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THE DEVELOPMENT OF EYE COLORS IN *DROSOPHILA* AS STUDIED BY TRANSPLANTATION¹

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INTRODUCTION

THE present report is an attempt to summarize briefly studies of eye color development in *Drosophila melanogaster*, carried out, for the most part, jointly by Dr. Boris Ephrussi of the Institut de Biologie physico-chimique, Paris, and the writer. Detailed evidence for statements made here have been or will be published elsewhere (see references at the end of this paper).

Those developmental reactions leading to the formation of specific types of eye colors in *Drosophila* presumably constitute a very small part of the general reticulum of developmental reactions. This particular small group, which of course in reality is probably very complicated, has several advantages for experimental study: (1) the genetic basis of eye color inheritance is relatively well understood; (2) eye colors have convenient characteristics which presumably can eventually be expressed in terms of definite chemical pigments (see Schultz, 1935); and (3) experience has shown that the reactions are approachable with a simple technique of transplantation (see Ephrussi and Beadle, 1936a, and Beadle and Ephrussi, 1936).

DIFFUSIBLE SUBSTANCES AND EYE COLOR

A series of eye-transplant experiments has indicated the existence of three specific diffusible substances, all of which are necessary for the production of wild-type eye color. The names assigned to these and their characteristics are as follows:

¹ Paper presented in a discussion session on Genetics and Development before the Genetics Society of America in a joint session with the American Society of Zoologists and the American Society of Naturalists at Atlantic City, December 30, 1936.

- (1) *ca⁺ substance*—a substance which a claret (a pink eye color) host can not supply to a genetically wild-type implant.
- (2) *v⁺ substance*—a substance which will result in the production of wild-type eye color when supplied to a genetically vermilion (a bright red eye color) eye.
- (3) *cn⁺ substance*—a substance which when supplied to a genetically cinabar (a bright red eye color, like vermilion) eye results in the production of wild-type eye color.

From experiments described by Ephrussi and Beadle (1937c) and by Beadle and Ephrussi (1937a) it has been concluded that these three substances are interdependent in some manner such that the relationship can be represented by a succession of three steps in a linear series, thus

→ *ca⁺ substance* → *v⁺ substance* → *cn⁺ substance*.

It is assumed that *ca⁺ substance* is somehow essential for the formation of *v⁺ substance* and that, similarly, *v⁺ substance* is necessary for the formation of *cn⁺ substance*. There is no sound basis for assuming that this interdependence in formation is referable to a direct chemical transformation of one substance into the one next in the series.

The evidence for the existence of three distinct diffusible substances and also the evidence for the sequential relations as indicated will be found summarized in the papers referred to above.

NATURE OF THE DIFFUSIBLE SUBSTANCES

Howland, Glancy and Sonnenblick (1937) have found that wild-type flies of *Drosophila melanogaster*, *D. simulans*, *D. pseudoobscura* and *D. virilis* all produce *v⁺ substance* which is active in changing vermilion eyes of the same species and also in changing vermilion eyes of any of the other species in this group. Ephrussi and Harnly (1936) have shown that *Galleria* and *Calliphora* pupae contain substances active in modifying vermilion and cinabar eyes of *D. melanogaster*; presumably these substances are identical with the *v⁺* and *cn⁺* substances of

Drosophila. These results suggest that these two substances are non-specific in nature and that they are widely distributed in insects.

Working with pupae of *Calliphora*, Khouvine, Ephrussi and Harnly (in press) have shown that v^+ and cn^+ substances are insoluble in ether but are soluble in 96 per cent. ethyl alcohol-ethyl ether mixtures and in 96 per cent. ethyl alcohol. Thimann and Beadle (in press) have obtained essentially similar results. It is found that these same two substances extracted from *Drosophila* pupae are insoluble in acetone and in sesame oil but are readily soluble in water. Both substances are heat-stable at 100° C., can be freed of proteins and are apparently inactivated by enzymic oxidation. It seems clear from the above facts that the two substances are not enzymes and are not proteins.

TIME OF APPEARANCE OF SUBSTANCES IN BODY FLUID

Transplants of wild-type eye anlagen to claret hosts at different stages of development have shown that the wild-type eye must normally take up ca^+ substance at a stage of development reached during the period of 24 hours prior to puparium formation (Ephrussi and Beadle, 1937d). On the other hand, v^+ substance appears not to be present in the body fluid in appreciable quantities until after puparium formation (Ephrussi, Clancy and Beadle, 1937); it is apparently present in the body fluid throughout most of development after puparium formation. The workers just cited have shown that vermilion eyes are sensitive to the addition of v^+ substance during a period extending from the late larval stage (or possibly earlier) to a stage reached at about 80 hours after puparium formation (at 25° C.).

SOURCE OF DIFFUSIBLE SUBSTANCES

It is evident from the manner in which it is detected that ca^+ substance is not produced in the eye. Tests for its

production by wild-type ovaries have given negative results (Ephrussi and Beadle, 1937d). Aside from this negative information, nothing is known as to the source of ca^+ substance in the fly.

Sturtevant's experiments on vermilion-wild-type mosaics in *D. simulans* (1932) can be interpreted as indicating that v^+ substance must be produced by wild-type eye tissue itself. Wild type implants grown in vermilion hosts develop wild type eye color; this is interpreted in a similar manner—formation of v^+ substance by the wild-type implant (Beadle and Ephrussi, 1936a). Eyes of certain genetic types have been shown to release v^+ substance (Ephrussi and Beadle, 1937b). Ovaries give negative results in tests for v^+ substance (Ephrussi and Beadle, 1935), as do salivary glands (Ephrussi, unpublished, and Beadle, in press). Both fat bodies and Malpighian tubes of wild-type flies have been found to liberate v^+ substance (Beadle, in press). Apparently any part of the fat body is active. It makes no difference whether an ovary is transplanted simultaneously with the fat body or not. Fat bodies are active when transplanted about 40 hours before puparium formation or when transplanted shortly before puparium formation.

By transplantation experiments it has been shown that cn^+ substance, like v^+ substance, is produced by wild-type eye tissue (same references). Ovaries give negative results in tests for this substance (Ephrussi and Beadle, 1935 and unpublished). More recently salivary glands, gastric caeca and that portion of the hind gut regenerated by its imaginal ring (see Robertson, 1937) have also given negative results (Beadle, in press). In contrast to the tests for v^+ substances, wild-type fat bodies give no test for cn^+ substance. On the other hand, wild-type Malpighian tubes do liberate cn^+ substance, even though they are transplanted as early as about 24 hours before puparium formation. Thus far, then, only eye tissue and Malpighian tubes are known to produce cn^+ substance.

RELATION OF VARIOUS GENES TO DIFFUSIBLE SUBSTANCES

From transplantation experiments of various kinds it has been assumed that many different genes must be concerned with the production of the postulated diffusible substances. For example, in a cinnabar fly, which differs genetically from wild type at a single gene locus, *cn*⁺ substance is deficient in amount as compared with wild type. Since, aside from the color of its eyes, a cinnabar fly is essentially normal, it is assumed that the normal allele of the cinnabar gene is in some way more or less directly necessary for the production of this diffusible substance. As to how direct this relation may be and as to precisely what the relation is, no information is available. For the sake of a simple working hypothesis it may be assumed that one or more products of the normal allele are not produced by the particular mutant allele known as cinnabar and that these are necessary for the reactions leading to the production of *cn*⁺ substance.

Numbering the steps in the sequence of substances

and making assumptions similar to those just considered for cinnabar, it has been postulated that the normal allele of the claret gene is concerned with step 1, that of vermilion with step 2 and that of cinnabar with step 3 (Beadle and Ephrussi, 1937a). No specific assumption need be made as to the number of reactions actually represented by each step in this scheme.

Considering other eye color genes, several types of experiments have indicated that many of them are concerned in the production of these substances. By testing directly for the presence of *v*⁺ and *cn*⁺ substance by growing vermilion and cinnabar implants in various eye color mutant hosts (Beadle and Ephrussi, 1936a), it has been found that carnation, carmine, garnet-2, peach and ruby flies are characterized by reduced amounts of *v*⁺ and *cn*⁺ substances as compared with wild-type flies. The normal

alleles of the genes associated with these eye colors, then, are assumed to be concerned with step 2 in the sequence. In a similar way, the eye color mutants bright and mahogany are found to be deficient in only cn^+ substance, indicating that the normal alleles of the bright and mahogany genes have to do with step 3.

By growing eyes of the various mutant types in vermillion hosts Ephrussi and Beadle (1937a) were led to conclude that the amounts of v^+ or cn^+ (or both) substances formed by bordeaux, clot, Henna-recessive, purploid (?), prune-2, purple, raspberry-2, sepia, sepiaoid and safranin-2 eyes are less than the amounts they use in their normal positions. It may be assumed that the normal alleles of the genes differentiating these characters are concerned with either step 2 or 3. In a similar way there is evidence that the Bar gene (known to be a duplication and normally not influencing eye color) influences the production of v^+ substance in the eye, indicating a relation to step 2.

Under specific genetic conditions, implanted eyes release diffusible substances which can be detected by effects on the eyes of the host. In such release, a scarlet eye (also others) has been shown by Ephrussi and Beadle (1937b) to differ from a wild-type eye.

The recessive gene suppressor of vermillion brings about a change such that measurable amounts of v^+ and cn^+ substances are produced by a fly homozygous for the vermillion gene (Beadle and Ephrussi, 1936b); presumably this gene has something to do with step 2.

Beadle (in press) has shown that Malpighian tubes from the eye color mutants light, maroon and white produce less cn^+ substance than do wild-type Malpighian tubes.

From the above it can be seen that 24 eye color genes are somehow concerned with the production of one or more of the three diffusible substances. Of the 26 eye color mutants which have been worked with, only two, brown and cardinal, have not been shown to differ measur-

ably from wild type in their diffusible substances; in these two, as a matter of fact, there are indirect indications that the diffusible substance relations differ from wild type. Thus it is seen that it is a fair assumption that any mutation that brings about a visible change in the eye color of the fly will alter in some way the production of one or more of the three eye color diffusible substances for which we have evidence.

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