments at 28°C indicate that the dorsoventral correlation is of the same magnitude as the parent-offspring correlation for the stock. It is concluded that genetic heterogeneity is adequate to account for the correlations observed. Variability in environmental agencies such as temperature and culture conditions also contribute to an increase in correlation between lobes. If these conclusions apply equally to all Bar stocks then the degree of correlation between lobes serves as a measure of uniformity of all factors, both genetic and environmental, which affect facet number.

An analysis on the effects of different methods of seriation of the data is presented. It is demonstrated that seriation of the facet data on the basis of total eye size leads to the impression of a functional relation between dorsal and ventral lobes where, in fact, no demonstrable relation exists, as evidenced by complete absence of regression or correlation.

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