

tion of germ layers with different developmental fates. In experimental conditions, the primitive streak can be functionally replaced by other (any?) parts of the ectoderm. These findings seem to explain the appearance of mesodermal tissues in teratomas derived from the head-fold stage ectoderm. However, it is not possible to decide whether the

newly formed mesenchyme in this experiment originates from prospective mesodermal or neural crest cells, or from any other undetermined cells which have assumed unexpected morphogenetic and differentiative capacities in response to atypical environmental conditions in the experiment.

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Alteration of thoracic macrochaet development in *Drosophila*

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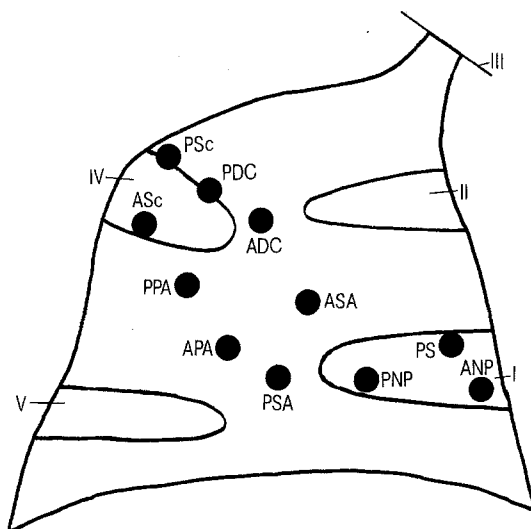
Summary. Incisions into 5 areas of the right dorsal mesothoracic disc in mature *Drosophila* larvae produced 2 types of alteration of macrochaet development. Macrochaets tended to be lost most commonly in the notopleural areas, and duplicated in the scutellum.

Methods. The 11 macrochaets of each side of the dorsal mesonotum of *Drosophila melanogaster* have been mapped with increasing accuracy on the dorsal mesothoracic imaginal disc in recent years^{1,2}. Their locations were determined by transplantation of parts of the disc taken from mature third instar larvae into hosts of the same age³. Metamorphosis of the implanted tissue coincident with that of the tissues of the host reveals which macrochaet is produced in each case. Since removal and surgical cutting of the disc necessarily place stress on its constituent cells, it is possible that alterations could be caused in both the number and location of macrochaets destined to develop from the tissue⁴. Therefore surgical incisions in situ could reveal the extent of such changes without the additional trauma of transplantation of the whole disc^{5,6}. This report summarizes a series of such operations whose effects were evaluated by examining the macrochaets of the operated animal after its eclosion.

All operations were performed on mature third instar larvae of the Oregon-S wild type strain. Larvae were grown on standard medium from eggs collected over a 6-h period. The operations were performed within the last 2 h before pupariation. Ether was applied for 1 min⁷, and the anesthetized animals were attached to a glass slide by allowing saline solution to evaporate to dryness beneath them⁸. Tungsten needles sharpened in molten sodium nitrite were inserted through the posterior dorsolateral margin of the third annulus in the anterior direction toward the right disc in operations on the lateral side of the disc. For operations on the medial side, the needle was inserted posteriorly through the posterior edge of annulus one slightly to the right of the midline. The incisions could then be made in the disc and the needle withdrawn quickly with minimal damage to other tissues. An average of 69.8% of all operations performed were followed by successful metamorphosis and eclosion of the operated animal. One incision was made in the right disc of every operated animal. 5 areas were chosen for the incisions in the thoracic portion of the disc, as shown in the figure. A total of 301 animals survived the operations.

Results. Table 1 summarizes the results of the 5 types of operations. In each of the 5 areas, the most common result of the operation was the deletion of a macrochaet together with its socket, and multiple deletions were not uncommon. Duplication of certain bristles and their sockets was also observed, and in 2 cases extra macrochaets appeared in positions not parts of the normal complement. Results for each macrochaet are summarized in table 2.

Area I. Incisions into area I produced the highest incidence of macrochaet anomalies of any of the 5 areas tested, and



Location of areas of incision in the thoracic portion of the right dorsal mesothoracic disc, viewed from the dorsal aspect. Fate map positions of macrochaets after Bryant². Abbreviations: ANP: anterior notopleural; PNP: posterior notopleural; PS: presutural; ASA: anterior supraalar; PSA: posterior supraalar; APA: anterior postalar; PPA: posterior postalar; ADC: anterior dorsocentral; PDC: posterior dorsocentral; ASC: anterior scutellar; PSc: posterior scutellar.

Table 1. Operation results

Operation type	Total survivors	Normal chaetotaxy (%)	Abnormal chaetotaxy (%)	Anomalies per survivor	Total anomalies
I	43	25 (58.2)	18 (41.8)	0.67	29
II	51	38 (74.5)	13 (25.5)	0.35	18
III	104	97 (93.3)	7 (6.7)	0.19	27
IV	57	47 (82.4)	10 (17.6)	0.26	15
V	46	39 (84.4)	7 (15.2)	0.15	7
Totals	301	246 (81.5)	55 (18.5)		

Table 2. Distribution of observed macrochaet anomalies

Bristle*	Number of deletions (%)	Number of duplications (%)
ANP	15 (16)	0 (00)
PNP	10 (11)	1 (01)
PS	13 (14)	0 (00)
ASA	6 (06)	1 (01)
PSA	8 (08)	0 (00)
APA	8 (08)	0 (00)
PPA	5 (05)	0 (00)
ADC	7 (07)	0 (00)
PDC	5 (05)	0 (00)
ASc	3 (03)	11 (12)
PSc	1 (01)	1 (01)
Totals	81 (85)	14 (15)

* Abbreviations as in the figure.

these were concentrated in the notopleural and presutural areas. In contrast however, 3 cases were observed in which the anterior scutellar bristle was duplicated while still in its normal position.

Area II. Operations in area II produced similar results except that the incidence of missing presutural macrochaets was substantially greater than in operations on area I. Again, duplication of the anterior scutellar bristle was observed (2 cases).

Area III. Area III consisted of the hypodermal stalk at the proximal end of the disc and the operation consisted of cutting it completely so that the disc was no longer attached to the body wall. This type of incision produced a low rate of abnormal bristle development with uniform distribution of deletions throughout the field. Anomalies were found at each macrochaet site, including the posterior scutellar in one case.

Area IV. Incisions in area IV produced more disturbances in the scutellar and posterior dorsocentral areas than had been seen previously, although cases were seen of missing notopleural and supra alar bristles. The anterior scutellar bristle was missing in 2 cases and duplicated in a third, and this type of operation also produced the only incident obtained of a duplication of the posterior scutellar bristle.

Area V. Operations on area V produced results in considerable contrast to those of the other 4 types. Except for a

single instance of a missing posterior supraalar and an anomalous scutellar bristle located intermediate between the normal anterior and posterior sites, every case of altered bristle development following incision into area V was a duplicated anterior scutellar bristle. This area thus responded in opposite fashion to the other 4.

In order to rule out the possibility of influence of damaged hypodermal tissue on the developing imaginal disc after the operation, mock operations were performed in which all steps of the above procedure were carried out except for the actual cutting of the disc. Mortality in such operations was similar to that seen previously, but no bristle anomalies were obtained.

Discussion. The fate map derived by Bryant² by means of transplantation of disc parts tends to be substantiated by these experiments, especially those of types I–III. Presumably, cutting through the area in which prospective socket and bristle forming cells lie exerts a strong enough influence on their development in many cases to completely prevent the formation of the bristle. It is noteworthy that in no case was a socket found without its bristle, or vice-versa, and duplications were always complete. In many cases (81.5%) no bristle anomalies were found in the entire complement after the operation, possibly indicating that sufficient time remained for repair processes to be completed before the last mitotic divisions took place. Experiments with more precisely aged larvae will be necessary to answer this point. An alternative explanation could be that incisions which passed prospective macrochaet sites by a sufficiently wide margin would not result in failure of bristle development.

The role of the hypodermal stalk remains unexplained^{8,9}. Operations in area III in which the stalk was severed completely were associated with a relatively low incidence of bristle deletion in other parts of the disc, although it is interesting that the anterior dorsocentral bristle was most commonly deleted. Bryant's fate map² places this bristle closest of all to the hypodermal stalk, yet it is unlikely that any incisions in the stalk could have reached as far as the dorsocentral area. Although the inadvertent removal of pieces of disc tissue by the needle on either side of the incision cannot be ruled out completely, it is also unlikely.

The most notable alterations in bristle development following any of these operations were the duplications, since they seem to represent a complete reversal of the deletion process. In addition, they were almost entirely limited to the anterior scutellar bristle. 14 instances of duplication were noted out of the total of 95 bristle anomalies (15%), and of these 14, 11 were at the site of the anterior scutellar bristle. There was in contrast only one instance of duplication of the posterior scutellar, and the remaining 2 were supra alar and posterior notopleural. There thus seems to be a strong tendency toward duplication at bristle sites in the anterior region of the scutellum, in marked contrast to the posterior area which produced only 2% of the anomalies seen. Thus 2 poles of reaction to the incisions in the thoracic area as a whole can be seen in the results of these operations: a tendency toward duplication in the scutellar region and a corresponding tendency toward deletion in the notopleural region.

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