THE PATTERN OF ABDOMINAL MICROCHAETAE IN *DROSOPHILA*

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Summary

The distribution pattern of abdominal microchaetae on the second and third tergites was examined in *wild-type* and *scute Drosophila melanogaster*. *Scute* was found to alter the pattern on each tergite, as well as bristle number and bristle density. An explanation of these results is given in terms of a prepattern–precursor complex involving competition among potential bristle-producing cells.

I. Introduction

Several current theories are concerned with genetic control of the development of bristle patterns on different parts of the body in *Drosophila*. Stern (1954) proposed that the position of the thoracic macrochaetes was determined by a "prepattern" or differential organization of the pupal hypodermis during the period of bristle differentiation. Maynard Smith (1960) discussed the genesis of prepatterns, and suggested that their origin may be explained in terms of chemical instabilities in morphogenetic fields (Turing 1952). Maynard Smith and Sondhi (1960, 1961) developed the concept of prepattern, considering it as the distribution of an inducing substance with regions of high concentration where bristles and ocelli of the head and thorax later differentiate. Bristle and ocelli differentiation also depend on the presence, in sufficient quantity, of a hypothetical bristle–ocelli-forming substance, or "precursor", which alternatively might be regarded as a varying competence of the tissues to react to a common bristle and ocelli-inducing stimulus (Stern 1954). They considered that several systems of genes were concerned with bristle determination. The prepattern is thought to be extremely stable, although two possible exceptions have been reported (Hannah-Alava 1958; Gottlieb 1964); in contrast, it is thought that the level of precursor or competence of the hypodermal cells may be altered easily by selection (Maynard Smith and Sondhi 1960; Reeve 1961; Rendel 1963; Sondhi 1965) or by the action of such mutant genes as *achaete*, *ocelli-less*, *scute*, *hairy*, *Theta*, and *engrailed* (listed by Gottlieb 1964). The action of *scute*, for example, has been shown to be autonomous in genetic mosaics (Stern and Swanson 1957; Young and Lewontin 1965), indicating that the competence of cells to react to the inducing stimulus, or prepattern, is altered in *scute* tissues.

Rendel (1962), considering the number of abdominal (sternite) bristles rather than their arrangement, suggested the term "make" to describe the sum of all influences, both genetic and environmental, which tend to produce bristles. The precursor of Maynard Smith and Sondhi may be considered as forming an integral part of Rendel's make. Whether the precursor is a specific chemical substance or a state of competence of the tissues is, in this case, immaterial.

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Claxton (1964) investigated a model, based on the proposals of Wigglesworth (1940, 1948), to explain some of the patterns of microchaetes. In the case of macrochaetes, the prepattern of Maynard Smith and Sondhi is assumed to consist of a series of peaks, and each peak determines the site of formation of a single bristle. Claxton suggested that with abdominal microchaetae, however, the prepattern peaks may be replaced by plateaux such that more than one bristle can form in the region bounded by a single plateau. With this modification the resulting pattern of microchaetes is controlled essentially by a competitive mechanism, bristle formation being inhibited only in areas immediately adjacent to other bristle sites. Stern (1954) also suggested that some form of inhibition occurs with thoracic macrochaetes which commence differentiating at predetermined sites, and apparently prevent further macrochaetes from developing in adjacent areas.

Such a competitive mechanism for the formation of microchaetae need not be held in direct opposition to the prepattern–precursor theory. Maynard Smith and Sondhi (1961) for reasons of economy sought to explain the arrangement of macrochaetes and microchaetes "by similar mechanisms, differing only in the accuracy with which they are regulated". However, they assumed specificity of the prepattern, whereas Claxton supposed the prepattern to be non-specific for the location of the microchaetes.

In the present work, the effect of the *scute* gene on the pattern of abdominal tergite microchaetae has been examined, and the results interpreted in relation to the above two theories of bristle initiation. The abdominal bristle pattern can be measured in terms of such characters as the total tergital bristle number, the "area ratio" (the area in which bristles are found relative to the total segmental area), the bristle density, and the spatial distribution of the bristles. Knowledge of these characters would also be useful in selection experiments designed to disrupt such patterns.

II. Methods

Flies were from a stock which had been maintained in the laboratory for several generations, and which was derived from the mating of several *wild-type* Oregon RC flies of both sexes with homozygous *scute*, *non-Curly* flies from a *Curly*, *scute* stock. Ten flies each of the five genotypes $++$, $+sc$, $scsc$, $+$, and sc were obtained from controlled matings of a few flies of known genotype. These matings were made in all possible genetic combinations, and the 10 flies of any one genotype came from several types of matings, except in the case of $++$ females, which were only obtained from the cross $++$ females $\times +$ males. Thus any differences between bottles were included in the within-genotype error variance, except that some bias may have been given to the results for $++$. But there was no indication of this type of bias in the results and therefore such effects have been assumed to be unimportant.

No statistically significant differences were found between the genotypes $++$ and $+sc$ for any of the traits examined, although an interaction significant at the 1% level ($F_{1:18} = 13{\cdot}96$) was found between genotype and tergite for bristle number. However, this was coupled with a highly significant difference between tergites ($F_{1:18} = 23{\cdot}65$, $P < 0{\cdot}1\%$), and a similar interaction for R (see below) was

only just significant at the 5% level. With the exception of bristle density, which was slightly higher in $+/sc$, all traits were very similar in the two genotypes. It was concluded that any real differences between $++$ and $+sc$ were negligible; consequently $+sc$ was excluded from further study.

Flies were taken at random about 2 days after eclosion. The only restriction, in the interests of uniformity, was that *scute* flies lacked all scutellar bristles. Individual flies were squashed whole in a drop of mounting medium under a coverslip, the wings being retained to aid positioning of the body before squashing. Drawings of the second and third abdominal tergites were made on squared millimetre graph paper, using a projection microscope. Since the zone of pigmentation of tergites did not appear to be affected by genotype, the anterior and posterior limits of pigmentation of each tergite were taken as the approximate anterior and posterior segmental boundaries. The real anterior boundaries of tergites were indeterminate and the real posterior boundaries frequently distorted and folded during squashing. Bristle sites were represented as small circles drawn around the individual bristle socket cells. The total bristle number of each tergite was recorded.

The total "tergital" area, and the area in which bristles were found, were calculated from the drawings on graph paper. On each tergite the posterior boundary of the area occupied by bristles was determined by the row of posterior medium-sized chaetae, and the anterior and lateral boundaries by straight lines connecting the most anterior and lateral microchaetae, respectively.

The bristle density was measured directly from the projection-microscope drawings, by taking a number of bristle counts in small rectangles of constant area located at random over the tergite, and also from the ratio of bristle number to the area occupied by bristles. Both methods had their disadvantages. The former was based on counts of very small numbers of bristles (range 5–15) and was influenced by any distortion of the mounted tergite; the latter was dependent on the location of boundaries of the area covered by bristles, and ignored any density variation across the tergite. A high positive correlation was found between the two estimates of bristle density ($r = 0{\cdot}90$, $P < 0{\cdot}1\%$ for all flies). For this work, therefore, bristle density estimations were obtained by the former method of direct counting in small constant areas, and these were probably least subject to bias. It was not considered necessary to transform the density data before analysis as a good approximation to a normal distribution was obtained.

The spatial distribution of bristles was measured by means of the formula $R = 2\bar{r}\sqrt{\rho}$, where $\bar{r}$ is the mean distance to nearest neighbour and ρ is the density (Clark and Evans 1954). The value of R, which varies according to $0 \leqslant R \leqslant 2{\cdot}1491$, indicates whether the distribution tends towards maximum uniform spacing or aggregation respectively, a value of R equalling unity indicating a random distribution. However, the use of R in the present study was somewhat limited. The bristle density across a tergite varied considerably, and its measurement was subject to both error and bias. For this reason, R was expected to show considerable

variation within genotypes alone. Its main use in the present study was to indicate any consistent differences in bristle arrangement rather than to measure such changes.

Some experimental error was introduced by the failure to obtain perfectly flat segments by squashing whole flies, and from the use of flies of different sizes and

TABLE 1

ABDOMINAL TERGITE CHARACTERISTICS OF THE FIVE GENOTYPES: MEANS AND STANDARD DEVIATIONS

Character	Genotype	Second Tergite	Third Tergite
Bristle number	*sc*	79·3 ± 7·9	77·8 ±10·7
	scsc	83·6 ±16·4	87·6 ±14·6
	+	113·5 ± 7·7	114·4 ± 9·7
	++	120·0 ±11·9	134·5 ±10·2
	+*sc*	128·4 ± 9·2	130·3 ± 7·1
Total tergite area (mm^2)	*sc*	63·64 ± 7·77	68·48 ± 6·32
	scsc	83·15 ± 9·04	88·61 ± 7·99
	+	66·28 ± 7·10	67·98 ± 9·15
	++	96·78 ± 5·44	104·76 ± 5·00
	+*sc*	97·36 ± 4·89	100·29 ± 3·65
Area of region in which bristles are found (mm^2)	*sc*	32·54 ± 3·86	32·95 ± 2·89
	scsc	42·74 ± 7·28	45·90 ± 7·25
	+	40·93 ± 5·19	42·01 ± 6·04
	++	59·18 ± 4·81	63·92 ± 3·52
	+*sc*	60·15 ± 3·41	61·40 ± 2·98
Area ratio	*sc*	0·513± 0·05	0·484± 0·05
	scsc	0·512± 0·05	0·517± 0·06
	+	0·618± 0·05	0·618± 0·03
	++	0·612± 0·04	0·610± 0·03
	+*sc*	0·618± 0·02	0·613± 0·03
Bristle density (No./mm^2)	*sc*	1·69 ± 0·23	1·71 ± 0·27
	scsc	1·48 ± 0·14	1·49 ± 0·17
	+	2·23 ± 0·25	2·17 ± 0·24
	++	1·70 ± 0·14	1·76 ± 0·31
	+*sc*	1·81 ± 0·15	1·81 ± 0·11
R	*sc*	1·55 ± 0·07	1·58 ± 0·07
	scsc	1·52 ± 0·06	1·54 ± 0·05
	+	1·65 ± 0·04	1·64 ± 0·04
	++	1·61 ± 0·04	1·64 ± 0·07
	+*sc*	1·65 ± 0·04	1·62 ± 0·05

weights. Correction of bristle density and total tergite bristle number according to fly weight would possibly have been more suitable but was not attempted. It was unlikely that such errors would seriously affect the experimental results, since differences between genotypes and sexes remained clear.

III. Results

Ideally the effects on the pattern of tergite microchaetae obtained by substituting the *scute* gene for its normal allele should be studied when the microchaetae first become established in the hypodermis. In the adult, the number of structures per unit area, for example, depends on the growth of the integument after bristle initiation, and this growth in turn may take place at different rates in different directions, thus distorting the initial spatial relationships between bristles.

Table 2

Analysis of variance of bristle number between *wild-type* and *scute* flies

Source of Variation	Degrees of Freedom	Mean Square	*F*
(1) Total flies			
Between flies			
Wild-type–scute (*P*)	1	29683·5	133·1***
Sex (*S*)	1	2070·6	9·3**
P × *S*	1	195·3	0·9
Replication	36	223·0278	
Within flies			
Tergite (*T*)	1	400·5	9·6**
P × *T*	1	208·0	5·0*
S × *T*	1	456·0	10·9**
P × *S* × *T*	1	82·1	2·0
Error	36	41·8583	
(2) Tergites separate			
Second tergite			
Wild-type–scute (*P*)	1	12460·9	93·4***
Sex (*S*)	1	291·6	2·2
P × *S*	1	12·1	0·1
Error	36	133·472	
Third tergite			
Wild-type–scute (*P*)	1	17430·6	132·6***
Sex (*S*)	1	2235·0	17·0***
P × *S*	1	265·3	2·0
Error	36	131·41388	

*$P < 0·05$. **$P < 0·01$. ***$P < 0·001$.

In the present study, at least total tergite bristle number and the relative size of the area in which bristles are found should, in the adult, be similar to the parameters existing in the juvenile stage immediately after bristle initiation. Due to growth following such initiation, bristle density, tergite area, and spatial distribution as measured by *R* may not be in such close agreement with the corresponding juvenile parameters.

(*a*) *Number of Bristles per Tergite*

The total bristle number of individual tergites was clearly altered in the presence of the *scute* gene (Table 1). The statistical significance of such differences

in bristle number was tested by variance analysis (Table 2). Since two of the two-factor interactions were significant, analyses were also performed separately for each tergite. The latter indicated that sex differences were more marked with the third tergite.

Although bristle number was higher on the third than on the second tergite in all except *scute* males, the tergite difference was only significant within *wild-type* females. Also bristle number was generally lower in males than in females. Evidently the significant interactions in the variance analysis were mainly a consequence of the relatively large differences in bristle number on the third tergite between *wild-type* and *scute* females.

TABLE 3

ANALYSIS OF VARIANCE OF TOTAL TERGITE AREA BETWEEN *WILD-TYPE* AND *SCUTE* FLIES

Source of Variation	Degrees of Freedom	Mean Square	F
Total flies			
Between flies			
Wild-type–scute (P)	1	1273·608	12·5**
Sex (S)	1	14288·788	140·6***
$P \times S$	1	954·962	9·4**
Replication	36	101·642	
Within flies			
Tergite (T)	1	498·800	70·6***
$P \times T$	1	0·475	0·1
$S \times T$	1	59·859	8·5**
$P \times S \times T$	1	40·044	5·7*
Error	36	7·060	

*$P < 0{\cdot}05$. **$P < 0{\cdot}01$. ***$P < 0{\cdot}001$.

Despite the demonstration that there are at least some real differences in bristle numbers between sexes and between the second and third tergites, these appear to be small in relation to the reduction in bristle number which accompanies the substitution of *scute* for its *wild-type* allele.

(*b*) *Differences in Tergite Area Measurements*

Two sets of data on tergite area were available, namely total tergite area (A_t) and tergite area in which bristles were found (A_b); in addition the relative area of each tergite in which bristles were found (area ratio = A_b/A_t) was determined for each tergite. The latter is most likely, in the adult, to represent the situation found in the pupa. Variance analysis of area ratio showed only a significant difference between *scute* and *wild-type* flies ($F_{1:36} = 67{\cdot}75$; $P < 0{\cdot}1\%$). But similar analyses for A_t and A_b (Tables 3 and 4) indicated significant sex and tergite differences, and also several significant interactions involving sex. Separate analyses for A_t and A_b for each sex indicated that area differences were higher in females than in males.

The difference in A_t between *scute* and *wild-type* males was not statistically significant. Differences in A_t between tergites within females were higher than differences in A_b, but this could be merely because A_t covered a larger area than did A_b.

Since no real differences in area ratio were found between sexes, it could be argued that the higher bristle number in females compared to that in males might result from differences in abdominal size at the time of bristle initiation. In this respect, A_b and A_t gave some indication of abdominal size and rate of growth, and both showed tergite area to be smaller in adult males than in adult females. However, area ratio might be expected to be less affected by these factors and more directly related to the tergite area at the time of bristle initiation.

TABLE 4

ANALYSIS OF VARIANCE OF TERGITE AREA IN WHICH BRISTLES WERE FOUND BETWEEN *WILD-TYPE* AND *SCUTE* FLIES

Source of Variation	Degrees of Freedom	Mean Square	F
Total flies			
Between flies			
Wild-type–scute (P)	1	3367·4018	64·8***
Sex (S)	1	5009·0873	96·4***
$P \times S$	1	361·4624	7·0*
Replication	36	51·937597	
Within flies			
Tergite (T)	1	110·5205	22·1***
$P \times T$	1	6·3000	1·3
$S \times T$	1	51·2160	10·2**
$P \times S \times T$	1	1·0466	0·2
Error	36	4·997425	

*$P < 0·05$. **$P < 0·01$. ***$P < 0·001$.

(*c*) *Differences in Bristle Density*

The results presented in Table 1 suggest that bristle density was dependent on both genotype and sex, and this was confirmed by variance analysis (Table 5). Additional analyses performed separately for each sex provided further evidence that no significant differences in bristle density existed between tergites. The presence of *scute* caused a reduction in bristle density in both sexes, and also a reduction of the difference between sexes. This is consistent with the reduction of the sex difference in A_b in the presence of *scute*, as both depend on relative abdominal and tergite growth after bristle initiation.

The higher bristle density in adult males compared to that in females could be due to a slower rate of growth of tergites in males after bristle initiation, i.e. initially bristle density may be the same in both sexes. This cannot, however, explain the lower bristle density in *scute* flies, since if A_t or A_b is used as an index of size and growth rate, the prediction would be for a higher bristle density in *scute* flies. One explanation is that the bristle density is lower in such flies at the time of initiation.

(*d*) *Differences in Spatial Distribution*

The ratio R, used as a measure of spatial distribution, was found by variance analysis to differ significantly at the 0·1% level between *scute* and *wild-type* flies only ($F_{1:36} = 44{\cdot}78$). R was lower in *scute* flies, indicating that bristle distribution was less uniform in the absence of the *wild-type* allele. However, such an apparent difference in R between *scute* and *wild-type* flies may not be due to real differences in the pattern of bristle initiation, as it could result from an increase in bristle density variation across a tergite in *scute* flies. An attempt was made to distinguish between these two alternatives by estimating bristle density separately in the lateral and central tergite areas in a small sample of male flies. Although a definite conclusion was impossible due to low numbers of bristles, particularly in such areas in *scute* flies,

TABLE 5

ANALYSIS OF VARIANCE OF BRISTLE DENSITY BETWEEN *WILD-TYPE* AND *SCUTE* FLIES

Source of Variation	Degrees of Freedom	Mean Square	F
Total flies			
Between flies			
Wild-type–scute (P)	1	2·7195	35·6***
Sex (S)	1	2·3427	30·7***
$P \times S$	1	0·3290	4·3*
Replication	36	0·076383	
Within flies			
Tergite (T)	1	0·0025	0·3
$P \times T$	1	0·0002	0·0
$S \times T$	1	0·0138	1·8
$P \times S \times T$	1	0·0183	2·3
Error	36	0·007847	

*$P < 0{\cdot}05$. **$P < 0{\cdot}01$. ***$P < 0{\cdot}001$.

there was some indication that increased bristle density variation across a tergite was found in the presence of scute. The coefficient of variation of mean distance to nearest neighbour measurements was also higher in these flies. It may be therefore that the difference in R between *scute* and *wild-type* flies resulted from a relatively lower bristle density in the central tergite areas of *scute* flies.

The main use of R in the present study was, as stated earlier, to give an indication of any change in bristle spatial distribution, rather than to measure such changes. It may be tentatively concluded that *scute* affects the relative spacing of the bristles. However, it should be recognized that a difference in mean R between *scute* and *wild-type* flies could be due to one or more of the following:

(1) A change in spatial distribution of bristles as well as in tergite bristle number due to the action of *scute*;
(2) Increased density gradients across tergites in *scute* flies;
(3) A reduced period of bristle initiation in *scute* flies; and
(4) Biased estimates of bristle density in *scute* flies due to low numbers of bristles.

IV. Discussion

(*a*) *Practical Results*

Comparisons of the bristle-distribution characters of *scute* and *wild-type* flies were partly limited, as most results were complicated to some degree by differences between sexes and between tergites. Nevertheless several definite conclusions could be reached. Substitution of the *scute* gene for its *wild-type* allele—in double dose in females since the gene is a sex-linked recessive—caused a decrease in bristle number, bristle density, and relative area covered by bristles. The magnitude of such differences was, however, difficult to establish. There was an unavoidable degree of experimental error, while the interactions with sexes and tergites in the analyses of variance lessened the significance of the differences between *scute* and *wild-type* flies. In particular, the magnitude of the sex difference often appeared to be dependent on genotype.

There was a query as to how much of the variation in the adult characters was due to different rates of expansion of the integument after bristle initiation, or alternatively due to differences in the initial size of tergites. That some differences in growth of tergite areas occurred between sexes, probably after bristle initiation, was strongly suggested by the finding of a higher bristle density in adult males than in females. There was no reason for supposing bristle density to be initially higher in males, especially since area ratio was similar in adults of both sexes. On the other hand, the results indicated that bristle density was probably lower in *scute* flies at the time of initiation. The smaller bristle number in mutant flies may therefore be attributed both to a decrease in bristle density and to a decrease in the magnitude of the area ratio.

Bristle density, A_b, and A_t were probably the only characters affected by growth after bristle initiation. Area ratio and R were only affected by the *scute* gene, whereas bristle density was affected by both sex and genotype, and in addition bristle number, A_b, and A_t showed differences between tergites.

(*b*) *Theoretical Implications*

By the use of genetic mosaics Stern and Swanson (1957) and Young and Lewontin (1965) have shown that *scute* alters the distribution of macrochaetes on the head and scutellum of *Drosophila*, and of microchaetes on the fifth adbominal sternite, by altering the competence of the hypodermal cells to react to an invariant prepattern. In the case of tergite microchaetae, it would appear that there is also present another system independent of, and in addition to, that determining whether bristles appear or not, since in *wild-type* flies, in particular, the spacing between bristles is fairly regular. This regularity of spacing suggests a competition between bristle-producing cells for an essential bristle-initiating substance (Wigglesworth 1940, 1948; Claxton 1964). The bristle-initiating substance may be regarded as a component of the competence, i.e. the precursor of Maynard Smith and Sondhi (1961). However, it could also be a substance independent of the prepattern–precursor complex. In what follows the bristle-initiating substance will be referred to simply as the bristle precursor. It should be noted that in this context the term precursor is

given its usual embryological meaning, which differs from Maynard Smith and Sondhi's definition.

Typical tergite microchaetae distribution patterns for *scute* and *wild-type* flies are shown in Figure 1. A possible explanation for such patterns, based on the assumptions outlined above, follows.

Maynard Smith and Sondhi (1961), utilizing Turing's (1952) diffusion-reaction theory of morphogenesis, considered the specific prepattern, responsible for the distribution of the macrochaetes and ocelli on the head of *Drosophila*, to consist of a series of peaks and valleys of concentration of some inducing substance or substances,

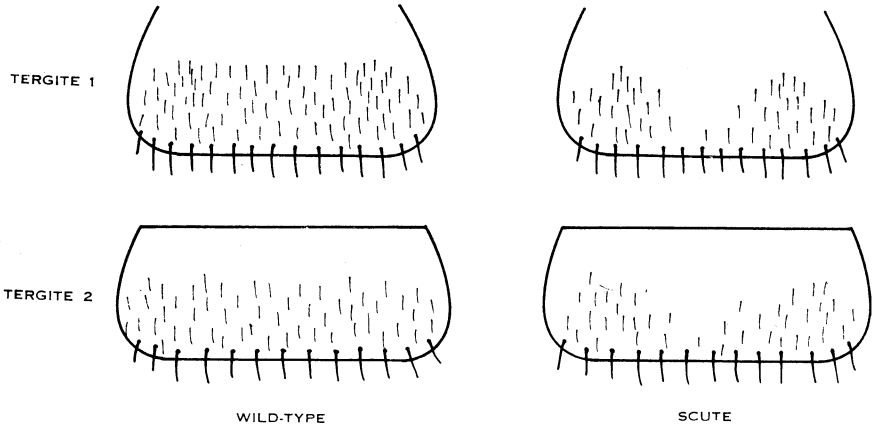

Fig. 1.—Typical tergite microchaetae distribution patterns—both sexes (semi-diagrammatic).

the peaks occurring at sites where bristle or ocelli later form. Now suppose that in the case of the abdominal tergites the peaks of the prepattern are somewhat flattened, or replaced by plateaux (Claxton 1964), so that each plateau corresponds to one tergite (or one-half tergite). This concept of one (unspecific) prepattern "peak" per tergite agrees well with Maynard Smith's (1960) observation that if variation is modal, a Turing-type mechanism should give rise to only between 5 and 7 integral structures.

The bristle precursor is pictured as being distributed in a series of gradients, as shown in Figure 2. The existence of both axial and lateral morphogenetic gradients, both intersegmental and abdominal, is well substantiated in the Insecta (Locke 1959, 1960; Maynard Smith and Sondhi 1961; Sondhi 1965). Two major axial gradients per tergite are postulated since the two halves of each tergite have separate embryological origins. The higher density of bristles in the lateral areas of the most anterior tergite (Fig. 1) is further support for the concept of two major axial gradients. Such lateral areas of higher bristle density are sometimes visible also on second tergites.

It is postulated that bristles form on the unspecific prepattern extending across a tergite wherever the amount of precursor reaches a threshold level; and the density of the bristles is related to the intensity of competition among bristle sites for the precursor. Considerably more precursor is needed to produce bristles from the less responsive hypodermal cells in *scute* flies, and thus bristles tend to be concentrated along the gradients. The distribution pattern is less regular in scute than in *wild-type*

flies. This could be the result of more intense competition for precursor among hypodermal cells coupled with a greater average distance between bristles, causing less sharply defined areas of inhibition around the bristle sites. Alternatively, the period of bristle initiation may be shorter in *scute* flies, resulting in a lower density and less regular distribution.

Assuming that the *scute* gene alters bristle density at the time of initiation in addition to altering the pattern of distribution, there remains the problem of differences in bristle number and density between sexes and between tergites. These differences are probably due to a difference in tergite area both before and after bristle initiation, or less likely to a difference between sexes, irrespective of genotype, in the

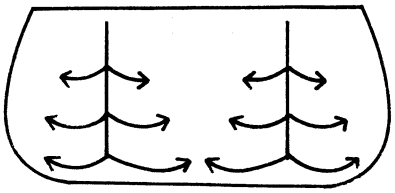

Fig. 2.—Distribution gradient of bristle precursor substance.

competitive ability of bristle-producing cells. A higher growth rate of the tergites in female flies after bristle initiation probably leads to the differences in density between sexes; such differences may be less marked in *scute* flies because the overall growth rate appears to be lower, *scute* flies being smaller than *wild-type* individuals of the same age and sex (Claxton, personal communication).

The size of the chaetae on the posterior border of each tergite appears to be governed by the prepattern as well as by the amount of precursor, since density should merely be increased if only the amount of precursor was increased. In this regard the mean distance between the bordering medium-sized chaetae and between them and neighbouring microchaetae is greater than the distance between the microchaetae alone, as would be expected from competition effects if a large amount of precursor is required for the development of the bordering chaetae. Whether the relative size of the microchaetae is affected by genotype has not been investigated although there is some indication that the size of remaining scutellar macrochaetae in *scute* flies is reduced (Rendel 1959*a*, 1959*b*).

Thoday and colleagues (reviews in Thoday 1961; Spickett 1963) have recently analysed the polygene system controlling sternopleural chaeta number in *D. melanogaster* and located three high chaeta number "factors" which function and interact in different ways, one having a generalized effect and the other two local effects. It is quite possible that a similar complex will eventually be discovered for abdominal bristle number. Each component could control its own morphogenetic field, and abdominal bristle number could then depend on the developmental balance between such fields, as suggested by Robertson and Reeve (1952). In this context Maynard Smith and Sondhi (1960) postulate at least three separate genetic systems, one affecting the precursor, one the prepattern, and one determining the actual formation of bristles, given sufficient precursor. Rendel (1963) suggests at least four.

At the present stage, with respect to tergite microchaetae, it is only possible to state that *scute* has a direct effect on the number of abdominal bristles, and that it appears to act autonomously by decreasing the competence of the pupal hypodermal tissue to react to an inductive field.

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VI. References

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