The Control of the Ocellar Bristle by the Scute Locus in *Drosophila melanogaster*

By

Curt Stern and David L. Swanson

(Department of Zoology, University of California, Berkeley, California)

(*With 1 Text-figure*)

The formation of the macrochaetae in *Drosophila* is a typical example of differentiation. At strictly localized regions of the imaginal discs, single hypodermal cells divide into three or perhaps more likely four cells which diverge developmentally from the course of the surrounding cells. They transform themselves into specialized sense organs consisting of a receptor bristle cell, a socket cell which surrounds the bristle, and a peripheral nerve cell which connects with the central nervous system. In the presence of the normal genotype, a specific number of macrochaetae is formed on the head and thorax. Mutant genes may lead to the development of either more or less bristle organs than are formed under the influence of their wild type alleles. Some of these mutants act rather indiscriminately over the whole surface of the fly or at least over whole areas. Thus hairy wing (*Hw*), for instance, increases the number of bristles in the dorsocentral regions of the mesothorax and hairless (*H*) and shaven (*sv*) eliminate bristles at many sites. Other mutants are more specific in their effects. Thus, the effect of achaete (*ac*) is primarily restricted to three bristles, the anterior and posterior dorsocentral and the posterior supra alar.

Earlier studies have shown that the developmental effect of different alleles at the achaete locus is cell autonomous. Regardless of its wild type or achaete genotype the hypodermal layer of a mesothoracic disc possesses regions in which the appearance of a bristle is predetermined. The actual initiation of bristle differentiation is, however, dependent on the specific genotype of the cells of these regions. A cell with the wild allele is competent to respond to the "prepattern" but a cell with the *ac* allele lacks this competence.

The present study extends these findings to different genotypes and different bristle organs.

Material and methods

The scute (*sc*) locus, at 0.0 in the X-chromosome, has yielded many mutant alleles, all of which result in the formation of fewer than the wild-type number of macrochaetae. The specificity of the scute alleles has been a subject of much

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study (e.g.Dubinin 1929, Goldschmidt 1931, Sturtevant and Schultz 1931). Each different allele is responsible for the absence of differentiation of particular assemblies of bristles. Attempts to discover topographic or developmental regularities underlying the actions of the different alleles have been unsuccessful. Scute-1 (sc^1), the mutant allele employed in the experiments to be reported here, affects among others the ocellar bristles which in flies with the normal allele, sc^+, are located on the dorsal surface of the head, one on each side of the midline anterior to the lateral ocelli (Fig. 1A). In many sc^1 flies the ocellar bristle is absent while in others it is present as a rudimentary structure greatly reduced from its size when on a sc^+ fly.

The following problem was to be solved. Is the organization of the developmental field of the eye disc in a sc^1 fly different from that in a sc^+ fly so that the

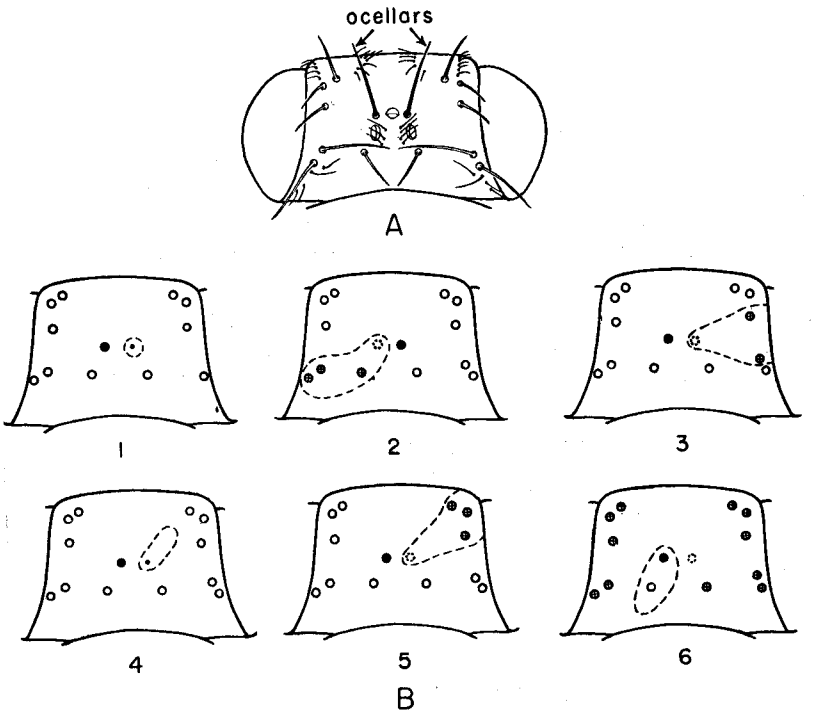

Fig. 1. A. Dorsal view of the head of *D. melanogaster*. B. Diagrams of dorsal views of six heads of gynanders, eyes omitted. ●=normal bristle; • =rudimentary ocellar bristle; ○=ocellar bristle absent, sc^1; ○=bristles other than ocellars, sc^+; ⊕=bristles other than ocellars, sc^1. 1. A very small sc^1 area on a sc^+ head. 2–5. Four small to medium sized sc^1 areas on sc^+ heads. 6. A sc^+ area on a sc^1 head.

ocellar region in sc^1 does not provide the stimulus to one of its cells to differentiate a bristle organ, while in sc^+ flies such a localized stimulus is produced ?

The method of attack was one employed earlier (Sturtevant 1932, Stern and Hannah 1950, Stern 1954, '56). Making use of the frequent mitotic elimination of a ring X-chromosome (X^{c2}), gynandromorphs were collected which were wild type, heterozygous for sc^+ (sc^+/sc^1) in their female tissues and hemizygous for sc^1 in their male tissues. Among numerous gynandomorphs those were selected for study in which the region of the ocellar bristle was genetically different from its surroundings. The rod-shaped X-chromosome which carried sc^1 was in addition to sc^1 itself marked by the recessives yellow (y, 0.0) and singed-3 (sn^3, 21.0). Since the ring-shaped X-chromosome carried the dominant alleles y^+, sc^+ and sn^+ the presence of a hemizygous area was recognizable by the yellow color of the body surface and of macro- and microchaetae as well as by the singed shape of the chaetae.

The gynanders were obtained in the cross $y\ sc^1\ sn^3/y\ sc^1\ sn^3$ ♀ × $+++\ (X^c)$ ♂. In the following pages references to the markers y and sn^3 will usually be omitted.

Results

Forty-four gynanders were found in which one or both ocellar bristle regions consisted of sc^1 cells. In 16 of these gynanders the whole dorsal surface of the head was sc^1. Since each dorsal surface is derived from two separate imaginal disc, the left and right eye discs of these 16 gynanders correspond to 32 discs. Another gynander had a mosaic left and a sc^1 right disc. There were 6 gynanders in which exactly one lateral half of the dorsal surface was sc^1 thus making a total of 39 mutant non-mosaic discs. The ocellar bristle was absent in 23 and, in small rudimentary form, present in the remaining 16 (Table 1).

Table 1. The state of the ocellar bristle in different gynanders.

Genotype of disc	oc rudimentary	oc absent	Total
non-mosaic, sc^1	16	23	39
ocellar region sc^1, rest sc^+/sc^1	12	5	17
ocellar and neighboring region sc^1, rest sc^+/sc^1	1	3	4

It may be asked whether the inability of the sc^1 discs to form a normal ocellar bristle is inherent in them or whether it is imposed on them by other parts of the flies. This question can be answered after a consideration of the very variable composition of the gynanders some of which expose none or little other $y\ sc^1\ sn^3$ areas on their surface than the head region and others of which show considerable such areas. In spite of this variability every one of the 39 non-mosaic sc^1 discs failed to differentiate a normal ocellar bristle. This suggests independence of

the disc but it may be objected that internal tissues rather than external ones would be the cause of possible dependency of the discs on other parts of the fly. There exist only very limited means of ascertaining the genotypes of internal organs and these organs were not studied. It is relevant, however, to point out that the areas adjacent to the head as represented by the dorsal mesothoracic surfaces had the following genotypes: sc^1 both mesothoracic sides 7 cases, one side 22 cases, no sc^1 on mesothorax 10 cases. This variability in constitution of neighboring discs makes it likely that similar genetic variability existed in tissues surrounding or underlying the eye discs. In spite of this presumed variability the uniform lack of normal ocellar bristles argues strongly for the independence of eye discs in ocellar differentiations.

In twentyone gynanders one eye disc had formed a non-mosaic sc^+ dorsal surface, with a normal ocellar bristle, while the other was a mosaic with a very small or a somewhat larger sc^1 area in the region of the ocellar bristle (Table 1; Fig. 1B, 1–5). The 17 very small spots just covered more than the ocellar site, while the four somewhat larger spots covered, in addition, various other bristles or a number of microchaetae. These cases are of particular importance. Since nearly the whole dorsal surface derived from these discs was sc^+/sc^1, one would expect that this genotype would result in the predetermination of a nomal ocellar bristle if such predetermination is sufficient for differentiation. The formation of a rudimentary ocellar bristle indeed shows that the predetermination has occurred but its rudimentary size clearly shows that predetermination is not sufficient. The response of the sc^1 cells to the predetermination stimulus is the decisive factor. The sc^1 cells are not competent to furnish normal differentiation.

There was only a single gynander in which most of the dorsal surface of the head was sc^1 with the exception of one ocellar bristle and a small area around it (Fig. 1B, 6). The dorsal mesothorax of this fly was completely sc^1. The ocellar bristle in the sc^+/sc^1 spot was present and normal. This case shows the competence of wild-type tissue to respond by normal differentiation to a predetermination of the ocellar region accomplished by the genetically mainly sc^1 disc.

It has been shown, in another case of bristle determination, that low competence of cells in mosaics may sometimes be increased by the presence of fully competent cells in the immediate neighborhood (Stern 1956). There is an indication of a similar phenomenon in the differentiation of the ocellar bristles. In those 39 half heads which were exclusively sc^1 the ocellar bristle was absent in nearly 60 per cent, while in the 17 cases in which sc^+/sc^1 tissue surrounded a very small sc^1 spot only about 30 per cent of the bristles remained unformed. The difference is not significant but might well become so when larger numbers of gynander are available.

Summary

The normal allele sc^+ of *Drosophila melanogaster* leads to the differentiation

of normal ocellar bristles. In sc^1 flies this bristle is absent or present in rudimentary form only. Experiments with gynanders yielded dorsal head surfaces mosaic for sc^+/sc^1 and sc^1 tissues. Regardless of the relative sizes of the two areas and, presumably, regardless of the genotype of other parts of the gynanders, the ocellar bristle was absent or rudimentary if in sc^1 areas and present if in sc^1/sc^+ areas. It is concluded that both sc^+ and sc^1 flies form a prepattern which predetermines differentiation of the ocellar bristle but that only sc^+ endows cells with full competence to respond to the prepattern.

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