DOSAGE AT THE *SCUTE* LOCUS, AND CANALISATION OF
ANTERIOR AND POSTERIOR SCUTELLAR BRISTLES
IN *DROSOPHILA MELANOGASTER*

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AN extensive analysis of the genetic variation underlying the canalised character scutellar bristle number in *Drosophila melanogaster*, has led to the development of the following model by RENDEL (1959, 1962). A population of individuals has an observed mean phenotypic value which is a continuous function of a single developmental variable. This variable has been termed "make" to avoid the implication that a particular substance is necessarily involved (RENDEL 1962). A number of scutellar bristles greater or less than four occurs only when the level of make in an individual falls outside a range of values bounded by an upper and a lower threshold. Assuming the variation among individuals in a population to be normally distributed on the underlying scale, the frequency of flies with missing bristles (3 or less), or with additional bristles (5 or more), can be related to the mean and variance of the distribution of make by use of the probit transformation. Control of development to give the normal four bristles on the scutellum operates over a range of approximately six standard deviations on this underlying scale (RENDEL, SHELDON and FINLAY 1965).

ROBERTSON (1965) has questioned the biological validity of using the probit transformation to analyse this character, since the formation of four bristles in their normal sites may not be a sequential or cumulative process. ROBERTSON suggested an alternative model in which the primary phenomenon is the control of development leading to one and only one bristle at each site, and argued that the probit transformation would then be applicable only to the events at a single site. Total scutellar bristle number is then a secondary measure which is a function of the respective site probabilities, which ROBERTSON assumed to be independent in any given individual.

In support of his model, RENDEL (1965) presented convincing evidence for a lack of independence of bristle formation at different sites in populations homozygous for the sex-linked mutant *scute*. This mutant leads to a marked, average reduction in scutellar bristles. From observations of the respective probabilities of formation of a bristle at anterior and posterior sites on the scutellum, RENDEL calculated the expected distributions of scutellar bristle patterns for a number of populations based on ROBERTSON's model of independence. In all populations the observed frequencies were shown to depart from expectation in a characteristic manner, which in *scute* populations of high mean bristle number led to a higher

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degree of canalisation of the four bristle phenotype than is predicted by ROBERTSON's model. On the other hand, STURTEVANT (1932) and YOUNG and LEWONTIN (1966) have shown that in bilateral scutellar mosaics, *scute* and wild-type tissue is autonomous in bristle formation.

An additional dose of the *scute* locus was shown by FRASER and GREEN (1964) and by RENDEL, SHELDON and FINLEY (1965) to lead in all cases to an increase in total scutellar bristle number. RENDEL *et al.* (1965) observed that the magnitude of the dosage effect, measured on the underlying scale, is considerably reduced in populations with a mean level of make approximating that of wild-type stocks. They have interpreted these observations in terms of a model in which the activity of the *scute* locus is under the control of the developmental system as a whole, the gene being progressively "switched off" as the wild-type level of make is approached.

The present study is concerned with the effects on both scutellar bristle number and pattern of multiple doses of mutant *scute* alleles in an unselected genetic background. Three *scute* alleles differing in activity at normal dose, and differing in the relative frequency of anterior and posterior bristles on the scutellum, have been employed. The objective of the study was to examine the adequacy of the hypothesis of a single scale of "make" in accommodating the effects of multiple doses of qualitatively different alleles at a single locus.

MATERIALS AND METHODS

The three *scute* alleles used in this study are sc^1 , $sc^{+60e17.4}$ (sc^{60}) and sc^{+59k9} (sc^{59}). The sc^1 allele has a mean scutellar bristle number of 0.55 ± 0.02 in males and 1.39 ± 0.02 in females. The other two alleles are X-ray induced revertants of sc^1 ; the mean number of bristles in sc^{60} being 3.88 ± 0.01 in males and 4.08 ± 0.01 in females, while for sc^{59} the means are 4.00 ± 0.01 and 4.02 ± 0.01 in males and females, respectively. The last mentioned allele is phenotypically indistinguishable from the standard wild-type allele.

Two classes of chromosomes were produced for this study. (1) Several Y-chromosomes were constructed each of which carried one of three *scute* alleles. The techniques for their construction are described by FRASER and GREEN (1964) using methods developed by BROSEAU, NICOLETTI, GRELL and LINDSLEY (1961). One Y carried sc^1 , and two Y-chromosomes were constructed independently for each of the alleles sc^{60} and sc^{59} . From Table 1 it can be seen that each of these Y-chromosomes carried few other X-chromosome genes. (2) From each of the above Y-chromosomes, an attached-XY stock was constructed carrying one of the alleles sc^1 , sc^{60} or sc^{59} in double dose. These were recovered as detachments from attached-X females carrying one or other of the specific Y-chromosomes described above. For sc^{60} and sc^{59} the genotypic constitution of the attached-X females which yielded the XY detachments was $\gamma^2 sc^x su-w^u w^u := \gamma^2 sc^x su^+-v su^+-w^u.Y$ (sc^x refers to either $sc^{+60e17.4}$ or sc^{+59k9}). These detachments, which would be of the constitution $X.Y.\gamma^2$, $\gamma^2 sc^x su-w^u w^u.Y$, $su^+-w^u su^+-v sc^x \gamma^2$, were recognised as unsuppressed white-apricot males. The attached-XY chromosome carrying the sc^1 allele was recovered as a detachment from $\gamma^2 sc^1 w^{i-p} := \gamma^+ sc^1 su^+-v su^+-w^u.Y$ females and recognized as a γ^+ male. The genetic constitution of these attached-XYs is shown in Table 1.

With these chromosomes, populations of individuals were independently produced carrying 1, 2 or 3 doses of the *scute* locus in males, and 2, 3 or 4 doses in females. The genotypes of these individuals are shown in Table 2. In a number of cases, for a given dose level, a number of populations differing in genetic background were scored. Females carrying 3 doses of sc^1 were also produced from the attached-X stock $\gamma^2 sc^1 w^{i-p} :=$ and $sc^1.Y$. Individuals from each of four replicate cultures were scored for each population.

TABLE 1

Genotypic constitution of the chromosomes used and their respective text references

Genotype	Text reference
<i>sc</i> ¹	
γ^2 <i>sc w</i> ^{i-p}	<i>sc</i> ¹
γ^+ <i>sc su</i> ⁺ - <i>v su</i> ⁺ - <i>w</i> ^a . <i>Y</i>	<i>sc</i> ¹ . <i>Y</i>
γ^2 <i>sc w</i> ^{i-p} : =	<i>sc</i> ¹
<i>X.Y.</i> γ^2 , γ^2 <i>sc w</i> ^{i-p} . <i>Y.</i> <i>su</i> ⁺ - <i>w</i> ^a <i>su</i> ⁺ - <i>v sc</i> γ^+	<i>sc</i> ¹ . <i>sc</i> ¹ . <i>Y</i>
<i>sc</i> ^{60e17.4}	
γ^2 <i>sc su-w</i> ^a <i>w</i> ^a	<i>sc</i> ⁶⁰
γ^2 <i>sc su</i> ⁺ - <i>v su</i> ⁺ - <i>w</i> ^a . <i>Y</i> ₁	<i>sc</i> ⁶⁰ . <i>Y</i> ₁
γ^2 <i>sc su</i> ⁺ - <i>v su</i> ⁺ - <i>w</i> ^a . <i>Y</i> ₂	<i>sc</i> ⁶⁰ . <i>Y</i> ₂
<i>X.Y.</i> γ^2 , γ^2 <i>sc su-w</i> ^a <i>w</i> ^a . <i>Y</i> ₁ . <i>su</i> ⁺ - <i>w</i> ^a <i>su</i> ⁺ - <i>v sc</i> γ^2	<i>sc</i> ⁶⁰ . <i>sc</i> ⁶⁰ . <i>Y</i> ₁
<i>X.Y.</i> γ^2 , γ^2 <i>sc su-w</i> ^a <i>w</i> ^a . <i>Y</i> ₂ . <i>su</i> ⁺ - <i>w</i> ^a <i>su</i> ⁺ - <i>v sc</i> γ^2	<i>sc</i> ⁶⁰ . <i>sc</i> ⁶⁰ . <i>Y</i> ₂
<i>sc</i> ^{+59k9}	
γ^2 <i>sc su-w</i> ^a <i>w</i> ^a	<i>sc</i> ⁵⁹
γ^2 <i>sc su</i> ⁺ - <i>v su</i> ⁺ - <i>w</i> ^a <i>su</i> ⁺ - <i>f.</i> <i>Y</i> ₁	<i>sc</i> ⁵⁹ . <i>Y</i> ₁
γ^2 <i>sc su</i> ⁺ - <i>v su</i> ⁺ - <i>w</i> ^a . <i>Y</i> ₂	<i>sc</i> ⁵⁹ . <i>Y</i> ₂
<i>X.Y.</i> γ^2 , γ^2 <i>sc su-w</i> ^a <i>w</i> ^a . <i>Y</i> ₁ . <i>su</i> ⁺ - <i>f su</i> ⁺ - <i>w</i> ^a <i>su</i> ⁺ - <i>v sc</i> γ^2	<i>sc</i> ⁵⁹ . <i>sc</i> ⁵⁹ . <i>Y</i> ₁
<i>X.Y.</i> γ^2 , γ^2 <i>sc su-w</i> ^a <i>w</i> ^a . <i>Y</i> ₂ . <i>su</i> ⁺ - <i>w</i> ^a <i>su</i> ⁺ - <i>v sc</i> γ^2	<i>sc</i> ⁵⁹ . <i>sc</i> ⁵⁹ . <i>Y</i> ₂

In high dose males, bristles were formed in regions not usually carrying a bristle in individuals of the normal genetic constitution. The convention used to identify the various scutellar bristle sites is depicted schematically in Figure 1. The anterior (a) and posterior (p) bristles are slightly curved bristles directed caudally and located on the anterior and posterior regions of the scutellum respectively (Figure 1B). The interstitial (i) bristles are located in a position intermediate between the anterior and posterior bristles on the side of the scutellum, and are curved dorsally and/or cephalically. Occasionally straight, caudally directed bristles occurred in an intermediate region. These were classified as anterior or posterior bristles, depending on their proximity to one or the other region.

The fourth class, the postscutellars (psc) (Figure 1A), which appeared only in three dose males, are located near the antero-dorsal margin of the metanotum (postscutellum). These bristles are approximately $\frac{2}{3}$ rd the size of the normal scutellar bristles and are curved dorsally.

Throughout this paper we will use the term *scutellar bristle number* to refer to all bristles on the scutellum. *Total bristle number* will be used when postscutellar bristles are also included.

In this analysis extensive use is made of the probit transformation (FINNEY 1947) which was developed for the statistical treatment of threshold phenomena. The use of this transformation

TABLE 2

Genotypes yielding the various doses employed for males and females

Dose	Sex	Genotype*
1	♂	<i>sc/Y</i>
2	♂	<i>sc-sc.Y/Y</i> or <i>sc/sc.Y</i>
	♀	<i>sc/sc</i>
3	♂	<i>sc-sc.Y/sc.Y</i>
	♀	<i>sc-sc.Y/sc</i> or <i>sc/sc.Y</i>
4	♀	<i>sc-sc.Y/sc-sc.Y</i>

* See Table 1 for description of chromosomes.

FIGURE 1.—Lateral (A) and dorsal (B) schematic views of the scutellum of *Drosophila melanogaster* showing the relative location of the bristle types.

to analyse phenotypically discontinuous characters, whose inheritance is polygenic, is discussed by FALCONER (1960). Its application to scutellar bristles in *Drosophila melanogaster* is discussed by RENDEL (1959, 1962) and LATTER (1964).

RESULTS

Table 3 summarizes the bristle counts for all the individual populations involved in the study. The frequency distributions of scutellar bristle number are given separately for males and females, for each of the three alleles studied, and for each genotype. The two independently produced sc^{60} and sc^{59} *Y* chromosomes and the corresponding attached-XY's are shown separately. In addition to total bristle number, mean bristle number in each of the four regions, *viz.* anterior, posterior, interstitial and post-scutellar, are also presented in the Table.

It can be seen from Table 3 that the bristle number distributions are not wholly determined by the combination of *scute* allele, gene dosage and sex. Comparable populations can be seen to differ appreciably in mean bristle score because of differences in genetic background, or because of differences between duplicate *Y* and attached-XY chromosomes derived by the same procedure. Despite this heterogeneity, the overriding effects of *scute* allele, dosage and sex are readily detected from the overall means presented in Figure 2.

There is clear evidence of an increase in bristle number in both sexes with increasing dosage of *scute*, and this affects both the number of bristles on the scutellum proper, and the frequency of postscutellar bristles at high dosage. As far as scutellar bristle number is concerned, the effect of dose is particularly marked in the case of sc^1 , but there is also a measurable increase with higher doses of sc^{60} and sc^{59} , which is analogous to the response to dose observed by RENDEL *et al.* (1965) in stocks with mean bristle number in the vicinity of 4.0. There is a suggestion that sc^{59} gives a greater response with dose than sc^{60} , but this difference between the two alleles must be gauged against the heterogeneity between populations evident from Table 3.

It can also be seen from Figure 2 that responses to dose are conspicuously

TABLE 3

Frequency distribution of scutellar bristle number, with means for individual regions

		Scutellar bristle number										Mean bristle number				
Allele	Dose*	0	1	2	3	4	5	6	7	8	Anterior	Posterior	Interstitial	Postscutellars	Total	
<i>sc</i> ¹ ♀ ♀	2	295	692	931	74	1	..	..	..	..	1.19	0.20	..	..	1.39	
	3A	1	17	421	870	1080	..	..	..	..	1.84	1.42	..	..	3.26	
	3A	13	6	277	1138	2566	..	..	..	..	1.92	1.64	..	..	3.56	
	3B	..	1	121	443	1059	..	..	..	..	1.93	1.65	..	..	3.58	
	4	..	..	25	206	1630	1	..	..	..	2.01	1.86	..	..	3.86	
♂ ♂	1	987	647	163	3	..	..	..	..	..	0.48	0.06	0.01	..	0.55	
	2C	..	1	68	399	1343	..	..	..	..	1.88	1.82	..	..	3.70	
	2C	..	3	139	397	1052	..	..	..	..	1.80	1.76	0.01	..	3.57	
	2D	..	4	125	578	1261	..	..	..	..	1.82	1.75	..	..	3.57	
	3	..	..	..	50	854	2	..	..	..	2.05	1.89	..	0.93	4.87	
<i>sc</i> ⁶⁰ ♀ ♀	2	..	..	..	4	974	24	5	..	..	2.05	1.98	..	..	4.03	
	2	..	..	..	1	1225	34	1	..	..	2.03	2.00	..	..	4.03	
	2	..	..	..	2	1216	178	32	..	..	2.19	1.98	..	..	4.17	
	3A ₁	..	..	..	..	1483	227	41	..	..	2.17	2.00	0.01	..	4.18	
	3A ₂	..	..	..	2	1359	279	70	..	..	2.24	2.00	..	..	4.24	
	4 ₁	..	..	..	2	706	282	113	..	..	2.45	2.00	0.01	..	4.46	
	4 ₂	..	..	..	..	866	153	31	..	..	2.20	2.00	..	..	4.20	
♂ ♂	1	..	1	8	107	914	2	..	..	..	2.04	1.84	..	..	3.88	
	2C ₁	..	..	..	3	1044	115	8	..	..	2.11	2.00	..	..	4.11	
	2C ₂	..	..	..	..	806	222	33	..	..	2.26	2.00	0.01	..	4.27	
	2D ₁	..	..	..	..	1074	82	..	..	..	2.07	2.00	..	..	4.07	
	2D ₂	..	..	..	..	1085	11	..	..	..	2.01	2.00	..	..	4.01	
	3 ₁	..	..	..	1	73	47	24	..	..	2.64	2.02	..	1.75	6.42	
	3 ₂	..	..	..	1	782	302	70	..	..	2.34	2.00	0.04	1.24	5.62	
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
<i>sc</i> ⁵⁹ ♀ ♀	2	..	..	1	4	1302	16	2	..	..	2.01	2.00	..	..	4.01	
	2	..	..	..	..	1751	31	1	..	..	2.02	2.00	..	..	4.02	
	2	..	..	..	..	2122	26	1	..	..	2.01	2.00	..	..	4.01	
	3A ₁	..	..	..	..	811	161	38	..	..	2.19	2.01	0.03	..	4.23	
	3A ₂	..	..	..	..	595	305	105	2	..	2.39	2.01	0.12	..	4.52	
	4 ₁	..	..	..	1	480	150	124	7	2	2.44	2.02	0.10	..	4.56	
	4 ₂	..	..	..	..	118	313	619	30	2	3.25	2.05	0.22	..	5.52	
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
♂ ♂	1	..	..	..	6	1216	..	..	..	..	2.00	2.00	..	..	4.00	
	2C ₁	..	..	..	..	1094	216	30	..	..	2.12	2.01	0.08	..	4.21	
	2C ₂	..	..	..	2	1272	261	41	1	..	2.12	2.01	0.09	..	4.22	
	2D ₁	..	..	..	2	756	100	37	1	..	2.13	2.00	0.07	..	4.20	
	2D ₂	..	..	..	..	400	396	221	2	..	2.68	2.01	0.13	..	4.82	
	3 ₁	..	..	..	..	63	42	44	3	1	2.67	2.01	0.25	0.99	5.92	
	3 ₂	..	..	..	..	44	58	68	2	..	2.68	2.08	0.41	1.48	6.65	
	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	

* Letters refer to chromosome constitution thus:

A—*sc-sc.Y/sc*B—*sc/sc.Y*C—*sc/sc.Y*D—*sc-sc.Y/Y*Subscripts refer to the independent origin of *sc.Y* chromosomes and their related *X.Y* chromosomes (see Table 1).

Populations having the same dose designation for any given allele have different genetic backgrounds.

FIGURE 2.—Mean scutellar, anterior and posterior number as a function of dose for each of the three *scute* alleles. Total bristle number refers to scutellar + postscutellar bristles.

different if measured separately for anterior and posterior scutellar bristles. A doubling of the dose of *sc¹* in males, which at normal doses have mean numbers of anterior and posterior bristles of roughly 0.5 and 0.1, respectively, leads to an increase in both means to approximately 1.8 bristles, and the addition of a further *sc¹* allele results in only a minor change. The effect of doubling the dosage of *sc¹* in females is again to bring the mean anterior and posterior bristle numbers to near equality, i.e. 2.0 and 1.9, respectively, by a disproportionate increase in posterior bristle frequency relative to anteriors. In each case the tendency is towards a regular configuration of two anterior and two posterior scutellar bristles per fly.

Apart from the effect on postscutellar bristles in 3 dose males, increases in dosage of *sc⁶⁰* and *sc⁵⁹* have influenced the anterior and interstitial bristles almost exclusively, with virtually no observable effects on the posterior scutellars (Table 3 and Figure 2). The absence of a measurable response in posterior bristle number with increasing dose could imply either (i) a greater degree of canalisation of the posterior sites by comparison with the anteriors, or (ii) a lack of effect of increasing dose on the underlying scale appropriate to posterior sites. A probit analysis of the data is therefore necessary to examine these alternatives in greater detail.

Probit analysis: A summary of the probit distances spanned by the important bristle number classes is given in Table 4 for each combination of *scute* allele, sex and gene dosage, considering in turn scutellar bristle number, anterior bristles and posterior bristles. No overall pattern of change in mean probit distance with increasing dose can be discerned, though a highly significant difference in the span of the "4" bristle class for scutellar bristles has been recorded for *sc⁵⁹*, in going from two to four doses in females. A comparable difference can also be inferred in *sc⁵⁹* males from the distribution of Table 3.

With regard to the probit distances pertinent to the anterior and posterior bristles separately, there are no clear-cut differences due to either *scute* allele or sex, though significant heterogeneity can be detected in the spans of the "2" bristle class in each case. The limited data suggest that females are more variable than males in the *sc⁶⁰* series for anterior bristles, and that the reverse is true for *sc⁵⁹*. No analogous significant differences exist for posterior bristles in the *sc⁶⁰* and *sc⁵⁹* series.

Despite this heterogeneity, the probit distances have been averaged over all populations to define the scale of measurement for each of the three variables, scutellar bristles, anterior bristles and posterior bristles. In the interpretation of response curves plotted in relation to these scales, the complications due to inequalities in variance must therefore be kept in mind. It should be emphasised that the three *scute* allele series did not contribute equally, if at all, to the overall average probit distances. The estimate of the width of the two-bristle class for scutellar bristles, and that of the one-bristle class for anteriors and posteriors, depended solely on observations of the *sc¹* series. However, the spans of the 2, 3, 5 and 6 scutellar bristle classes are in close agreement with those characteristic of populations with normal dosage of the *scute* locus, but the mean probit distance of 3.95 for the four-bristle class is conspicuously less than that normally observed in wild-type populations.

TABLE 4

Probit intervals for scutellar, anterior and posterior bristle classes

Allele	Dose	2	3	Scutellars 4	5	6	1	Anterior 2	3	1	Posterior 2	3
<i>sc</i> ¹ ♀	2	1.79 ± 0.05	1.51 ± 0.28				1.17 ± 0.03			1.33 ± 0.07		
	3	1.34 ± 0.11	1.05 ± 0.02				1.24 ± 0.05	3.85 ± 0.06		1.11 ± 0.02		
	4		1.06 ± 0.08	4.43 ± 0.29				4.34 ± 0.11	1.18 ± 0.28	1.11 ± 0.08		
	Means	1.57 ± 0.04	1.21 ± 0.10	4.43 ± 0.29			1.20 ± 0.03	4.10 ± 0.07	1.18 ± 0.28	1.18 ± 0.04		
♂	1	1.61 ± 0.18					1.29 ± 0.05			1.38 ± 0.18		
	2	1.47 ± 0.11	1.06 ± 0.03				1.24 ± 0.05	3.91 ± 0.11		1.12 ± 0.04		
	3			4.45 ± 0.24				4.21 ± 0.18		1.60 ± 0.23	4.32 ± 0.31	
	Means	1.53 ± 0.11	1.06 ± 0.03	4.45 ± 0.24			1.27 ± 0.04	4.06 ± 0.10		1.37 ± 0.10	4.32 ± 0.31	
<i>sc</i> ⁶⁰ ♀	2			4.48 ± 0.13	0.91 ± 0.07				0.95 ± 0.07			
	3			3.87 ± 0.22	0.94 ± 0.04				0.94 ± 0.04		6.39 ± 0.27	
	4			3.27 ± 0.22	0.92 ± 0.04			3.49 ± 0.30	0.93 ± 0.04		5.81 ± 0.34	
	Means			3.87 ± 0.11	0.92 ± 0.03			3.49 ± 0.17	0.94 ± 0.03		6.10 ± 0.22	
♂	1	0.72 ± 0.28	1.17 ± 0.12	4.10 ± 0.23				4.09 ± 0.14	1.43 ± 0.30			
	2			4.05 ± 0.19	1.18 ± 0.06			4.18 ± 0.23	1.17 ± 0.06		5.74 ± 0.25	
	3			3.15 ± 0.23	1.06 ± 0.05				1.17 ± 0.06		5.72 ± 0.29	
	Means	0.72 ± 0.28	1.17 ± 0.12	3.77 ± 0.13	1.12 ± 0.04			4.14 ± 0.13	1.26 ± 0.10		5.73 ± 0.19	
<i>sc</i> ⁵⁹ ♀	2		0.5 ± 0.33	4.88 ± 0.18	0.95 ± 0.14			4.96 ± 0.19	0.94 ± 0.14			
	3				0.99 ± 0.04	1.64 ± 0.22			0.99 ± 0.05		5.56 ± 0.33	
	4			3.34 ± 0.31	0.82 ± 0.03	1.90 ± 0.07			0.88 ± 0.03		4.77 ± 0.19	1.00 ± 0.14
	Means		0.5 ± 0.33	4.11 ± 0.18	0.92 ± 0.05	1.77 ± 0.12		4.96 ± 0.19	0.94 ± 0.05		5.17 ± 0.19	1.00 ± 0.14
♂	2			3.46 ± 0.13	0.99 ± 0.03	1.68 ± 0.15		3.63 ± 0.15	1.05 ± 0.04		5.60 ± 0.24	1.04 ± 0.28
	3				0.79 ± 0.07	1.68 ± 0.17			0.92 ± 0.08			
	Means			3.46 ± 0.13	0.89 ± 0.04	1.68 ± 0.11		3.63 ± 0.15	0.99 ± 0.05		5.60 ± 0.24	1.04 ± 0.28
	Overall means	1.39 ± 0.18	1.06 ± 0.13	3.95 ± 0.18	0.96 ± 0.04	1.73 ± 0.06	1.23 ± 0.03	4.07 ± 0.14	1.05 ± 0.05	1.28 ± 0.08	5.49 ± 0.23	1.02 ± 0.02

It can be seen from Table 4 that a marked contrast is shown in the span of the two-bristle classes for anterior and posterior bristles. In spite of the fact that the probit distances for the one- and three-bristle classes are comparable in magnitude, the span of the two-bristle class for posteriors is 35% greater than that for anteriors (last line, Table 4). Throughout Table 4, wherever direct comparisons are possible for the same combination of allele, dose and sex, the ratio of the two probit distances is consistently greater than unity for the sc^{60} and sc^{59} populations. There is, therefore, direct evidence of a higher degree of control over the normal phenotype for posterior bristles than that for anterior bristles.

Responses to increasing dose of the three *scute* alleles are plotted in probit units in Figure 3 for scutellar bristles, posterior bristles and anterior bristles separately. The probit distances of the bristle number classes are those given in the last line of Table 4. Probit values are plotted relative to the thresholds indicated in the figure. Where there are several estimates for a given dose, all such points are plotted relative to the same threshold. It is evident from the figure that for *each* of the *scute* alleles, the response to increased dose is quite different for anterior and posterior bristles, and this difference cannot be accounted for in terms of differences in variability of some of the populations on the probit scale.

In both males and females of the sc^i series, the changes in anterior probit score with increasing dose are close to linear, though there is some falling off at higher doses. For posteriors on the other hand, a single extra sc^i allele causes an increase of 3.69 units in males and 2.58 in females, while a further increase in dose adds only 0.40 and 0.76 probit units, respectively. In the sc^{60} and sc^{59} series the significant responses shown by scutellars and anteriors are essentially linear. For posteriors in the sc^{59} series there is a slight, though non-significant increase over the entire dose range, while for the sc^{60} populations only the first additional dose in males has a significant effect on posteriors.

Canalisation at 4 bristles: In view of the fact that anterior and posterior scutellar bristles have been shown to differ in both their degree of canalisation, and their response to increases in dosage of the *scute* locus, it is important to examine the nature of the canalisation of scutellar bristle number at a value of four. What in fact is the $\frac{3}{4}$ threshold on RENDEL's scale of "make," and how is it determined? In the same way, can we specify the factors determining the position of the $\frac{4}{5}$ threshold?

Figure 4 shows quite clearly the respective roles of the anterior and posterior bristles in determining the span of the four-bristle class for scutellar bristle number. In Figure 4A the percentage of flies with more than 3 scutellar bristles (Sc3), and the percentage of flies with more than 4 scutellar bristles (Sc4), are plotted as functions of mean probit score for scutellar bristles on the underlying scale. All populations scored in this study have been plotted, and cumulative unit normal distribution curves were kindly computed by Mr. C. E. NOVITSKI by the method of least squares for each set of points. It can be seen that the 50% points on the ordinate correspond as expected with the positions of the $\frac{3}{4}$ and $\frac{4}{5}$ thresholds, the span of the four-bristle class being 3.95 units (Table 4).

In Figures 4B and 4C the same percentages characterising scutellar bristle

FIGURE 3.—Response in probit units to increasing dose of the *scute* locus for the three alleles. Scutellar, anterior and posterior bristles are plotted separately (○—males; □—females). Vertical lines represent the maximum confidence interval for points at a given dose, displaced to the left for males and to the right for females where necessary.

FIGURE 4.—The percentage of flies with more than three scutellar bristles (Sc3, A3, P3), and with more than four scutellar bristles (Sc4, A4, P4), plotted as a function of mean probit score of the population for each of: (A) Scutellar bristle number; (B) Anterior bristle number; (C) Posterior bristle number. Cumulative normal distribution curves have been fitted by the least squares procedure.

number are plotted as a function of the mean probit score for anterior and posterior bristles, respectively. Cumulative unit normal curves of best fit are drawn for each set of points. It can readily be seen from curve A4 that a population with 50% of flies having more than four scutellar bristles (i.e. with the median of the distribution corresponding to the position of the $\frac{4}{5}$ threshold) also has a mean on the underlying scale for anteriors which is almost coincident with the position of the $\frac{2}{3}$ threshold. On the other hand it can be seen from curve P4 that the same population has a mean on the underlying scale for posteriors which is 2.95 standard deviations below the $\frac{2}{3}$ threshold. Similarly, the comparison between curves A3 and P3 show that the specification of the position of the $\frac{3}{4}$ threshold for scutellar bristle number is primarily a function of the $\frac{1}{2}$ threshold for posterior bristles.

Table 5 summarizes tests of goodness-of-fit of the unit normal curve for each set of points. The deviations of observed percentages from curve Sc4 are not statistically significant, while the significant χ^2 value for departure from curve Sc3 is due almost entirely to populations of females with two doses of *sc⁵⁹*. The span of the 4-bristle class for these populations is conspicuously different from the overall average (Table 4), and the deviant points give some guide to the scatter expected from heterogeneity in variance on the underlying scale. The four remaining curves in Figure 4 (A3, A4, P3, P4) all leave an appreciable proportion of the variation unexplained; the relative magnitude of the residual variation again reflecting the different role of anterior and posterior bristles in the determination of the $\frac{3}{4}$ and $\frac{4}{5}$ thresholds (Table 5).

The nature of the canalisation of scutellar bristle number at a value of four is, therefore, clearly demonstrated by the results of this study. Populations with a high frequency of four-bristle flies, i.e., those with mean values near the centre of the canalisation zone on the underlying scale, show a frequency of phenotypic deviants with 5 or more bristles which is determined essentially by the frequency of flies with 3 or more anterior bristles (Figure 4B). Deviants with 3 or fewer scutellar bristles occur with a frequency closely related to that of flies with 1 or 0 posterior bristles (Figure 4C).

In view of this obvious difference between anterior and posterior bristles in the determination of the zone of canalisation at four scutellar bristles, it is important to give some details of bristle patterns in these populations. Table 6 sets out the

TABLE 5

The proportion of the total variation accounted for by regression, calculated for the observed percentages of figure 4

Underlying scale	Scutellar bristle number threshold	
	$\frac{3}{4}$	$\frac{4}{5}$
Scutellar bristles	0.995*	1.000
Anterior bristles	0.891*	0.958*
Posterior bristles	0.980*	0.583*

* Denotes significant χ^2 value for departure from the fitted theoretical curve.

TABLE 6

Percent of three and four bristle individuals with various bristle patterns

	Dose	a_3	3 bristles a_2p_1	a_1p_2	a_4	4 bristles a_3p	a_2p_2	Mean scutellar number
sc^1 ♀ ♀	2	..	90.4	9.6	..	..	..	1.39
	3	0.5	79.7	19.8	..	0.7	99.3	3.47
	4	1.5	89.3	9.2	..	1.8	98.2	3.86
	Homo 2*	2.5	95.0	2.5	..	3.2	96.6	3.92
sc^1 ♂ ♂	2	0.2	55.8	43.9	..	0.2	99.8	3.61
	3	..	91.8	8.2	..	5.6	94.4	3.94
	Homo 2*	..	62.1	37.9	0.2	0.3	99.5	3.80
sc^{60} ♀ ♀	2	..	..	..	..	1.1	98.9	4.08
	3,4	..	..	..	..	..	100	4.21, 4.33
sc^{60} ♂ ♂	1	0.9	93.5	5.6	0.1	4.9	95.0	3.88
	2,3	..	..	..	..	..	100	4.12, 4.50
sc^{59} ♀ ♀	2,3,4	..	..	..	..	..	100	4.01, 4.38, 5.04
sc^{59} ♂ ♂	2,3,4	..	..	..	..	..	100	4.00, 4.36, 4.72

* Data from Rendel (1965).

† The notation a_2p indicates a configuration of two anterior bristles and one posterior bristle.

distribution of the various patterns for individuals with three and four scutellar bristles. For comparison, data from RENDEL (1965) are also included. Patterns were not scored in this study for left and right hand sides of the scutellum, and the notation a_2p means 2 anteriors and 1 posterior bristle. Observations during scoring indicated that the frequency of individuals with two bristles on one side of the anterior or posterior region, and none on the other side, were extremely rare. It is obvious from Table 6 that a "prepattern" of two anterior and two posterior bristles, i.e., a_2p_2 flies, is preferentially satisfied. The distributions of bristle patterns from this study are comparable with those of RENDEL (1965) for populations having similar mean scutellar bristle number. The frequency of deviant patterns, namely the a_3 and a_3p types are low. In all cases where the mean bristle number is greater than four, essentially all four bristle flies are a_2p_2 .

Considerations to this point have been restricted to bristles occurring in close proximity to regions characteristically possessing bristles in wild-type populations. Table 7 summarises the mean number of the two supernumerary bristles (postscutellars and interstitials) in three dose males. The mean number of these supernumerary bristles in sc^1 is 0.93 while in the near wild-type alleles sc^{60} and sc^{59} , it is 1.50 and 1.57, respectively. The contribution of the interstitials to supernumeraries in sc^{60} was of no consequence, but in sc^{59} they contributed some 21% to the supernumerary mean.

The probit intervals for the postscutellar bristle classes for 3 dose males for each allele (Table 8) are quite different in magnitude from the normal scutellar bristles (see Table 6). In every case the probit intervals for the 1, 2, 3 and 4

TABLE 7

Mean number of the two supernumerary bristles in males carrying 3 doses of the scute locus

Male genotype	Postscutellars	Interstitials
$sc^1 \cdot sc^1 \cdot Y / sc \cdot Y$	0.93 ± 0.03	
$sc^{60} \cdot sc^{60} \cdot Y_1 / sc^{60} \cdot Y_1$	1.75 ± 0.10	
$sc^{60} \cdot sc^{60} \cdot Y_2 / sc^{60} \cdot Y_2$	1.24 ± 0.03	
Mean	1.50 ± 0.05	
$sc^{59} \cdot sc^{59} \cdot Y_1 / sc^{59} \cdot Y_1$	0.99 ± 0.11	0.25 ± 0.03
$sc^{59} \cdot sc^{59} \cdot Y_2 / sc^{59} \cdot Y_2$	1.48 ± 0.09	0.41 ± 0.05
Mean	1.24 ± 0.07	0.33 ± 0.03
Mean number of postscutellars + interstitials 1.57 ± 0.08 .		

bristles classes are less than unity, and no one bristle class appears to be more highly canalised than any other.

DISCUSSION

The results of this study indicate that a single developmental scale does not provide an adequate description of the phenomenon of canalisation of scutellar bristles in *D. melanogaster*. Three facts have emerged from this study: (i) posterior bristles are more strongly canalised than anteriors; (ii) there is a different response of anterior and posterior bristles to increasing dosage of the *scute* gene; and (iii) posterior bristles play a different role from anteriors in defining the $\frac{3}{4}$ and $\frac{4}{5}$ thresholds responsible for canalisation at 4 bristles.

Though it is possible to accommodate the observations of *total scutellar* bristle number on a single scale, our results reinforce ROBERTSON'S (1965) suggestion that scutellar number should be resolved into its more basic components. Whereas an interpretation of total scutellar bristle number might suggest a gradual "switching-off" of the *scute* locus as the four bristle zone is approached (RENDEL *et al.* 1965), the observations reported here show this to be particularly marked

TABLE 8

Probit intervals of postscutellar bristles in males carrying 3 doses of the scute locus

Male genotype	Probit interval			
	1	2	3	4
$sc^1 \cdot sc^1 \cdot Y / sc^1 \cdot Y$	0.66 ± 0.04	0.88 ± 0.06	0.73 ± 0.10	0.69 ± 0.21
$sc^{60} \cdot sc^{60} \cdot Y_1 / sc^{60} \cdot Y_1$	0.61 ± 0.10	1.00 ± 0.12	0.78 ± 0.14	
$sc^{60} \cdot sc^{60} \cdot Y_2 / sc^{60} \cdot Y_2$	0.70 ± 0.03	0.80 ± 0.04	0.67 ± 0.06	0.97 ± 0.16
Means	0.69 ± 0.03	0.82 ± 0.04	0.68 ± 0.05	0.97 ± 0.16
$sc^{59} \cdot sc^{59} \cdot Y_1 / sc^{59} \cdot Y_1$	0.19 ± 0.06	0.52 ± 0.09	0.70 ± 0.15	0.86 ± 0.34
$sc^{59} \cdot sc^{59} \cdot Y_2 / sc^{59} \cdot Y_2$	0.63 ± 0.09	0.76 ± 0.10	0.67 ± 0.13	
Means	0.32 ± 0.05	0.63 ± 0.07	0.68 ± 0.10	0.86 ± 0.34

for the posterior bristles, with correspondingly little reduction in response at the anterior sites.

It has been shown quite conclusively by RENDEL (1965) that the formation of a bristle at one scutellar bristle site is not entirely independent of the formation of a bristle at the others when scutellar bristle number is less than four. In this region of the scale there is a direct relationship between bristle number and the underlying variable (i.e. position on the probit scale) not only for total scutellars, but also for the component anterior and posterior bristles. Consequently any preferential utilisation of a limited amount of morphogenetic substance by the anteriors for example, will reduce the amount available to the posteriors and thus lower posterior bristle number. However, in individuals with four bristles, where both the anterior and posterior bristles are canalised at a bristle number of two, change in bristle number is relatively insensitive to change of the underlying variable. It is then likely that the bristle number distribution will approach independence. In fact RENDEL (1965) found that the observed distribution which gave the best fit to an expectation based on the product of the respective bristle site probabilities was a selected population with the great majority of flies having four bristles.

STERN (1954) concluded that the reduction in thoracic bristle number occasioned by the mutant *achaete* was not due to a change in "prepattern." Our results are in agreement with these conclusions in that a prepattern of four scutellar bristles at normal positions is preferentially satisfied in populations carrying extra doses of *sc¹*.

RENDEL *et al.* (1965) argued that the degree of control of the activity of the *scute* locus is a function of the mean level of make. The higher the level of make, the greater the suppression of gene activity, with maximal control presumed to operate at a mean of four bristles. However, the appearance of appreciable numbers of postscutellar bristles in three dose males (Table 3) suggests considerable activity of the *scute* locus in populations which, by virtue of their scutellar bristle number, have reached a level where control of the *scute* locus should be maximal. An alternative to the hypothesis of a progressive switching-off of the *scute* gene as the four bristle zone is approached, might then be based on the ability of scutellar tissue to respond to increased gene product. The present study has shown that such a model must account for quite different responses at the anterior and posterior scutellar bristle regions.

SUMMARY

The effects on scutellar bristle number in *Drosophila melanogaster* of one, two and three doses of the *scute* locus in males, and two, three and four doses in females have been determined for three different alleles. It has been clearly demonstrated that the posterior scutellar bristles are more strongly canalised than the anterior scutellars and that they respond differently to increasing dosage of the *scute* locus. Further, the bristle thresholds responsible for canalisation at four scutellar bristles are quite differently determined. The specification of the $\frac{3}{4}$

bristle threshold on the underlying scale for scutellars is primarily a function of the $\frac{1}{2}$ threshold for posterior bristles, while the $\frac{4}{5}$ threshold depends almost exclusively on the relative position of the $\frac{2}{3}$ threshold for anterior bristles. These findings indicate that a single developmental scale does not adequately describe the phenomenon of canalisation of scutellar bristles.

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