GENETIC CONTROL OF PATTERN DETERMINATION IN DROSOPHILA. II. NONRANDOM DISTRIBUTION OF MOSAIC TISSUES¹

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SOMATIC crossing over, which can be induced by irradiation, can lead to the formation of genetic mosaics. It is generally assumed that crossovers are induced randomly among the cells exposed to the irradiation. Since the induced somatic exchange may occur in any cell and since no mechanism has been described for preferential orientation of homozygous chromosomes on the basis of genotype during mitosis in somatic tissue, it follows that the positions of the homozygous twin patches, resulting from such a somatic exchange, should be random. In the course of a mosaic analysis of the sex-linked dominant mutation Hairy-wing 49c (*Hw^{49c}*) (GOTTLIEB 1964) certain observations gave indications that the location of twin patches on the thorax may not always be random.

The present investigation enables us (1) to test the assumption that there is random distribution of alternative homozygous tissue patches in twin spot genetic mosaics, and (2) to ascertain the degree of interaction between such tissue patches as it affects relative patch location.

MATERIALS AND METHODS

Stocks: Hairy-wing is at $0.0 \pm$ on the X chromosome. The extreme mutant allele *Hw^{49c}* (POULSON and KING 1949) was used. The mutants yellow (*y*) and singed-3 (*sn³*), at 0.0 and 21.0 respectively, served as morphological markers (superscripts will be omitted in the following discussion). Stocks were maintained at $26^\circ \pm 1^\circ\text{C}$, experimental animals at $25^\circ \pm 1^\circ\text{C}$.

Mosaic production: The genetic mosaics were obtained following BECKER's (1957) techniques utilizing ionizing irradiation to increase the frequency of somatic crossing over. Larvae from the cross *y/y* $\times$ *Hw sn* were irradiated with 1200, 1500, 1800, 2000 or 2400 r of hard X rays (250 kv, 15 ma, with total filtration equivalent to 3 mm Al + .25 mm Cu) at a dose rate of 100 r/min, and at ages ranging from 15 to 70 hr after hatching. *Hw sn/Hw sn* and *y/y* tissue patches on a *Hw sn/y* background were recovered among the female offspring. These mosaics will be referred to as "experimental."

In addition, larvae from the cross *y/y* $\times$ *sn* were irradiated with 1800 r of gamma rays from a cesium source at a dose rate of 120 r/min, at ages ranging from 20 to 60 hr after hatching. Patches of the genotypes *sn/sn* and *y/y* on a *sn/y* background were recovered among the female offspring. These mosaics will be referred to as "control," as they are the *Hw⁺* control group. The *y/y* and *sn/sn* stocks used to produce *y/sn* mosaics were the Iso (2;3) stocks (see GOTTLIEB 1964) which were co-isogenic, i.e., homozygous for one second and one third chromosome from the original *Hw sn* stock.

Classification of mosaics: The mosaic flies were initially divided into four classes dependent upon the location of the patches with respect to the dorsocentral region (defined as the area

¹ This investigation was supported by Public Health Service Research Grant GM 11084.

bounded anteriorly by a line connecting the anterior dorsocentrals, posteriorly by the scutoscute-lar suture and on the sides by lines extended from the anterior dorsocentrals, through the posterior dorsocentrals to the suture) (1) a class in which both the *Hw sn/Hw sn* (or *sn/sn*) and the γ/γ patch enter the dorsocentral region ("both-in"); (2) a class in which only the *Hw sn/Hw sn* (or *sn/sn*) patch enters the dorsocentral region and the γ/γ patch, if present, lies outside the region ("*Hw sn*-in" or "*sn*-in"); (3) a class in which only the γ/γ patch enters the dorsocentral region and the *Hw sn/Hw sn* (or *sn/sn*) patch, if present, lies outside the region (" γ -in"); and (4) a class in which neither the *Hw sn/Hw sn* (or *sn/sn*) nor the γ/γ patch enters the dorsocentral region ("neither in"). These classes, except the "both-in" class, can be subdivided into "Twin," where both homozygous patches are present on the half-thorax and "Single," where only one homozygous patch is present on the half-thorax. Since the four dorsocentral bristles, along with the scutoscute-lar suture, determine the dorsocentral region, (Figure 1) these bristles were not considered as "in" so that their phenotype does not enter into the assignment to mosaic classes.

A number of the mosaic thoraces to be measured were dissected, mounted on slides, and sketched with a camera lucida. Additional size comparisons were made on all mosaic animals by direct observation with a stereomicroscope at 100 $\times$.

RESULTS

What predictions can be made with respect to the expected frequencies of individuals in the four mosaic classes? There is no definite prediction about the relative numbers of the "both-in" class *vs.* the "neither-in" class, short of the expectation that the latter class should be larger since the dorsocentral region occupies but a small portion of the total dorsal mesothorax. The other two classes, by virtue of the assumed random nature of the irradiation induction process, should occur with equal frequencies.

A total of 610 *Hw sn/\gamma* animals with thoracic mosaic patches were identified and scored. Of these, 47 could not be classified by the usual means. All of these were animals which had been irradiated late in their larval life, between 67 and 70 hr after hatching. Instead of small localized twin patches of several bristles each, *Hw sn/Hw sn* and/or γ/γ bristles were scattered all over the thorax, as if numerous mosaic events had occurred. These animals ("Scatters") were not included in the distribution of mosaic animals among the mosaic classes (Table 1a).

FIGURE 1.—Diagram of the thorax of *Drosophila melanogaster* showing the dorsocentral region (crosshatched).

TABLE 1

Distribution of mosaic events among the mosaic classes

a. <i>Distribution of 610 Hw sn/y mosaics</i>					
	Mosaic class				TOTAL
	1 "Both-in"	2 "Hw sn-in"	3 "y-in"	4 "Neither-in"	
Twin	29	82**	35**	148	294
Single (No Hw sn/Hw sn)	..	..	16	39	55
Single (No y/y)	..	62	..	152	214
TOTAL	29	144	51	339	563
				"Scatters"	47
				GRAND TOTAL	610
b. <i>Distribution of 349 sn/y mosaics</i>					
	Mosaic class				TOTAL
	1 "Both-in"	2 "sn-in"	3 "y-in"	4 "Neither-in"	
Twin	18	40*	26*	116	200
Single (No sn/sn)	..	..	10	37	47
Single (No y/y)	..	10	..	91	101
TOTAL	18	50	36	244	348
				"Scatters"	1
				GRAND TOTAL	349

** $\chi^2 = 18.880$ $P \leq .001$.* $\chi^2 = 2.970$ $P > .05$.

The deviation from the expected equality of "Hw sn-in" and "y-in" classes for twin spot mosaics is highly significant ($P \leq .001$), and is manifested by an excess of "Hw sn-in." To determine whether the observed deviations were due to Hw, a "control" mosaic series was set up using heterozygotes of the two morphological marker mutants *sn* and *y*. In this series, 349 *sn/y* mosaics were collected and classified. The distribution was checked for the equality of the two comparable classes: "sn-in" and "y-in." The twin group shows no significant excess of the "sn-in" class ($.10 > P > .05$, Table 1b), however, it should be remembered that the significance of such comparisons depends not only upon the differences between the two classes but also upon the size of sample. A homogeneity Chi-square run on the "experimental" and "control" twin ratios (85:35 and 40:26) indicates that these two sets show the same nonrandom distribution.

If the average Hw sn/Hw sn patch were significantly larger than the average y/y patch, the observed differences in the frequencies of the two tissue location classes could be attributed to the increased probability of the larger patch falling in a selected region of the dorsal mesothoracic surface, such as the dorsocentral region. To check this possibility, camera lucida drawings were made of 77 mounted mosaic thoraces and the areas of the Hw sn/Hw sn and y/y twin spots were measured on these drawings. In order to minimize the introduction of bias due to differences in the age of animals at the time of irradiation and the effect of such age differences on patch size, total area measurements of the two types

of patches have not been reported. Instead, the difference (D) in area between the twin patches [$D = (Hw\ sn/Hw\ sn\ area) - (\gamma/\gamma\ area)$] has been employed. The averages of the differences obtained are listed in Table 2. When the 77 mosaics are pooled, irrespective of their tissue location class, they show no significant differences in patch size between the two tissue genotypes. When the mosaics are listed separately according to the locations of their tissue patches on the dorsal mesothorax, the "both-in" and "neither-in" classes still show no significant differences in patch sizes. In the " $Hw\ sn$ -in" class the average $Hw\ sn/Hw\ sn$ patch is significantly ($.05 > P > .02$) larger than the average γ/γ patch. In the " γ -in" mosaics, however, the converse is true, γ/γ patches are significantly ($.02 > P > .01$) larger than $Hw\ sn/Hw\ sn$ patches (Table 2).

To make possible a comparison of differences in patch sizes in the "experimental" ($Hw\ sn/\gamma$) mosaics with those of the "control" (sn/γ) mosaics every specimen was classified as to the relative size of the twin patches. Three possibilities were apparent: One in which the $Hw\ sn\ Hw\ sn$ (or sn/sn) patch was larger than its γ/γ twin; one in which the γ/γ patch was larger than its twin; and one in which the twin patches were of equal size. In a small number of cases (17 sn/γ and 36 $Hw\ sn/\gamma$ mosaics, (*) in Table 3) the twin patches were both very small in size, usually containing one microchaeta each. Since relative size was difficult to determine in these cases, they were omitted from the calculations (their inclusion in the = class has no effect on the significances of the differences between the distributions of the experimental and control animals). These distributions of twin spot mosaics on the basis of their relative patch size are presented in Table 3. The pooled values of the experimental (Table 3A) and control (Table 3B) groups were found to differ significantly ($.05 > P > .02$). The distributions of three of the four tissue location classes ("both-in," " $(Hw)\ sn$ -in," and "neither-in") showed no significant difference between experimental and control series, while those of the fourth class (" γ -in") were quite different ($0.01 > P > 0.001$). At the same time the mosaics were classified as to which patch came closest to the mid-line. The distributions of mediality results are also given in Table 3. There is no significant difference between the "experimentals" and "controls" for the pooled distributions nor for the "both-in," " $(Hw)\ sn$ -in" and "neither-in" classes. In the

TABLE 2

Average area differences between $Hw\ sn/Hw\ sn$ and γ/γ twin spots in 77 mosaics
 $(D = (Hw\ sn/Hw\ sn\ area) - (\gamma/\gamma\ area))$ D expressed in cm^2 on camera lucida
 drawings; $1\ cm^2$ (drawings) = $59.172\ \mu^2$ (specimen)

	N	$D \pm S_D$	Significance of D
Pooled	77	0.299 ± 0.901	Not significant
"both-in"	20	2.307 ± 1.590	Not significant
" $Hw\ sn$ -in"	15	5.642 ± 2.272	$.05 > P > .02$
" γ -in"	19	-4.834 ± 1.845	$.02 > P > .01$
"neither-in"	23	-0.691 ± 1.007	Not significant

TABLE 3

Relative sizes and relative location of twin patches in Hw sn/y and sn/y mosaics

	Relative patch size			Relative location			
	<i>sn</i>	Larger <i>γ</i>	=	<i>sn</i>	Medial <i>γ</i>	=	(*)
A) Experimental (<i>Hw sn/γ</i>)							
Pooled	148	52	58	130	66	62	(36)
"Both-in"	18	4	7	7	7	15	
" <i>Hw sn</i> -in"	66	5	10	59	1	21	(1)
" <i>γ</i> -in"	7	24	4	3	27	5	
"neither-in"	57	19	37	61	31	21	(35)
B) Control (<i>sn/γ</i>)							
Pooled	83	46	54	83	44	56	(17)
"both-in"	9	3	5	7	5	5	(1)
" <i>sn</i> -in"	29	6	5	28	0	12	
" <i>γ</i> -in"	5	9	12	4	11	11	
"neither-in"	40	28	32	44	28	28	(16)
Significance of differences between experimental and control							
Pooled	.05 > P > .02			P > .30			
both-in	P > .80			P > .30			
(<i>Hw</i>) <i>sn</i> -in	P > .20			P > .90			
<i>γ</i> -in	.01 > P > .001			.02 > P > .01			
neither-in	.20 > P > .10			.10 > P > .05			

Hw sn/y series the " γ -in" class does show a significant (.02 > P > .01) excess of γ medial and lack of (=) mediality as compared with the *sn/y* controls.

DISCUSSION

Can we assume that, in twin spot mosaics, there is random distribution of the tissue patches on the surface of the thorax? If we consider the *sn/y* heterozygote which forms *sn/sn* and γ/γ twin patches, we would expect that if the distribution of the patches is random the frequency of *sn/sn* patches entering the scoring region should be equal to the frequency of γ/γ patches entering the region. Since the "both-in" class contributes equally to both "*sn/sn*" and " γ/γ -in" events and to avoid counting these animals twice, we need only compare the "*sn*-in" and " γ -in" classes to test for the expected equality. On the basis of the data collected (Table 1) we must conclude that twin patches are not distributed randomly on the thorax, as there is a highly significant excess of *Hw sn/Hw sn* patches entering the dorsocentral region. Since the *sn/y* "control" data are consistent with the *Hw sn/y* results, we can conclude that there is a tendency for *sn/sn* patches to enter the dorso-central region. While it is not presently possible to distinguish the role of *Hw* in this phenomenon, it should be noted that the *sn* bearing X chromosome as well as the second and third chromosomes of the co-isogenic strains used in the control series were derived from the *Hw sn* stock (GOTTLIEB 1964).

Does the location of one patch affect the location of its twin? If the relative locations of twin patches are independent we would expect that the frequency of

"both-in" animals should be equal to the product of the frequencies of "*sn/sn-in*" and "*γ/γ-in*" events; the frequency of "*sn-in*" to the product of the frequencies of "*sn/sn-in*" $\times$ the "*γ/γ-out*" events; etc. Thus we should test for the existence of any preferential association of the twin patches on particular areas of the dorsal mesothorax. Although there is a relationship between patch location and relative patch size (Tables 2 and 3) there is no significant preferential association of the location of twin patches in either the experimental or control series. That is to say, the association of "in" and "out" locations of the twin tissue patches is random, both for the experimental and control groups, and thus each combination, such as "both-in", reflects the product of the combined probabilities of each genotype tissue falling the way it does, relative to the dorsocentral region.

The lack of positional association and the homogeneity of the "*sn-in*": "*γ-in*" twin patch results does not imply that the frequencies of "in" events are the same for the experimental and control series. When we compare the experimental and control twin patch data by genotype we find that the locational distribution of *γ/γ* patches is homogeneous (Table 4). In the experimental group there is a significant excess ($.05 > P > .02$) of *Hw sn/Hw sn* patches entering the dorsocentral region as compared to the *sn/sn* controls. These results indicate that homozygous *Hw^{49c}* patches on the thorax have a somewhat greater tendency to locate themselves within the dorsocentral region (i.e., posteriomedially) than do their *Hw⁺* twins.

Neither mutation nor differential survival of tissue patches of the two genotypes can be the cause of the twin spot tissue distribution differences, since both tissues must be present for a mosaic to be classified as a "Twin" event. Differential recovery of patches due to the inability to find one patch or the other as function of phenotype is probably not a major factor either. Although yellow has been reported to be non-autonomous on the abdomen of gynandromorphs

TABLE 4

Comparisons between experimental and control twin patches by genotype

<i>γ/γ</i>	In	Out	
Experimental	63	230	293
Control	44	156	200
	107	386	493
$\chi^2 = 0.012$			
$P > .90$			
<i>sn/sn</i>	In	Out	
Experimental (<i>Hw sn/Hw sn</i>)	111	182	293
Control (<i>sn/sn</i>)	58	142	200
	169	324	493
$\chi^2 = 4.195$			
$.05 > P > .02$			

(HANNAH 1957), no such difficulties are present in $2X$ tissue or in large tissue patches. Indeed, studies of mosaics formed by the introduction of dissociated wing disc cells showed no sign of nonautonomy of γ (URSPRUNG and HADORN 1962). STURTEVANT (1932) noted that, although there was some weakening of the yellow effect, possibly due to the action of the underlying non-yellow tissue, yellow "must be classed as a gene whose effects are weakened in small spots but not in large areas of mosaics." In the present investigation the patches recovered were large, usually representing a number of bristles. Indeed, in the experimental series, the γ/γ tissue patches in the " γ -in" class have a tendency to be larger than their $Hw\ sn/Hw\ sn$ twins (Table 3).

Genetic background has been shown to be able to act as a modifier of spot size (STERN 1936). There is also evidence of an interaction between $Hw\ sn/Hw\ sn$ and γ/γ tissues which leads to the increase in chaetal density in γ/γ tissue lying adjacent to $Hw\ sn/Hw\ sn$ tissue (GOTTLIEB 1964). The present results indicate that a similar situation exists with respect to patch size. When γ/γ tissue patches lie medial to $Hw\ sn/Hw\ sn$ patches and in the dorsocentral region, there is a pronounced tendency for the yellow tissue patch to be larger (Tables 2 and 3). It may well be that the same interacting system which affects chaetal density is responsible for the differences in relative patch size. It should be noted that Hw , in the homozygous animal, increases the width of the thorax in the dorsocentral region (GOTTLIEB 1964) and that this site of action corresponds to region of greatest tissue patch interaction.

While it is not possible at present to delimit the roles of sn and Hw in the disposition of twin spots, it is clear that the relative distribution of these tissue patches on the thorax is not random. There is an interesting parallel between this nonrandom distribution of mosaic tissues and meiotic drive. In both instances there is a distinguishing of homologues carrying different genes during division and a subsequent differential behavior. PEACOCK and ERICKSON (1965) propose that the spindles of primary spermatocytes regularly possess a polar differentiation and that the SD bearing second chromosome preferentially moves to one pole. PEACOCK (1965) also showed that the X and Y chromosomes respond to the same polar differentiation. The simplest way of explaining the present results is to suggest that there also may be spindle polarity during mitosis. The somatic re-combinational event and subsequent segregation which produces the genetic mosaic permits the manifestation of preferential chromosome orientation as a function of chromosome genotype. From the mediality results (Table 3) it is further suggested that there may be preferential chromosome orientation as a function of chromosome genotype. From the mediality results (Table 3) it is further suggested that there may be preferential orientation of spindles during the mitotic divisions in the imaginal disc. Such mitotic spindle orientation could be a function of cell geometry, a concept similar to one first proposed by ERRERA (1888) to explain cell division orientation in plants.

Single spot mosaics: The scanning technique employed is such that the discovery of a patch of homozygous tissue of one genotype of the thorax would enhance the probability of finding its twin were it present. Singles, thus, represent

those animals where no twin patch was found after several careful examinations. No significant association between patch location and genotype was found among the single spot mosaics, experimental or control (Table 5). Indeed, single patch locations were in agreement with twin patch results for γ/γ patches in both the experimental and control series (Table 6). The *Hw sn/Hw sn* and *sn/sn* patches show a significant excess ($.05 > P > .02$, for experimentals and $P \ll .001$, for the controls) of "in" events among the twin spot mosaics and a concomitant excess of "out" events among the single spot animals (Table 6). STERN (1936) performed a number of experiments in which γ and *sn* were in repulsion configuration. He reported his results with the data separated as to patch size, using the number of chaetae as a measure of size. If we compare his results for single spot patches whose size is greater than two bristles with the present results (Table 7) we find that there is no significant difference in relative patch recovery frequency in the controls but a significant ($.05 > P > .02$) excess of *Hw sn/Hw sn* single patches.

TABLE 5

Chi-square tests for independence of genotype and patch location in single patch mosaics

	Experimental				Control		
	In	Out			In	Out	
<i>γ/γ</i>	16	39	55	<i>γ/γ</i>	10	37	47
<i>Hw sn/Hw sn</i>	62	152	214	<i>sn/sn</i>	10	91	101
	78	191	269		20	128	148
	$\chi^2 = 0.001$				$\chi^2 = 3.440$		
	$P > .95$				$.10 > P > .05$		

TABLE 6

Chi square heterogeneity comparisons between twin and single results

	Experimental				Control		
	In	Out			In	Out	
<i>Hw sn/Hw sn</i>				<i>sn/sn</i>			
Twin	111+	183	294	Twin	58+	142	200
Single	62	152+	214	Single	10	91+	101
	173	335	508		68	233	301
	$\chi^2 = 4.271$				$\chi^2 = 14.003$		
	$.05 > P > .02$				$P \ll .001$		
<i>γ/γ</i>							
	In	Out			In	Out	
Twin	64	230	294	Twin	44	156	200
Single	16	39	55	Single	10	37	47
	80	269	349		54	193	247
	$\chi^2 = 2.240$				$\chi^2 = 0.012$		
	$.20 > P > .10$				$P > .90$		

(+) = in excess of expected.

TABLE 7

Comparison between single spot results of STERN (1936) and present data

	A) Control	B) Experimental		
A.		γ/γ	sn/sn	
STERN's 2		22	44	66
γ/sn Control		47	101	148
		69	145	214
	$\chi^2 = 0.049$ $P > .80$			
B.		γ/γ	sn/sn	
STERN's 2		22	44	66
$Hw\ sn/\gamma$ Experimental		55	214	269
		77	258	335
	$\chi^2 = 4.924$.05 > P > .02			

If STERN's smaller patches are included (a total of 124 γ/γ :234 sn/sn) the *Hw sn*/*Hw sn* patch excess is more pronounced ($P \ll .0001$) while the controls still show a good fit. Thus, the differences noted can not be attributed to differential recovery of yellow patches between twins and singles nor between experimentals and controls. Some of the single spot mosaics could represent cases where only one of the two segregating tissues was finally located in hypodermal tissue and was therefore detectable, as has been suggested by ABBADESSA and BURDICK (1963). It is also possible that, among the singles, some may have had their twin patch located on the wing or pleural segments which areas were not scanned. Whatever the cause, there are fewer γ/γ single patches recovered than sn/sn or *Hw sn*/*Hw sn*.

"Scatters": The "scatters" present a problem. STERN (1956) reports that "in nearly all cases in which segregation involves the mesothoracic imaginal disc, a coherent patch of segregated tissue is formed." Clearly this is not the case with the "Scatters". They may be the result of a heightened sensitivity to irradiation-induced chromosome breakage after 65 hr of age. They may also reflect the increase in the numbers of cells present in the dorsal mesothoracic disc. *Hw* clearly increases the frequency of occurrence of scatters (Table 1). This effect of *Hw* may explain the fact that scatters have not been previously encountered.

The author would like to express his gratitude to Dr. CURT STERN and to Dr. CALVIN SPECTOR for their suggestions on the manuscript, to Dr. C. C. LI for his statistical guidance and to Mr. WILLIAM HANRATTY for his technical assistance.

SUMMARY

Genetic mosaics, produced by the X irradiation of *Hw^{49c}sn^s/γ* and of *sn^s/γ*, Iso

(2;3) female *Drosophila melanogaster* and classified with respect to the location of thoracic tissue patches, were analyzed to determine whether alternative homozygous tissue twin spots are randomly distributed on the surface of the thorax and whether the position of one tissue patch affects the location of its twin. The results indicate that twin patches are not always randomly distributed on the thoracic surface. $Hw^{49c}sn^3/Hw^{49c}sn^3$ (and also sn^3/sn^3) tissue patches have a greater tendency to locate themselves within the dorsocentral region of the thorax than do their γ/γ twins. $Hw^{49c}sn^3/Hw^{49c}sn^3$ tissue patches were shown to affect the size of γ/γ patches lying medial to them in the dorsocentral region. Single spot mosaic data were also presented which indicate that there are fewer γ/γ single patches recovered than either sn^3/sn^3 or $Hw^{49c}sn^3/Hw^{49c}sn^3$ patches.

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