PHENOGENETIC STUDIES IN SCUTE OF *D. MELANOGASTER*

III. THE EFFECT OF TEMPERATURE ON SCUTE 5

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INTRODUCTION

THIS paper deals with the quantitative variations, at different temperatures, in the bristle numbers of *sc 1*, *sc 5*, and their compound *sc 1/sc 5*. The allele *sc 5* was found by GAISSINOVITSCH (1930). According to DUBININ (1929, 1932), *sc 5* is a less extreme allele than *sc 1*. (1) *Sc 5* effects fewer bristles and has a lesser effect on those bristles. (2) The bristles affected by both *sc 1* and *sc 5* are the only ones affected in the compound *sc 1/sc 5*. (3) The mean bristle numbers of the compound are intermediate between *sc 1* and *sc 5*.

It will be shown in this paper that these generalizations do not hold at all temperatures for all the bristles. These experiments further add to the growing amount of quantitative data which ultimately must be used to formulate definitely and test a quantitative theory of development such as proposed by GOLDSCHMIDT (1927) and PLUNKETT (1926).

MATERIALS AND METHODS

Culture conditions

The usual *Drosophila* culture methods were employed (banana-agar gel with added yeast) with added precautions to insure uniform conditions for large numbers of flies raised in half-pint bottles (CHILD 1935). To insure that the *sc 5*, *sc 1*, and the *sc 1/sc 5* flies had as similar an environment as possible, they were raised in the same culture in most of the experiments. Two methods were used to obtain the various genotypes in the same bottles. In some experiments males and females of both alleles were mated in the same bottle. In other experiments *sc 1/sc 5* flies were mated to *sc 1* and *sc 5* males in the same bottle.

Flies 4-7 days old raised under favorable conditions were used for egg laying. About 20-30 females were used per bottle with an egg-laying period of from 1 to 3 hours duration. The temperature was regulated in incubators held constant to within 0.1°.

Selection

The details of selection of the *sc 1* stock and the tests for the adequacy of selection were presented in a previous communication (CHILD 1935).

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The *sc 5* flies were made isogenic with the *sc 1* by twenty generations of backcrossing *sc 1/sc 5* by *sc 1* males. The only difference between these *sc* stocks is, therefore, the possession of one or the other of the *sc* alleles.

The original *sc 5* stock was actually *y sc 5*. During the course of these experiments one crossover was obtained between *y* and *sc 5*, thus eliminating the yellow. The bristle numbers of *y sc 5* and *sc 5* were found to be the same, however, and in reporting these data no distinction will be made as to whether the flies were yellow or wild type for color.

EXPERIMENTAL DATA

The flies were raised for their total period of development at temperatures ranging from 14° to 30°. The complete and more extensive data relat-

TABLE 1*
Effect of Temperature on mean bristle numbers.

Males

$T \pm 0.1^\circ$	<i>M a sc</i>		<i>M p sc</i>		<i>M i v</i>	
	<i>sc 5</i>	<i>sc 1</i>	<i>sc 5</i>	<i>sc 1</i>	<i>sc 5</i>	<i>sc 1</i>
14°	.11 ± .019	.020 ± .014	.24 ± .027	.060 ± .024	.62 ± .030	.68 ± .046
15°	.11 ± .023	.019 ± .004	.26 ± .032	.035 ± .005	.72 ± .033	.94 ± .029
16°	.10 ± .015	.027 ± .012	.14 ± .018	.049 ± .016	.91 ± .015	.99 ± .005
18°	.09 ± .018	.004 ± .002	.57 ± .014	.005 ± .002	.99 ± .006	1.
19°	.13 ± .036	.012 ± .012	.69 ± .015	.002 ± .001	1.0	1.
20°	.18 ± .036	.005 ± .001	.86 ± .026	.0	1.	1.
22°	.19 ± .033	.005 ± .003	.69 ± .021	.0	1.	1.
23°	.21 ± .017	.025 ± .014	.09 ± .004	.0	1.	1.
24°	.35 ± .036	.020 ± .014	.11 ± .005	.0	1.	1.
25°	.22 ± .022	.003 ± .002	.00	.0	1.	1.
26°	.28 ± .025	.008 ± .008	.06 ± .004	.0	1.	1.
27°	.27 ± .024	.007 ± .003	.00	.0	1.	1.
28°	.28 ± .025	.004 ± .002	.06 ± .004	.0	1.	1.
29°	.32 ± .023	.005 ± .002	.05 ± .004	.0	1.	1.
30°	.17 ± .016	.000	.22 ± .007	.0	1.	1.

* a sc, p sc, anterior and posterior scutellars; iv, pv, inner and posterior verticals; oc, ocellar.

ing to the effect of temperature on the mean bristle numbers of *sc 1* have been reported previously (CHILD 1935). The *sc 1* flies in these experiments served, therefore, as controls. Those few experiments were discarded in which the bristle numbers of the *sc 1* flies differed from the results previously obtained. This type of control served as a very careful check on the temperature and the culture conditions.

The results of these experiments are presented in tables 1 and 2, and are illustrated in figures 1 and 2. At each temperature, between 50 and 300 flies of each type were counted. The results are given as mean bristle

TABLE 2
Effect of temperature on mean bristle numbers.
 Females

$T \pm .1^\circ$	$M_{p\ sc}$			M_{pv}		
	$sc\ 5/sc\ 5$	$sc\ 1/sc\ 5$	$sc\ 1/sc\ 1$	$sc\ 5/sc\ 5$	$sc\ 1/sc\ 5$	$sc\ 1/sc\ 1$
14°	.54 ± .054	.47 ± .033	.28 ± .033	1.	.93 ± .017	.020 ± .019
15°	.54 ± .048	.42 ± .049	.23 ± .012	1.	.98 ± .014	.060 ± .006
16°	.46 ± .035	.35 ± .028	.15 ± .025	1.	.97 ± .010	.045 ± .015
18°	.36 ± .029	.20 ± .028	.07 ± .077	1.	.95 ± .015	.077 ± .088
19°	.34 ± .034	.18 ± .041	.04 ± .025	1.	.95 ± .023	.036 ± .025
20°	.25 ± .036	—	.02 ± .001	1.	—	.086 ± .008
22°	.09 ± .024	.09 ± .031	.01 ± .004	1.	.97 ± .018	.045 ± .009
23°	.07 ± .015	.08 ± .019	.01 ± .002	1.	.98 ± .009	.028 ± .014
24°	.09 ± .023	.04 ± .016	.00	1.	.98 ± .009	.000
25°	.06 ± .018	.04 ± .020	.01 ± .009	1.	.96 ± .020	.012 ± .003
26°	.04 ± .015	.02 ± .011	.00	1.	.94 ± .018	.009 ± .009
27°	.05 ± .017	.00	.00	1.	.97 ± .013	.000
28°	.06 ± .016	.01 ± .009	.00	1.	.96 ± .018	.001 ± .001
29°	.05 ± .012	.03 ± .012	.00	1.	.78 ± .031	.000
30°	.06 ± .015	.03 ± .011	.00	1.	.74 ± .026	.000

$T \pm .1^\circ$	M_{oc}			$M_{a\ sc}$		
	$sc\ 5/sc\ 5$	$sc\ 1/sc\ 5$	$sc\ 1/sc\ 1$	$sc\ 5/sc\ 5$	$sc\ 1/sc\ 5$	$sc\ 1/sc\ 1$
14°	1.	.93 ± .017	.00	.14 ± .037	.18 ± .025	.04 ± .026
15°	1.	.94 ± .024	.00	.13 ± .035	.18 ± .038	.09 ± .008
16°	1.	.96 ± .011	.00	.20 ± .028	.12 ± .019	.08 ± .021
18°	1.	.98 ± .009	.00	.25 ± .027	.23 ± .028	.09 ± .009
19°	1.	.99 ± .011	.00	.38 ± .035	.39 ± .052	.07 ± .035
20°	1.	—	.00	.49 ± .042	—	.13 ± .003
22°	1.	.99 ± .011	.00	.61 ± .039	.50 ± .054	.17 ± .006
23°	1.	1.	.01 ± .007	.63 ± .028	.55 ± .034	.22 ± .031
24°	1.	1.	.04 ± .018	.68 ± .037	.58 ± .033	.24 ± .040
25°	1.	1.	.08 ± .008	.69 ± .033	.51 ± .050	.17 ± .011
26°	1.	1.	.40 ± .050	.64 ± .036	.50 ± .038	.12 ± .033
27°	1.	1.	.41 ± .021	.61 ± .038	.46 ± .039	.14 ± .015
28°	1.	1.	.60 ± .013	.62 ± .033	.50 ± .044	.06 ± .006
29°	1.	1.	.75 ± .017	.61 ± .029	.50 ± .037	.05 ± .009
30°	1.	1.	.85 ± .020	.52 ± .030	.45 ± .030	.05 ± .009

$T \pm .1^\circ$	M_{is}		
	$sc\ 5/sc\ 5$	$sc\ 1/sc\ 5$	$sc\ 1/sc\ 1$
14°	.94 ± .022	.93 ± .018	.98 ± .019
15°	.99 ± .01	1.	1.
16°	1.	1.	1.

M. i.v. = 1 at higher temperatures.

numbers per half fly. The *sc 1* curves contain additional points from data previously obtained (CHILD 1935).

DISCUSSION OF RESULTS

With one exception, the i.v.,¹ the bristle numbers of the *sc 5* stock are higher than the *sc 1*. With respect to the i.v. bristle, *sc 5* is therefore a more extreme allele than *sc 1* (fig. 2). Furthermore, as pointed out previously (CHILD 1935) this variation in the M. i.v. is contrary to the subgene hypothesis (DUBININ 1929, 1932, GAISSINOVITSCH 1930), since the i.v. is in a center outside both the *sc 1* and *sc 5* centers as postulated by the Russian workers.

It is further evident from these data that the mean bristle number of a particular bristle (if at all variable) varies in the same way with temperature in the *sc 1*, *sc 5*, and *sc 1/sc 5* stocks.

The bristle numbers of the *sc 1/sc 5* are intermediate between *sc 1* and *sc 5*, although this relationship is somewhat obscured at low temperatures for the asc. The mean bristle numbers of *sc 1/sc 5*, moreover, are closer to those of *sc 5* than *sc 1*. In other words, *sc 5* appears to be "dominant" over *sc 1*. However, the degree of this dominance is not the same for all bristles, and, furthermore, it is not the same for the same bristle at different temperatures.

The data on the pv and the oc bristles (these should not have varied in *sc 1/sc 5* according to subgene hypothesis) illustrate a problem which has been recognized by *Drosophila* workers on other characters; PLUNKETT (1926) on *Dichaete*, MOHR (1932) on *vestigial*, BARON (1935) on *eyeless*, TIMOFEEF-RESSOVSKY (1934) on *venation*, and others. This point can be best made clear by citing specific examples. MOHR (1932) found that *vgⁿⁱ/vgⁿⁱ* (nicked) and the wild type are alike phenotypically, both giving normal wings. This, however, does not imply that the concentration of some substance or substances producing the character, normal wings, is the same in both genotypes. This was shown by comparing nicked and the normal allele in combination with the other mutant alleles of *vestigial*. In combination with *vg* alleles, the character nicked could be discerned. Other slight *vg* alleles showed a similar behavior, their expression depending also upon environmental conditions, especially temperature. BARON (1935) in analyzing isogenic populations of *ey* (*eyeless*) *drosophilae* found that there was a variation in the amount of eye producing substance among the "no-eyed" *eyeless*, although all the "no-eyed" flies had less than the amount needed to produce eyes.

At Minnesota with Dr. HURT (data unpublished) I found a similar situation in a character in *Gallus* known as "down defect," a bald spot

¹ For meanings of the bristle abbreviations see footnote to table 1.

FIGURE 1.—Effect of temperature on mean bristle number. Ordinates, mean bristle numbers; abscissae, temperature in °C.

○ = SC 1   ◐ = $\frac{SC\ 1}{SC\ 5}$ ● = SC 5

FIGURE 2.—Effect of temperature on mean bristle number. Ordinates, mean bristle number; abscissae, temperature in °C.

○ = sc 1   ◐ = $\frac{sc\ I}{sc\ 5}$ ● = sc 5

on the head of the fowl. In populations homozygous for down defect there is a variation in the size of the bald spot, a certain percentage of the fowls not showing the character at all, although genetically down defect. A statistical analysis of such a population indicated that a definite percentage of "normal" fowl were to be expected, if one assumed a distribution in amount of "down defect producing substance" among the individuals of a homozygous down defect population. The "normal" fowl in this analysis had varying quantities of a smaller amount of "down defect producing substance" than the threshold amount needed to show the character.

In all these instances where the expression of a character depends upon a threshold amount of character producing substance, any amount less than the threshold will have no effect. An analogous situation may be seen

FIGURE 3.—Hypothetical distributions in concentrations of bristle producing substance for a particular bristle. The numbers 1-6 refer to various populations. T is the threshold concentration.

in muscle contraction where any subminimal stimulus evokes no response. If the character is variable such as wing or eye size, varying amounts of substance above the threshold may produce varying degrees of character expression. With respect to bristle production, however, the situation is more complex. A particular bristle is either present or absent, like the all-or-nothing principle in the contraction of a single muscle fiber. Any amount of substance above the threshold amount will produce only one bristle.

The effect of the threshold with respect to a bristle is illustrated in figure 3. Populations such as 2-4 will have mean bristle numbers between 0 and 1 (curve 2 near 0, curve 4 near 1). Populations which do not cross the threshold value will have mean bristle numbers of 0 if on the left or of 1 if on the right of threshold, although these populations differ from one another, for example 5 and 6.

In *sc 5* (fig. 2) the oc bristle is never affected (is like the wild type) at all temperatures (like curves 5, 6 in fig. 3). In *sc 1* the oc bristle is absent in all flies raised under 22° (like curve 1 in fig. 3). The M. oc increases rather sharply with increasing temperature (like curves 2-4). In *sc 1/sc 5*

the M. oc equals 1 above 20°, and is less than 1 below 20°. These results indicate that although the M. oc in *sc 5* is 1 at all temperatures, the concentration of bristle producing substance is not the same at all temperatures and similarly for *sc 1* below 22°. The p.v. bristle (fig. 2) behaves in a somewhat similar manner. The temperature effect on *sc 1/sc 5* indicating that either *sc 1/sc 1* and *sc 5/sc 5* or both have a decreasing amount of bristle producing substance with increasing temperature above 25°. In *sc 1 sc 1*, since the amount is already below the threshold (curve 1 and 2, figure 3), no further effect on the bristle number can be seen. In *sc 5/sc 5* the inference is that the amount of bristle producing substance although decreasing above 25° does not cross the threshold.

According to this interpretation, in order to use mean bristle number as an exact quantitative character in a study of the chemical kinetics involved in bristle production, a statistical or experimental analysis of one bristle and no bristle must be made. PLUNKETT (1926) found that because of the arbitrary assumptions needed in a statistical analysis, a satisfactory result could not be obtained. It is hoped that experimental studies with combinations of other scute alleles will shed more light on the problem.

A study of the temperature effective periods of these stocks is being made. Preliminary results indicate that both the temperature-effective periods and the time of development differ in these three stocks.

SUMMARY

1. The mean bristle numbers in isogenic stocks of *sc 1*, *sc 5*, and *sc 1/sc 5* were determined at temperatures ranging from 14° to 30°.
2. *Sc 1* is a more extreme allele than *sc 5* for all bristles affected except the i.v. bristle.
3. The effect of temperature on the mean bristle number is in the same direction in the three stocks.
4. The mean bristle number of *sc 1/sc 5* is intermediate between *sc 1* and *sc 5* at all temperatures.
5. The problem of thresholds as applied to the presence and absence of a particular bristle is discussed.

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