DEVELOPMENT OF EYE COLORS IN DROSOPHILA: TRANSPLANTATION EXPERIMENTS ON THE INTERACTION OF VERMILION WITH OTHER EYE COLORS

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INTRODUCTION

IN WORK previously reported (BEADLE and EPHRUSSI 1936) it was found that by transplanting an eye anlage (imaginal disk) from a larva of one genetic constitution to a larval host of another constitution, an implant may be obtained with an eye color which does not correspond to its own genetic constitution. Thus it was found that:

(1) vermilion disk in wild type gives a wild type eye,
(2) cinnabar disk in wild type gives a wild type eye,
(3) vermilion disk in cinnabar gives a wild type eye, but
(4) cinnabar disk in vermilion gives a cinnabar eye.

From these results, it was postulated that two diffusible substances are involved in the development of wild type eye color, that a cinnabar fly is deficient in one of these (cn^+ substance), and that a vermilion fly is deficient in both (cn^+ and v^+ substances). There is evidence for the existence of a third substance necessary for the development of wild type eye color (ca^+ substance, so named because a genetically claret fly is deficient in this substance), but this substance need not concern us in the present paper.

Other known eye colors in *Drosophila melanogaster*, with the exception of three that are difficult to work with and consequently give doubtful results (bordeaux, bright, and mahogany), show autonomous development in transplants to wild type hosts. For example, a genetically carmine eye disk grown in a wild type host develops an eye color indistinguishable from a carmine control implant obtained by transplanting a carmine eye disk to a carmine host.

By growing vermilion and cinnabar eye disks in various eye color mutant hosts, it was found that in most cases the implants develop wild type eye color, indicating that the hosts were able to supply v^+ and cn^+ substances to the implants. However, vermilion and cinnabar eye disks grown in claret, carnation, carmine, garnet-2, peach, or ruby hosts develop a color

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either like vermilion and cinnabar (these two eye colors are phenotypically alike) or intermediate between vermilion or cinnabar and wild type. This suggests that these hosts supply the implants with reduced amounts of the two substances.

It is known from genetic studies that the combination of vermilion eye color with almost any other eye color results in a phenotype different from either of the simple eye colors. For example, vermilion is a bright red, garnet is a dark purplish pink, while the double recessive vermilion garnet is a light yellowish-red. This type of interaction would indicate that v^+ substance is involved in the production of these other eye colors; in the example chosen, that v^+ substance is necessary for the development of garnet eye color and that the essential difference between garnet and vermilion garnet is that a vermilion garnet eye normally develops in an environment deficient in v^+ substance. Following this interpretation, a vermilion garnet eye disk grown in a wild type host, which can supply the implant with v^+ substance, should develop garnet eye color. On the other hand, it is quite conceivable that the interaction between vermilion and garnet is less simple; the transplantation experiment should indicate the answer. The first section of this paper is concerned with transplants of eyes homozygous for vermilion and for one other recessive (*vvxx*)eye color gene to wild type hosts.

That flies containing certain eye color mutant genes show a deficiency of v^+ substance is indicated by the fact that when these are used as hosts to vermilion eyes the implant is not completely changed to the wild type. This deficiency of v^+ substance might be characteristic of the entire fly in which case we might expect, judging from the genetic interaction with vermilion in the double recessives, a partial modification of such eyes by a wild type host. The absence of such a modification (EPHRUSSI and BEADLE 1936) suggests the possibility of localized deficiencies of v^+ substance. When the results of transplanting the double recessive with vermilion (*vvxx*) to wild type are known, it should be possible to test whether v^+ substance is produced in a given mutant eye by transplanting it to a host unable to supply v^+ substance. For example, a garnet-2 host does not modify a vermilion implant completely to wild type, but a vermilion garnet-2 eye develops garnet-2 eye color when grown in a wild type host. By growing a garnet-2 eye in a vermilion host the garnet-2 eye color should develop provided the garnet-2 implant can itself produce sufficient v^+ substance; otherwise an eye with a color intermediate between vermilion garnet-2 and garnet-2 should develop. Tests of this kind are considered in the second section. Actually, since a vermilion host is deficient in cn^+ substance as well as in v^+ substance, these tests do not differentiate between production of v^+ substance and the related cn^+ substance. Additional experiments involving the use of cinnabar hosts are necessary to do this.

Supplementary tests, essentially similar in nature to those just outlined, are given in the third section. In these tests, eyes of the various color mutant types were grown in double recessives of vermilion and the mutants under test, that is, *x* disks in vermilion *x* hosts. According to the simple scheme of interaction of a given eye color with vermilion suggested above these tests should give identical results with those made by growing mutant *x* eyes in vermilion hosts; other types of interaction between *x* and vermilion might possibly lead to different results in this series of tests.

A case has been reported (BEADLE and EPHRUSSI 1936) of a difference in color of an eye implant dependent on the sex of the donor. Several additional instances were encountered during the course of the experiments considered here. The fourth section has to do with experiments bearing on the interpretation of this difference. Since one of these cases involved the character sepia which normally shows a marked age-change in eye color, experiments were made to determine the possible influence of age-change in implanted sepia eyes. These are presented in section 5.

The last section has to do with experiments in the development of eye color in genetically wild type eye disks grown in vermilion hosts which differed in age from the donors at the time the transplants were made.

EXPERIMENTAL

The technique of transplantation used in this work has been described (EPHRUSSI and BEADLE 1936). In addition to the mutants previously used and listed in an earlier paper (BEADLE and EPHRUSSI 1936), certain experiments involve a new eye color mutant, mahogany (*mah*).

1. Implants of v x eye disks in wild type hosts

Table 1 gives the results of implanting double recessive eye disks (*v x*) into wild type hosts. These data show that most of the implanted disks develop into eyes with pigmentation characteristic of the mutant *x*, for example, a *v bw* eye disk grown in a wild type host gives rise to a phenotypically brown eye.[3] Two cases show slight deviations from this general rule, *v* sf^2 and *v* $ras.^2$ Eyes from disks of these constitutions are slightly lighter than safranin-2 and raspberry-2 respectively. It should be emphasized that in these instances the resulting color was very close to that of the simple mutant, and it may be questioned whether the slight deviations observed are significant.

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[3] In the case of *v bo* the implant develops into an eye definitely darker than vermilion bordeaux and as dark as bordeaux; but the distinction between bordeaux and wild type is difficult; it is possible that *bo* in wild type is not autonomous in pigment development.

2. *Implants of x eye disks in v hosts*

Data concerning the implantation of mutant eye disks into *v* hosts are presented in table 2. It can be seen that *bw*, *ca*, *car*, *cd*, *cm*, *cn*, g^2, *lt*, *ma*, p^p, *rb*, and *st* disks develop eyes with pigmentation corresponding to their genotypic constitution. Eye disks from Hn^r, *pd*, pn^2, and *pr* larvae develop pigmentation slightly lighter than that corresponding to their genetic constitutions while disks from *bo*, *cl*, *mah*, ras^2, *se*, *sed*, and sf^2 larvae develop pigmentation definitely lighter than that characteristic of their controls. Here again it should be pointed out that in none of these last cases is the modification strong enough to result in a color close to that of the double recessive. A sex difference appears in the cases of *bo*, *cl*, Hn^r, *mah* pn^2, *pr*, ras^2, *se*, *sed*, and sf^2. In all ten cases the difference is in the same direction; disks from male donors give eyes lighter in color than those from females, that is, show a clearer deviation from the pigmentation of the single mutant controls.

TABLE 1

Data on the differentiation of double recessive v x eye disks implanted into wild type hosts. In this and the following tables, under the heading "number of individuals," are given the four sex combinations and the total in the order: female in female, female in male, male in female, male in male and total.

IMPLANT	HOST	NUMBER OF INDIVIDUALS	PHENOTYPE OF IMPLANT
v bw	+	6, 1, 4, 3; 14	*bw*
v ca	+	7, 1, 3, 2; 13	*ca*
v car	+	0, 1, 3, 2; 6	*car*
v cl	+	0, 4, 2, 1; 7	*cl*
v cm	+	4, 0, 1, 2; 7	♀♀—*cm*; ♂♂—possibly little darker.
v cn	+	5, 0, 2, 3; 10	+ (some implants little lighter).
$v\ g^2$	+	2, 2, 3, 0; 7	g^2
$v\ Hn^r$	+	4, 2, 4, 2; 12	Hn^r
v lt	+	2, 3, 3, 5; 13	*lt*
v ma	+	6, 1, 0, 0; 7	*ma*
$v\ p^p$	+	6, 3, 2, 5; 16	p^p
v pd	+	6, 1, 2, 2; 11	*pd*
$v\ pn^2$	+	3, 1, 1, 3; 8	pn^2
v pr	+	1, 3, 0, 2; 6	*pr*
$v\ ras^2$	+	0, 0, 3, 5; 8	Slightly lighter than ras^2; much darker than $v\ ras^2$.
v rb	+	1, 2, 4, 3; 10	*rb*
v se	+	5, 4, 3, 3; 15	*se*
v sed	+	2, 2, 3, 3; 10	*sed*
$v\ sf^2$	+	2, 4, 3, 1; 10	sf^2 (lighter ?)
$v\ w^a$	+	*	w^a

* Data previously published (Beadle and Ephrussi 1936) and confirmed by more extensive experiments.

3. Implants of x eyes in v x hosts

Data resulting from implants of mutants (x) disks into double recessive ($v\ x$) hosts are given in table 3. These experiments give results similar to those of the x into v series in so far as development of pigmentation corresponding to the genotype of the implant is concerned. Here again *bw*, *ca*, *car*, *cm*, *cn*, g^2, *ma*, p^p, and *rb* disks are apparently unaffected by the transplantation, while *cl*, Hn^r, pn^2, ras^2, *se*, *sed*, sf^2 and possibly *pd* and *pr* disks give eyes which deviate slightly in color from the single mutant controls in the direction of the double recessive. The only exception to this parallel is *lt*, which in this series (*lt* in *v lt*) is slightly lighter than the control (*lt* in *lt*) while in the previous experiment (*lt* in *v*) such a difference was not recorded.

TABLE 2

Data on the differentiation of mutant eye disks implanted in v hosts; arrangement as in table 1.

IMPLANT	HOST	NUMBER OF INDIVIDUALS	PHENOTYPE OF IMPLANT
bo	*v*	2, 1, 5, 2; 10	Lighter than *bo;* ♂♂ lighter than ♀♀.
bw	*v*	2, 2, 2, 2; 8	*bw*
ca	*v*	1, 0, 1, 1; 3	*ca*
car	*v*	2, 0, 5, 0; 7	*car*
cd	*v*	*	*cd*
cl	*v*	0, 1, 1, 6; 8	Lighter than *cl;* ♂♂ lighter than ♀♀.
cm	*v*	2, 0, 0, 0; 2	*cm*
cn	*v*	*	*cn*
g^2	*v*	6, 1, 1, 2; 10	g^2
Hn^r	*v*	3, 0, 3, 0; 6	Very little lighter than Hn^r; ♂♂ lighter than ♀♀; both darker than $v\ Hn^r$.
lt	*v*	1, 1, 1, 4; 7	*lt*
ma	*v*	1, 0, 1, 1; 3	*ma* (little lighter?)
mah	*v*	1, 3, 0, 1; 5	Lighter than *mah*, darker than *v*; ♂♂ lighter than ♀♀
p^p	*v*	4, 1, 1, 1; 7	p^p
pd	*v*	5, 0, 4, 2; 11	Probably slightly lighter than *pd;* Much darker than *v pd.*
pn^2	*v*	3, 1, 3, 2; 9	♀♀ possibly, ♂♂ clearly lighter than pn^2; both darker than $v\ pn^2$.
pr	*v*	2, 3, 1, 2; 8	Slightly lighter than *pr;* darker than *v pr;* ♂♂ lighter than ♀♀.
ras^2	*v*	1, 0, 1, 0; 2	Lighter than ras^2; much darker than $v\ ras^2$; ♂♂ lighter than ♀♀.
rb	*v*	5, 2, 1, 4; 12	*rb*
se	*v*	2, 1, 2, 3; 8	♂♂ Intermediate between *se* and *v se*, ♀♀ *se.*
sed	*v*	2, 0, 2, 1; 5	Lighter than *sed;* darker than *v sed;* ♂♂ lighter than ♀♀.
sf^2	*v*	1, 0, 2, 0; 3	Lighter than sf^2; ♂♂ lighter than ♀♀.
st	*v*	*	*st*

* Data previously published (Beadle and Ephrussi 1936).

A difference between implants originating from male and female donors was recorded in the cases of *cl*, *lt*, pn^2, ras^2, and sf^2. In all of these the implants from male donors were lighter than those from female donors.

4. Sex difference

The existence of a sex difference in sepia implants growing in vermilion hosts has been pointed out previously (BEADLE and EPHRUSSI 1936) but only a few experiments on the implantation of mutant eyes in *v* hosts had been made at that time. The more extensive data presented here show several cases of the same kind.

TABLE 3

Data on the differentiation of mutant eye disks implanted into double recessive v x hosts; arrangement as in previous tables.

IMPLANT	HOST	NUMBER OF INDIVIDUALS	PHENOTYPE OF IMPLANT
bw	*v bw*	5, 1, 2, 5; **13**	*bw*
ca	*v ca*	4, 1, 3, 5; **13**	*ca*
car	*v car*	1, 1, 0, 0; **2**	*car*
cl	*v cl*	3, 1, 3, 3; **10**	♀♀ little, ♂♂ much lighter than *cl*; both darker than *v cl*.
cm	*v cm*	2, 2, 2, 4; **10**	*cm*
cn	*v cn*	0, 0, 1, 0; **1**	*cn*
g^2	$v\ g^2$	2, 1, 2, 2; **7**	g^2
Hn^r	$v\ Hn^r$	0, 0, 1, 1; **2**	Lighter than Hn^r; darker than $v\ Hn^r$.
lt	*v lt*	3, 0, 2, 0; **5**	♀♀ *lt*; ♂♂ lighter than *lt*.
ma	*v ma*	5, 2, 5, 1; **13**	*ma*
p^p	$v\ p^p$	6, 2, 5, 3; **16**	p^p
pd	*v pd*	5, 2, 4, 2; **13**	*pd* (slightly lighter?)
pn^2	$v\ pn^2$	1, 2, 3, 3; **9**	♀♀ close to pn^2; ♂♂ lighter, but darker than $v\ pn^2$.
pr	*v pr*	3, 3, 1, 3; **10**	*pr* (slightly lighter?)
ras^2	$v\ ras^2$	4, 4, 4, 2; **14**	♀♀ very close to ras^2; ♂♂ little lighter.
rb	*v rb*	5, 2, 4, 1; **12**	*rb*
se	*v se*	1, 0, 2, 3; **6**	Slightly lighter than *se*; darker than *v se*.
sed	*v sed*	0, 0, 1, 1; **2**	Lighter than *sed*
sf^2	$v\ sf^2$	2, 2, 0, 2; **6**	Lighter than sf^2; ♂♂ lighter than ♀♀; darker than $v\ sf^2$.

It was suggested that the result of the implantation of *se* into *v*, that is, the development of pigmentation intermediate between sepia and vermilion sepia, might be due to a lowered rate of formation of v^+ substance in the *se* eye, which under normal conditions receives a part of the v^+ substance used from other parts of the body. (In the particular case of *se* there is unpublished evidence that the formation of v^+ rather than of cn^+ substance goes at a reduced rate in the eye since a *se* eye disk grown in a *cn* host gives an eye with straight sepia pigmentation.) According to this interpretation, the observed sex difference might be accounted for by the known fact that the development of male larvae is somewhat slower than that of female larvae. It might be supposed that disks from male larvae had received less v^+ substance from other parts of the body at the time of transplantation than had disks from female larvae.

If this interpretation is correct, the transplantation of *se* disks to *v* hosts at earlier stages of development, should lead to the formation of eyes still closer to the double recessive vermilion sepia and, possibly, to the disappearance of the sex differences. The results of an experiment of this type are given in table 4. Transplants made at about 90 and 78 hours after egg-laying (approximately 30 to 40 hours before pupation) led to the same result as those made shortly before pupation. In all cases the pigmentation was intermediate between sepia and vermilion sepia; the implants made earlier in development showed no appreciable difference from those made later.

TABLE 4

Data on implantation of se *eye disks into* v *hosts at various ages; arrangement under heading "Number of individuals" same as in previous tables.*

AGE OF IMPLANT AFTER EGG LAYING (HOURS)[*]	AGE OF HOST AFTER EGG LAYING (HOURS)	NUMBER OF INDIVIDUALS	PHENOTYPE OF IMPLANT
112 to 115 (control)	Close to puparium formation	4, 0, 0, 2; 6	Lighter than *se*
88¼ to 91	88¼ to 91	0, 1, 0, 1; 2	Very close to control
77 to 79¼	77 to 79¼	1[†], 0, 0, 0, 1	Very close to control

[*] Puparium formation occurs later in *se* than in wild type.

[†] Dissected as pupa.

The period of time during which *se* disks remain in their normal environment before pupation therefore seems to be of no appreciable significance. The difference between *se* and se^+ implants in *v* seems to be in the rate of production of v^+ substance by the eye itself. This interpretation is consistent with the results of direct tests which indicate that v^+ substance is not produced before pupation (BEADLE, CLANCY and EPHRUSSI in press). In the case of *se* the observed sex difference therefore cannot be accounted for by differences in the time during which eyes of the two types receive v^+ substance from the body. Another explanation is necessary. It is possible that the total amount of v^+ substance produced by an eye is different in the two sexes, less in the male than in the female. This assumption would account for the observed results. Such a difference in rate of production of v^+ substance in the two sexes would not necessarily lead to a sex difference in normal flies because, under these conditions, the body serves as a supplementary source of v^+ substance. It should be pointed out that in none of the eye color mutants in which this sex difference was recorded does there appear to be a deficiency of v^+ substance in the body. This was shown by experiments in which *v* eye disks were grown in various eye color mutant hosts (BEADLE and EPHRUSSI 1936).

5. *Age-change in sepia*

In connection with the experiments on *se* implants just referred to, it seemed desirable to make another series of experiments bearing on the question of age-change in eye transplants. It is known that several eye colors, including sepia, normally show a marked age-change. In sepia, freshly hatched flies have eyes of a yellowish color; within a few days the eyes become progressively darker. Experiments made to determine whether or not a similar change occurs in implanted sepia eyes and whether this is related to the sex difference considered above were made by implanting *se* eye disks in *se* hosts at successive intervals of several days. The implanted eyes were examined at the same time. The results of these experiments are given in table 5. All implants taken from flies less than 24 hours old appeared to be quite uniform in color. Eyes examined at 0–1, 3, 5, and 8 days after hatching show a series of gradually darker colors up to the fifth day. Little or no difference was observed between eyes which remained in the adult flies 5 and 8 days. It is clear that an age-change similar to that observed in normal sepia eyes takes place in implanted sepia eyes. From the characteristics of the age-change observed in sepia, time and intensity of color-change, there seems to be no clear relation between this age-change and the sex difference discussed above.

TABLE 5

Data on the age change in se implants grown in se hosts; arrangement under heading "Number of individuals" same as in previous tables.

EXPERIMENT	NUMBER OF INDIVIDUALS	DISSECTED (DAYS AFTER HATCHING)	PHENOTYPE OF IMPLANT
a	5*, 5*, 0, 0; **10**	0 to 1	Gradual darkening
b	2*, 5*, 0, 0; **7**	3	from a to c, and
c	5*, 5*, 0, 0; **10**	5	slightly or no change
d	2*, 2*, 0, 0; **4**	8	from c to d.

* Sex of donors not determined.

6. *Data on transplants of young wild type eye disks to older v hosts*

It has been shown (BEADLE and EPHRUSSI 1936) that wild type eye disks can develop into eyes with pigmentation close to that of vermilion if young wild type disks are transplanted in older *v* hosts. In the two experiments published previously, one did not have satisfactory controls; in the other, an eye color intermediate between vermilion and wild type was observed. In neither experiment was the age difference accurately known. Another series of experiments was made in order to determine more accurately the results of known age differences. It was believed that if the implants were taken early enough the resulting pigmentation of the implants would be identical with that of vermilion. Table 6 gives the results of these experiments. It can be seen that age differences of 17–21¼, 23¼–26¾ and 27–30½ hours (the host being close to pupation) were tried. In all three cases the implants were lighter than wild type controls and in the last two cases clearly intermediate between vermilion and wild type. Whether or not transplantation at still earlier stages would lead to pigmentation identical with that of vermilion remains unknown.

TABLE 6

Data on the differentiation of wild type eye disks from young larvae implanted into older v larvae. Arrangement under heading "Number of individuals" same as in previous tables.

IMPLANT		HOST		AGE DIFFERENCE (HOURS)	NUMBER OF INDIVIDUALS	PHENOTYPE OF IMPLANT
CONSTITUTION	AGE AFTER HATCHING (HOURS)	CONSTITUTION	AGE AFTER HATCHING (HOURS)			
v	45¼ to 47	*v*	70 to 72¼	23¼ to 26¾	2,* 1,* 0, 0; **3**	*v*
+	45¾ to 47¼	*v*	70½ to 73¾	23¼ to 26¾	2, 3, 2, 0; **7**	Intermed. between + and *v*
+	Approx. 24 hrs. before pupation	*v*	Close to pupation	17 to 21¼	9, 1, 1, 1; **12**	Lighter than +
v	Approx. 24 hrs. before pupation	*v*	Close to pupation	17 to 21¼	2,* 0, 0, 0; **2**	*v*
+	Approx. 24 hrs. before pupation	*v*	Close to pupation	27 to 30½	1, 1, 3, 1; **6**	Intermed. between + and *v*
+	Approx. 24 hrs. before pupation	+	Close to pupation	27 to 30½	4,* 0, 0, 0; **4**	+
v	Approx. 24 hrs. before pupation	*v*	Close to pupation	27 to 30½	2,* 4,* 0, 0; **6**	*v*

* Sex of donors not determined.

DISCUSSION

As stated in the introduction, it seemed probable that v^+ substance is necessary for the formation of the various mutant eye colors. The experiments involving implantations of different double recessives into wild type hosts show that by supplying v^+ substance to such disks, a change to not-vermilion pigmentation is brought about. They therefore confirm the conclusion that could be drawn from purely genetic data. Two cases were observed in which the *v x* implants developed into eyes with pigmentation slightly lighter than the *x* controls. The observed differences however were too small in these cases to justify a conclusion without further investigation. It is clear that all the eye colors tested in combination with vermilion do show autonomous development and that, in all cases, the *v* component shows a modification by the host. Under the conditions of these experiments there is no evidence that the interaction between *v* and *x* is different from that between *v* and x^+.

The experiments on implantation of mutant eye disks into *v* hosts show that in a series of cases (*bw*, *ca*, *car*, *cd*, *cm*, *cn*, g^2, *lt*, *ma*, p^p, *rb* and *st*) the pigmentation of the implant is unaffected by a deficiency of v^+ and cn^+ substances in the host. Since the necessity of one of these substances (v^+ substance) has been demonstrated, it must be concluded that the v^+ substance, and presumably cn^+ substance, is formed in these cases by the eye itself. On the other hand, in all cases where the pigmentation of the implant is modified by transplantation to *v* hosts (*bo*, *cl*, Hn^r, *mah*, *pd*, pn^2, *pr*, ras^2, *se*, *sed* and sf^2) we must conclude that the amount of at least one of the substances (v^+ or cn^+ substance or both) produced by the eye is less than that used by the eye in its normal position. That it is not completely blocked is demonstrated by the fact that the pigmentation is never as light as that of the double recessive *v x*. Transplants to *cn* hosts must be made in order to determine which of the two substances is involved. It is pointed out elsewhere (EPHRUSSI and BEADLE in press) that none of these mutant eyes, when transplanted to w^a *v* hosts, releases a detectable quantity of v^+ substance.

The third series of experiments (*x* in *v x*) gave essentially the same results. The only exception is *lt* (see above). From these two series of experiments, *x* in *v* as compared with *x* in *v x*, it appears that *v x* behaves like *v* with regard to its influence as a host on an *x* implant. In terms of deficiencies of diffusible substances alone, this is the expected result.

In cases in which mutant eye disks grown in *v* or *v x* hosts fail to show complete autonomy in development of eye color, the eye colors concerned appear to have in common the properties of being relatively dark and of showing a relatively strong age-change.

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SUMMARY

(1) Double recessive *v x* eye disks, implanted in wild type hosts, develop pigmentation like that of the mutant *x*.

(2) Eye disks from *bw, ca, car, cd, cm, cn,* g^2, *lt, ma,* p^p, *rb,* and *st* flies are unaffected by implantation in *v* hosts. Disks from *bo, cl,* Hn^r, *mah, pd,* pn^2, *pr,* ras^2, *se, sed* and sf^2 flies, implanted into *v* hosts develop pigmentation more or less intermediate between that corresponding to their genotype and that of the corresponding double recessive with *v*. In certain cases eye disks from male donors differ in color, when grown in *v* hosts, from genetically similar eye disks from female donors.

(3) Implantation of mutant eye disks (*x*) into double recessive *v x* hosts, gives results similar to those stated under (2).

(4) Implants of *se* disks grown in *se* hosts show an age-change similar to that occurring in sepia eyes *in situ*.

(5) The results of a series of experiments in which wild type eye disks were transplanted to older *v* hosts are given.

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