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Non-autonomy in achaete mosaics of *Drosophila*

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SUMMARY

Numbers of bristles are reduced in the dorsocentral regions of achaete *Drosophila melanogaster*. In achaete tissue of mosaics the effect is not uniform, and near the clone boundaries bristle numbers are significantly higher than they are elsewhere in the clone. It is argued that the cause of this non-autonomy stems from 'factors' that spread into the achaete clone from surrounding non-achaete cells.

1. INTRODUCTION

The study of genetic mosaics has provided a valuable concept of the developmental origin of biological patterns. Stern's (1945*a*, *b*) experiments with the arrangement of *Drosophila* bristles led him to the conclusion that these patterns are the result of two independent processes: (1) an underlying prepattern of spatial 'differentness' that provides potential inducement for some cells to behave differently to others, and that has reference to the size, shape and type of area on which a pattern later develops; and (2) a genetically determined competence of cells to respond, either in different ways or not at all, to the prepattern specificities. This dichotomy of determination stems from the discovery of pattern mutants in *Drosophila* that behave autonomously in mosaics, and that must therefore affect the local response of cells to an unaltered prepattern.

In fact the large majority of mutant pattern genes incorporated into mosaics show a response that is primarily autonomous. Of these genes though, achaete (Stern, 1954*a*) and Theta (Stern, 1956) are two that in rare instances seem to behave non-autonomously either in regions near the boundary of larger clones, or in very small clones. For this reason, these rare departures from autonomy have been attributed to 'factors' that spread into the clone from nearby non-mutant tissue.

Previous studies of achaete in mosaics (Stern 1954*a*, *b*; Roberts, 1961; Claxton, 1969) have been largely concerned with the effects it has on the dorsocentral macrochaetes, and it is because of the small number and specific locations of these bristles that apparent cases on non-autonomy have been detected rarely. But the achaete allele also causes a general reduction in the numbers of microchaetes in the dorsocentral region and this characteristic makes possible a statistical study of non-autonomy. By analysing microchaete numbers at varying distances from clone boundaries it seemed that evidence of non-achaete 'factors' spreading to a limited

extent into achaete clones could be reflected in: (i) the bristle numbers of achaete clones being larger than is typical for wholly achaete flies, and/or (ii) the bristle numbers of achaete clones being atypically higher near the clone boundary, and/or (iii) the bristle numbers in non-achaete tissue adjacent to the clone boundary being smaller than is typical for wholly non-achaete flies. The study secondarily gave the opportunity to compare bristle numbers in clones of different size, and thereby determine if the larger clones, in which the genotype of cells was changed relatively early in development, behaved similarly or differently to the smaller clones whose mosaic origin was later. Some information on regional differences in the frequency of occurrence of clones was also provided.

2. MATERIALS AND METHODS

The recessive mutants *yellow* (*y*, 1–0·0) and *multiple wing hairs* (*mwh*, 3–0·0) were used as phenotypic markers of *achaete* (*ac*, 1–0·0) tissue in mosaics. The flies in which somatic crossing over gave yellow, achaete and multiple wing-hair clones on a normal (non-yellow, non-achaete, non-multiple wing hairs) background were either homozygous or hemizygous for the *X*-linked *yellow* and *achaete* mutants; in addition, one of their IIIrd chromosomes contained the sc^{J4} translocation (carrying y^+ and ac^+, Lindsley & Grell, 1967) and the mwh^+ allele, while the other contained the *mwh* mutant but was structurally normal (Fig. 1). One of the two parental cultures whose cross gave these offspring was of this same genotype, while the other was homozygous for *mwh*, and either homo- or hemizygous for

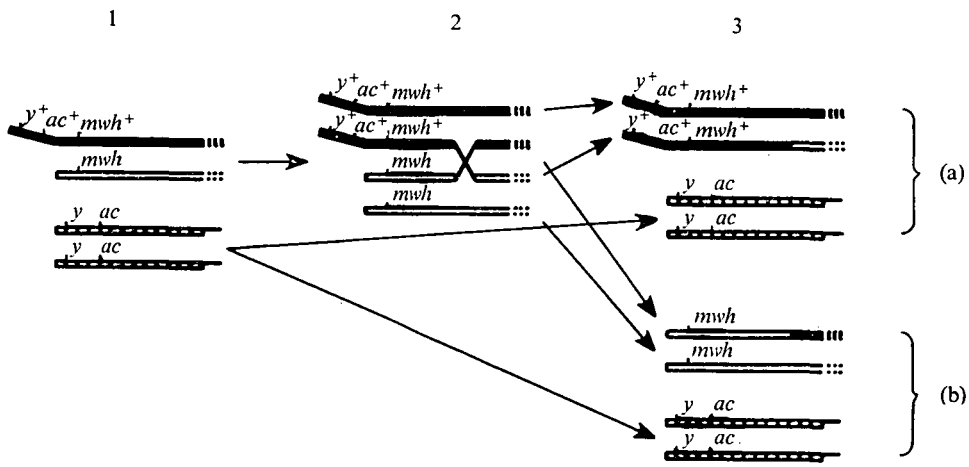

Fig. 1. Mitosis with somatic crossing-over in chromosome III. (1) A ♀ cell heterozygous for the sc^{J4} translocation (carrying y^+ ac^+) and for the *mwh* locus on chromosome III, and homozygous for *yellow* and *achaete* on chromosome 1. (2) Chromosomes duplicate and two of the IIIrd chromatids participate in somatic crossing-over. The phenotype of one daughter cell (3 a) may be potentially the same as parent cell 1 (i.e. non-yellow, non-achaete, and non-multiple wing hairs), whereas the other daughter cell (3 b) may potentially have a yellow, achaete and multiple wing hairs phenotype. The same potential phenotypes result if the parent cell is ♂ and hemizygous for *X*-linked *yellow* and *achaete*.

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X-linked *y* and *ac*. These latter parental genotypes also recurred in 50% of offspring from the parental crosses.

Somatic crossing over was induced with X irradiation (total ~1800 rad; 80 rad/min; 150 kV, 4 mA) given to larvae 48–72 h after egg laying. From the irradiated flies, three different types were recovered:

(1) A random sample of 50 ♂ and 50 ♀ normal controls (non-yellow, non-achaete, non-multiple wing hairs) in which there was no evidence of somatic crossing over having been induced.

(2) A random sample of 50 ♂ and 50 ♀ yellow, achaete and multiple wing hair controls.

(3) 111 ♀ and 64 ♂ mosaics with yellow, achaete and multiple wing hair clones on the dorsal thorax.

The dorsal thorax of each recovered fly was dissected from the remainder of the body, prepared histologically, and mounted upright on a glass slide (cf. Claxton,

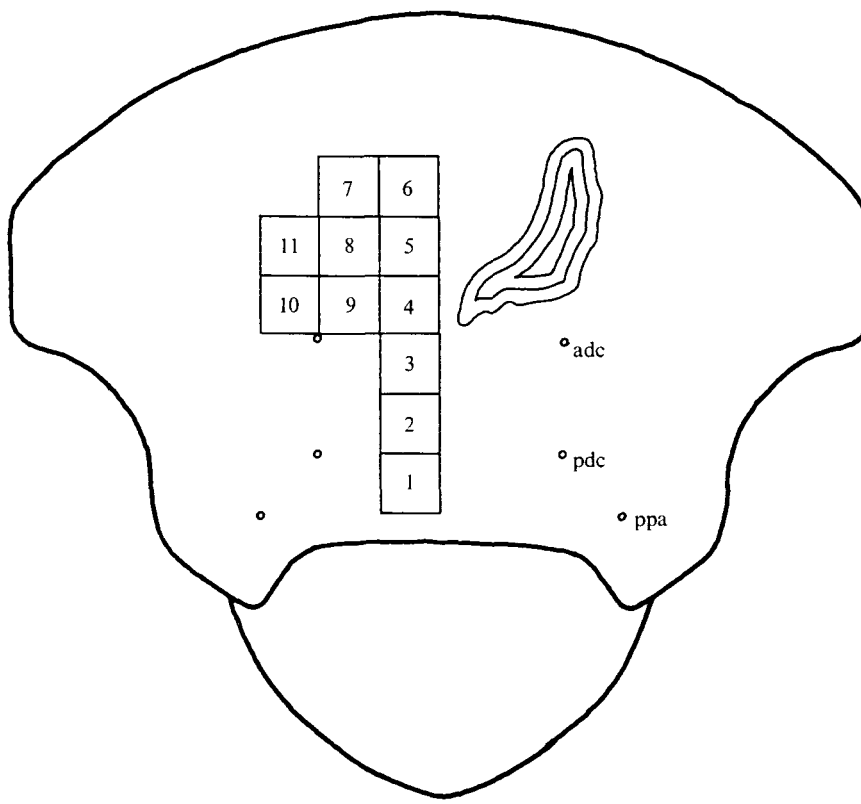

Fig. 2. Outline of *Drosophila* dorsal thorax with the standard locations of the anterior (adc) and posterior (pdc) dorsocentral bristles and the posterior postalars (ppa) (adapted from Plunkett, 1926). The size and location of the eleven dorsocentral regions to which observations were restricted in the present study are illustrated on the left hand side of the mid-dorsal line, while on the right, a typical achaete clone of a mosaic fly is outlined and divided into contours (three in this example) by lines evenly spaced and drawn parallel to the clone boundary.

1969). Observations were generally restricted to 11 contiguous dorsocentral regions on each side of the mid-dorsal line where the curvature of the thorax was small, and where curvature could reasonably be ignored in bristle density determinations; these regions are specifically defined in Fig. 2. As shown, the regions related to the position, and the distance apart, of the posterior postalar (ppa) macrochaetes which, regardless of variation in fly size, occupy approximately the same relative positions on the mesothorax. Further, these positions are not influenced by the achaete mutant.

Within each of the four groups of control flies bristle number was found to be positively related to distance apart of *ppa* (and hence to fly size). Accordingly, where bristle numbers in mosaic flies were compared with predicted numbers derived from the controls, the latter were adjusted for small average differences in size between the control and mosaic groups. The larger size differences between ♂ and ♀ are not of importance here because comparisons were kept on a within-sex basis.

In addition, comparisons were restricted to corresponding dorsocentral regions. As substantiated later, achaete does not reduce bristle numbers uniformly in all these regions.

To facilitate the collection of results, an image of each mounted thorax was magnified through a projection microscope to give an arbitrary, but constant, separation (60 mm) between ppa, and all the positions of the sockets of chaete in the dorsocentral regions were marked on mm^2 graph paper. For the mosaics, the clone boundaries between *mwh* and *mwh*$^+$ tissue were also marked.

To these drawings were added equally spaced (2 mm) lines, parallel with the clone boundary, and successively further from the boundary, either into achaete tissue (Fig. 2), or into non-achaete tissue. These lines provided the basis for another form of subdivision of the dorsocentral surface, so that bristles were not only assigned to regions, but also to different contours within each region.

As outlined in the introduction, the rationale for comparing bristle numbers in different contours was to detect inhomogeneities that might result from non-autonomous behaviour attributable to a spread of non-achaete 'factors' into the achaete clones. It was crucial then to eliminate inhomogeneities that might arise from causes other than non-autonomy. In non-achaete flies the microchaetes of the dorsal mesothorax are arranged in a series of longitudinal (acrostichal) rows. Because the width of contours was approximately half the distance between adjacent acrostichal rows, then wherever the boundary of an achaete clone followed a longitudinal direction, there was the possibility of bristles being confined mainly to alternate contours. However, provided this section of boundary was short, and provided its lateral position on different flies was random in relation to the acrostichal rows, any resulting inhomogeneities between the bristle numbers in different contours of one mosaic were likely to cancel with those of another.

But there were some mosaics where the longitudinal parts of the clone boundaries were not short, and where they were positioned regularly on the mid-dorsal line.

In such cases the contours in non-achaete tissue corresponding with these particular parts of the boundary were excluded from the analysis. However, the counterparts to these contours in achaete tissue were not excluded for two reasons. In the first place, the acrostichal rows of achaete flies (and of achaete tissue in mosaics) in the dorsocentral region, and the tendency for bristles to be arranged in rows is very much less pronounced than it is in non-achaete flies (Claxton, unpublished). Secondly, the distribution of bristles in the different contours of achaete clones was examined separately for those mosaics each having a part of their clone boundary in the mid-dorsal line; the distribution was not in any significant way different to that in the remaining mosaics.

3. RESULTS

(i) *Bristle numbers in control flies*

A summary of the number of bristles in the dorsocentral regions of control flies is given in Table 1; on average the achaete mutants had about one-third fewer bristles than the non-achaete flies. A comprehensive variance analysis of these results established the statistical significance ($P \ll 0{\cdot}001$) of this overall difference, and as well it showed all the 1st- and 2nd-order interactions involving differences between achaete and non-achaete phenotypes, sexes, and regions, to be significant at the 1% level at least. For this reason the subsequent examination of bristle numbers in mosaic flies was kept on a within-sex and within-region basis. In contrast, bristle numbers on right and left sides of the thorax were not significantly different overall (as expected *a priori*), and because only one of seven interaction terms involving sides reached significance, sides were subsequently combined.

(ii) *Total bristle numbers in achaete clones of mosaics*

The observed numbers of bristles in the achaete clones of mosaic flies are given in Table 2. Meaningful comparisons between these and the numbers of bristles that are typical for wholly achaete flies (Table 1) must take into account the fact that the size and location of clones varied between different mosaic flies, and as a result, the regions were not all represented equally in area. The average proportion of each region covered by achaete tissue in mosaics is listed in Table 2; multiplying these values with the corresponding bristle number of wholly achaete flies (Table 1), accomodating the numbers of flies, and also making the small correction for average difference in fly size between the mosaic and control groups, leads to the predicted bristle numbers of Table 2.

In both sexes the total observed bristle numbers in the achaete clones of mosaics were larger than those typical of wholly achaete flies. These differences were statistically significant even although at a regional level, some of the observations were lower than the corresponding predictions. (Utilizing a paired Student's t test: ♂, $t = 3{\cdot}40$, d.f. $= 10$, $P < 0{\cdot}01$; ♀, $t = 2{\cdot}55$, D.F. $= 10$, $P < 0{\cdot}05$).

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Table 1. *Total numbers of bristles on 11 dorsocentral regions of male and female achaete and non-achaete flies*

(Numbers for corresponding regions on right and left sides of the mid-dorsal line have been combined. Regions numbered 1, 2, ..., 11 are defined in Fig. 2.

Phenotype	Number of flies	Dorsocentral region 1	2	3	4	5	6	7	8	9	10	11	Total
Non-achaete ♀	50	162	234	328	356	377	374	411	390	346	347	338	3663
Non-achaete ♂	50	166	235	311	352	337	331	381	375	321	347	366	3522
Achaete ♀	50	7	93	179	235	244	287	303	335	251	134	199	2267
Achaete ♂	50	44	122	207	262	255	265	293	307	238	239	292	2524

Table 2. *Observed and predicted bristle numbers in achaete clones of mosaics partitioned among the 11 dorsocentral regions*

(The listed values for the average proportion of each region covered by achaete tissue were utilized in the predictions of bristle number (see text).)

	Region 1	2	3	4	5	6	7	8	9	10	11	Total
♀ (N = 111)												
Observed bristle number*	1	24	53·5	65·5	60·5	71	89	100	90·5	52·5	49	656·5
Predicted bristle number	1·1	25·4	49·8	64·2	64·5	66·1	65·1	94·4	80·6	31·9	38·4	581·5
Average proportion (per fly) of region covered by achaete tissue	0·0785	0·1349	0·1367	0·1341	0·1298	0·1131	0·1056	0·1383	0·1578	0·1168	0·0947	
♂ (N = 64)												
Observed bristle number*	6	24	36·5	37	33	32	35	61	56·5	33	45	399·0
Predicted bristle number	3·7	18·0	33·2	40·6	30·8	25·4	34·0	52·5	45·8	31·4	37·6	352·8
Average proportion (per fly) of region covered by achaete tissue	0·0626	0·1104	0·1196	0·1157	0·0900	0·0717	0·0866	0·1277	0·1438	0·0982	0·0960	

* Bristles falling exactly on the boundary of a region scored 0·5 bristle to the region.

(iii) *Distribution of bristle numbers in achaete clones of mosaics*

The data presented in Table 3 summarize the results of partioning each achaete clone not only between the eleven dorsocentral regions but also between contours running parallel to the clone boundary and numbered successively further from the boundary (Fig. 2).

Table 3. *Observed and predicted bristle numbers in successive contours of achaete clones*

	Contour								
	1	2	3	4	5	6	7	8	Total
♀ (N = 111)									
Observed bristle numbers	260·5	240·5	82·5	42·5	19·5	10·0	1·0	0	656·5
Predicted bristle numbers	258·5	159·1	85·4	45·4	22·7	8·1	2·1	0·5	581·6
♂ (N = 64)									
Observed bristle numbers	179·0	146·5	44·5	20·5	7·5	1·0	0	–	399·0
Predicted bristle numbers	174·4	104·8	50·3	17·4	5·2	0·6	0·0	–	352·8

As before, predicted bristle numbers were derived from wholly achaete flies but this time by utilizing the average proportion of each region covered by the individual contours of achaete tissue in mosaics. The predictions were initially separate for each region and each contour, and only subsequently were the results for corresponding contours summed over all regions in order to compare observed and predicted bristle numbers in the different contours. Table 3 shows that the discrepancies between observed and predicted bristle numbers are comparatively small except in contour 2 where the observed numbers are very much larger in both sexes. Further, the excess observed numbers in contour 2 account for about 90% of the difference between observed and predicted totals.

A simple and meaningful statistical test of the significance of these discrepancies was not possible, and instead this problem was approached differently. Beginning with the hypothesis that bristles occur with equal probability in all contours, then the observed numbers should be simply proportional to the relative areas of clone devoted to different contours. The regional total observed bristle numbers were partitioned in this way, and the results for corresponding contours were then summed over all regions finally giving a set of expected bristle numbers that were utilized in a chi-square test of the foregoing hypothesis. Because of the low numbers, and good match between observations and predictions, in contours 6, 7 and 8 of ♀, and contours 5, 6 and 7 of ♂, these were combined for the chi-square analysis.

Comparing the six pairs of observed and expected numbers for males, $\chi^2 = 29{\cdot}3$, D.F. $= 5$, $P < 0{\cdot}001$. Correspondingly for ♂, $\chi^2 = 11{\cdot}3$, D.F. $= 4$, $P < 0{\cdot}05$. To establish the individual contour(s) responsible for these significant chi-square values, contours were omitted from further analyses one at a time. In each case a new set of expected numbers was obtained and the chi-square recalculated. As a result of this procedure, chi-square always reached significant levels when contour 2 was

included, but not when it was omitted. Thus the probability of bristles occurring is not the same for all contours and it is higher for contour 2 than for the others.

(iv) *Distribution of bristle numbers in non-achaete tissue adjacent to achaete clones of mosaics*

As with the achaete clones, the non-achaete tissue adjacent to the clone boundaries of mosaics was also subdivided into contours (three in all) running parallel with the boundary and numbered successively moving away from the boundary. A summary of the bristle numbers in these contours is presented in Table 4 along with predicted bristle numbers calculated in a similar fashion to those of Table 3 with the single difference that they were derived from the non-achaete control flies.

Table 4. *Observed and predicted bristle numbers in successive contours of non-achaete tissue adjacent to the clone boundaries in mosaics*

	Contour			
	1	2	3	Total
♀♀(N = 111)				
Observed bristle numbers	393·5	336·6	292·0	1022
Predicted bristle numbers	396·5	347·0	305·2	1048·7
♂ (N = 64)				
Observed bristle numbers	214	195	168	577
Predicted bristle numbers	213·8	186·8	166·8	567·4

Differences between observations and predictions are small and the discrepancies which do exist in the totals are not clearly attributable to one contour more than any other. Nevertheless the hypothesis that bristles occur with equal probability in all three contours was routinely examined in the same statistical fashion as in the previous section. The chi-square values did not reach significant levels.

(v) *Distribution of bristle numbers in achaete clones of different size*

To determine if bristle numbers depended on the time of somatic crossing over it was not appropriate to compare discrepancies between observed and predicted bristle numbers in mosaics having achaete clones of different area. In these comparisons any effects of the time of somatic crossing over would be confounded with those resulting from the higher bristle numbers in contour 2 coupled with the fact that the proportion of clone area devoted to contour 2 varied with total clone area. Consequently observed bristle numbers were compared, not with predictions from the achaete control flies, but with expected numbers calculated as follows. The mosaic flies were divided into five groups according to the overall area of the achaete clone on each fly. As a result of this division there were five observed numbers of bristles (and five corresponding areas of achaete tissue on which the numbers were counted) for every region and every contour within each region. The subtotal of each set of five observed numbers was partitioned in proportion to the corresponding five areas of achaete tissue to give five expected numbers. Subse-

quently the observations (and expectations separately) were summed over all regions and all contours with the results listed in Table 5. The match between observations and expectations provided a test of whether or not bristles occurred with equal probability in clones of different size, and it was independent of the higher bristle numbers in contour 2.

Table 5. *Observed and expected bristle numbers in mosaics, grouped according to overall size (arbitrary units) of achaete clones*

(The method of deriving expectations is explained in the text.)

	Clone size					
	<100	100–300	300–500	500–700	>700	Total
Number of mosaics (♀)	12	27	22	29	21	111
Observed bristle number	13	90	130	156·5	267	656·5
Expected bristle number	12·9	87·1	132·3	155·4	268·8	656·5
Number of mosaics (♂)	7	14	18	13	12	64
Observed bristle number	12	53	94·5	106	133·5	399
Expected bristle number	9·7	54·7	99·3	107·6	127·7	399

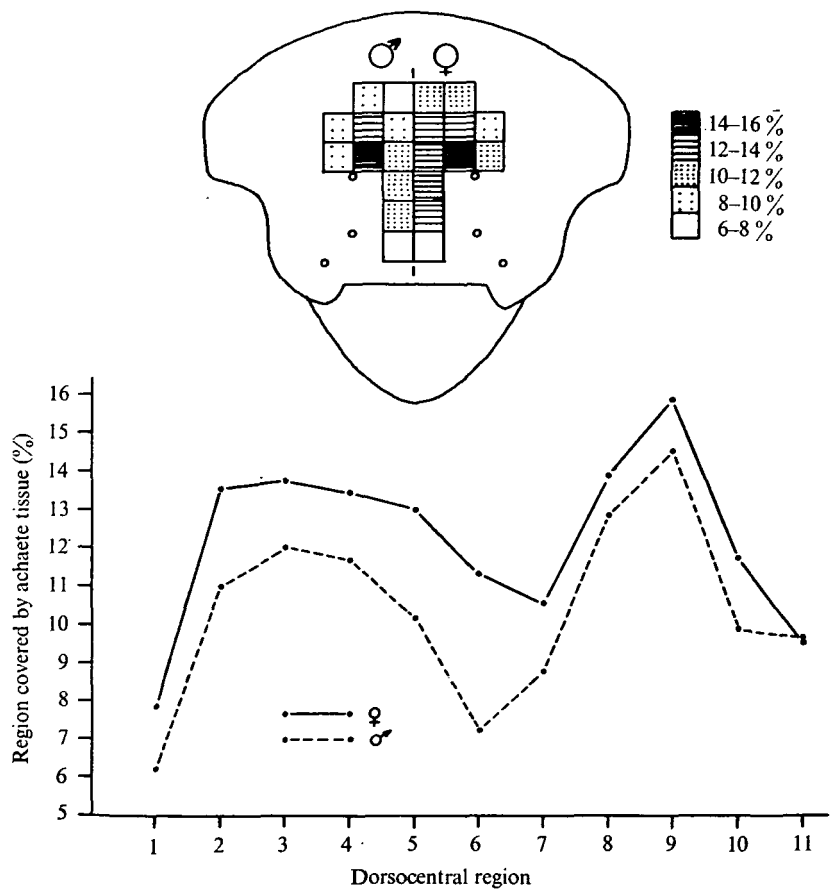

Fig. 3. Frequency of occurrence of achaete tissue in the dorsocentral regions of mosaics.

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It is clear from Table 5 that differences between observed and expected bristle numbers were small; further there was no evidence of a graded response such that the differences tended to be of one sign for the smaller clones and of the opposite sign for the larger ones. Statistical comparisons gave small and non-significant chi-square values.

(vi) *Frequency distribution of achaete clones in the dorsocentral regions*

Table 2 included values for the average proportion of each region covered by achaete tissue. This information is plotted in histogram style as well as graphically in Fig. 3, and illustrates, in effect, the relative frequencies with which achaete tissue occurs in the different dorsocentral regions. The pattern of frequency changes between the regions is very similar in both sexes ($r \simeq 0{\cdot}87$), and strongly suggests that real frequency differences exist between (at least some) regions. Achaete tissue occurred with greatest frequency in regions 8 and 9 immediately anterior and medial to the anterior dorsocentral macrochaetes. Adjacent to the mid-dorsal line the frequency was highest at a level between the dorsocentrals, and was lower posteriorly (toward region 1) and anteriorly (toward region 6)

4. DISCUSSION

The bristle numbers in achaete clones of mosaics were higher than those typical of wholly achaete flies. These differences were not uniform throughout the clones but instead were confined to contour 2, a narrow band of cells near and parallel to the clone boundary. The most reasonable explanation for non-autonomy patterned in this unique way is that bristle-producing 'factors' enter the clone from surrounding non-achaete cells and spread to a limited extent into the clone. This explanation is not inconsistent with the observation that bristle numbers in contour 1 were unaltered in spite of the fact that the cells here were nearer the clone boundary and also nearer the source of spreading 'factors'; there is good reason for this apparent anomaly.

A pattern feature of bristles in *Drosophila*, and indeed of epidermal structures in insects generally, is a tendency for many of them to be evenly spaced. There is now considerable indirect evidence that the origin of even spacing stems from a competitive-like process whereby an epidermal cell, once committed to differentiate a bristle, suppresses similar differentiation in its neighbours (Stern, 1956; Wigglesworth, 1959; Claxton, 1964; Lawrence, 1969). Coupling this with the conclusion that bristle differentiation is determined later in achaete than in non-achaete epidermal cells (Stern, 1954*a*; Claxton, 1969), then it follows that suppression across the clone boundary in achaete mosaics must be unidirectional, i.e. achaete bristles are restricted from differentiating near the clone boundary by already developing non-achaete bristles which are near but on the opposite side of the boundary. Our argument thus suggests that the bristle numbers of contour 1 are partly dependent on two opposing (and apparently roughly balancing) influences – one, a spread of non-achaete 'factors' tending to increase bristle numbers, and the

other, the fields around nearby non-achaete bristles that suppress differentiation and tend to decrease bristle numbers.

This argument is in line with the probable effective range of suppression around the non-achaete bristles. An upper limit of this range is the distance between non-achaete bristles, and observation showed this to be about twice the width of contours. Thus a circular field of suppression around a non-achaete bristle next to the clone boundary would influence achaete cells mainly in contour 1, and to a lesser extent in contour 2. Overall, non-achaete bristles sufficiently near the clone boundary to affect achaete cells at all, would obviously have their greatest influence in contour 1.

If the spread of non-achaete 'factors' into achaete clones depletes non-achaete cells near the clone boundary, this has not resulted in the differentiation of fewer non-achaete bristles. This might be explained, for example, if the concentration of 'factors' in non-achaete cells does not fall below a threshold, only beneath which a reduction in bristle numbers occurs. Another possibility is that the production of 'factors' in non-achaete cells may regulate to counter a depletion.

Unlike the abdominal histoblasts which are mitotically quiescent during the larval period (Garcia Bellido & Merriam 1971*b*; Guerra, Postlethwait & Schneiderman, 1973), mesonotal disk cells divide regularly until after pupariation. Thus, in general, the smaller clones in the thorax result from later somatic crossing-over events, and are the ones most likely to show non-autonomy, either from persisting effects of the non-achaete genotype after somatic crossing over or because bristle numbers are determined (at least partly) before somatic crossing over. In our study there was no significant tendency for the smaller achaete clones to have a higher bristle density than the larger ones. In so far as irradiation in the present experiments was administered almost exclusively in the second larval instar this result is in line with the work of Garcia-Bellido & Merriam (1971*a*), who found that the ability of achaete to suppress the hairy phenotype remains up until about mid-third instar, i.e. in its role as a suppressor of hairy, achaete behaves non-autonomously only if somatic crossing over occurs after about 8 h before puparium formation. The mid-third instar also seems a crucial time for the expression of genes such as hairy, Hairy Wing (Garcia-Bellido & Merriam, 1971*a*) and aristapedia (Postlethwait & Girton, 1974); changes in genotype before mid-third instar are the only ones accompanied by changes in phenotype.

The frequency with which marked tissue occurred in the different regions of mosaics was generally lower than that reported by Murphy, Tokunaga & Hogan (1970). This is a reflexion of the average size of achaete clones, which in our study were smaller because somatic crossing over was induced later. However, in broad terms, the relative frequency of marked clones in different dorsocentral regions was similar to that found by Murphy *et al.* (1970), the only notable discrepancy being immediately anterior to adc; in our regions 4 and 9, which correspond approximately to Murphy *et al.*'s regions 6 and 15 respectively, relative frequencies were reversed. Murphy *et al.* attributed regional differences in frequency of marked clones to unequal mitotic activity in different parts of the mesothoracic disk.

The foregoing discrepancy suggests that mitotic activity may also vary unequally with time in different parts of the disk.

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