A POSSIBLE INFLUENCE OF THE SPINDLE FIBRE ON CROSSING-OVER IN DROSOPHILA

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The distribution of genes in the second and third chromosomes of *Drosophila melanogaster* suggests that crossing-over may be influenced by the spindle fibre at least in neighboring regions. The disparity between the genetic and cytological maps of these chromosomes especially in the spindle fibre regions (Dobzhanzky[2,3]) is consistent with such a view. Sturtevant[4] suggests from studies of crossing-over in Drosophila stocks homozygous for inverted sections of the autosomes that crossing-over in a given region is a function of the material in that region rather than of its position in the chromosome. He found no significant changes in amount of crossing-over with change in position of a section of a chromosome with respect to the spindle fibre or the end of the chromosome. Muller and Stone[5] in a study of crossing-over in the case of a homozygous inversion in the X-chromosome of Drosophila apparently found that the regions in the inverted section gave normal crossing-over. However, since in none of these cases of homozygous inversions did the inversion include regions close to the spindle fibre, the possibility remains that the spindle fibre influences crossing-over in regions close to it.

Dobzhansky[6] studied crossing-over in a homozygous III–IV translocation in Drosophila (designated as translocation-*c*) and found no significant differences from normal controls. However, the regions which might have been expected to be influenced by the spindle fibre were not studied. At the suggestion of Professor Dobzhansky, the writer has made additional studies of crossing-over in flies homozygous for this translocation. The results are reported in the present paper.

In the translocation stock under consideration a distal segment made up of about three-fourths of the right limb of chromosome III (cytologically[3]) is broken off and attached to chromosome IV   The break in chromosome III is close to and to the left of the curled gene (0.7 unit according to Dobzhanky's data[3] and somewhat closer according to results obtained by the writer). Accordingly, in the homozygous translocation flies the section of the third chromosome including curled and regions to the right is closer to a spindle fibre (of the fourth chromosome) by a cytological distance equal to about one-fourth the length of the right limb of chromosome III. Genetically this distance represents about 2 crossover units (standard map[7]).

A stock of the homozygous translocation was made up carrying in one of the translocated third chromosomes the genes roughoid (*ru*), hairy (*h*), thread (*th*), scarlet (*st*), curled (*cu*), stripe (*sr*), sooty (*e^s*) and claret (*ca*) and in the homolog the normal allelomorphs of these genes. The constitution of this stock was therefore $\dfrac{+\ +\ +\ +}{ru\ h\ th\ st}\ \dfrac{+\ +\ +\ +}{cu\ sr\ e^s\ ca}$. All of the recessives were introduced, by crossing-over, from a normal stock. The normal allelomorphs of *ru*, *h*, *th*, *st*, *e^s* and *ca* were likewise introduced from a normal stock. Females of the above-mentioned constitution were used for a study of crossing-over by mating with homozygous translocation males carrying the above-named recessives in both third chromosomes. The control was made up by using the stocks which had been used in introducing the desired genes into the translocation stock.

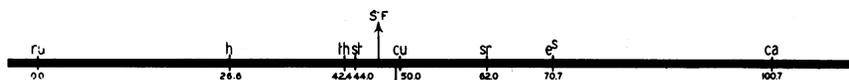The standard map[7] positions of the loci used are shown in figure 1.

FIGURE 1

Standard map positions of the loci used. S F refers to the spindle fibre.

Crossover data from the homozygous translocation stock and the control are presented in table 1. These data together with the crossover

TABLE 1

CROSSOVER DATA FROM HOMOZYGOUS TRANSLOCATION-*c* FEMALES

$$\left(\dfrac{ru\quad h\quad th\quad st\quad cu\quad sr\quad e^s\quad ca}{1\quad 2\quad 3\quad 4\quad 5\quad 6\quad 7}\ \times\ ru\quad h\quad th\quad st\quad cu\quad sr\quad e^s\quad ca\right)$$

AND A NORMAL CONTROL OF SIMILAR CONSTITUTION

(The class carrying the dominant allelomorph of *ru* is given first in each case)

CROSSOVERS REGION	TRANS-LOCATION	CONTROL	CROSSOVERS REGION	TRANS-LOCATION	CONTROL
0	519	140	2, 3	0	1
	330	107		0	0
1	199	50	2, 4	168	1
	255	57		131	0
2	140	36	2, 5	2	6
	151	45		3	6
3	3	1	2, 6	3	8
	3	0		6	5
4	450	8	2, 7	79	25
	442	8		84	27
5	6	25	3, 4	4	0
	3	20		0	0
6	29	34	3, 5	1	0
	21	22		0	0

TABLE 1 (*Continued*)

CROSSOVERS REGION	TRANS-LOCATION	CONTROL	CROSSOVERS REGION	TRANS-LOCATION	CONTROL
7	269	85	3, 6	2	0
	213	54		0	0
1, 2	45	12	3, 7	5	0
	25	7		7	1
1, 3	1	0	4, 5	6	1
	2	1		4	1
1, 4	240	2	4, 6	10	3
	199	5		25	2
1, 5	1	6	4, 7	200	8
	3	9		240	5
1, 6	8	9	5, 6	0	0
	7	9		0	1
1, 7	83	33	5, 7	1	12
	124	36		1	10
6, 7	1	3	2, 4, 7	82	2
	0	4		77	1
1, 2, 4	19	1	2, 5, 7	0	5
	30	1		0	8
1, 2, 5	0	1	2, 6, 7	0	0
	0	2		3	0
1, 2, 6	0	0	3, 4, 7	3	0
	1	3		7	0
1, 2, 7	13	4	4, 5, 7	2	0
	8	4		0	0
1, 3, 4	4	0	4, 6, 7	0	0
	1	0		1	1
1, 4, 5	2	0	5, 6, 7	0	0
	4	0		0	2
1, 4, 6	8	0	1, 2, 4, 7	13	0
	7	1		16	0
1, 4, 7	118	1	1, 2, 5, 7	0	1
	102	4		0	0
1, 5, 6	0	1	1, 3, 4, 7	0	0
	0	0		1	0
1, 5, 7	0	3	1, 4, 5, 7	0	0
	0	7		1	1
1, 6, 7	0	3	1, 4, 6, 7	2	0
	0	6		0	0
2, 4, 5	1	1	2, 4, 5, 7	0	1
	3	2		1	0
2, 4, 6	6	0	2, 4, 6, 7	2	0
	9	1		0	0
			1, 2, 4, 5, 7	0	0
				1	0
			Total	5303	1019

data from the heterozygous translocation flies (from Dobzhansky[5]) are summarized in table 2. As compared with the control, crossing-over in

TABLE 2

SUMMARY OF CROSSOVER DATA FROM HOMOZYGOUS TRANSLOCATION-*c*, HETEROZYGOUS TRANSLOCATION-*c* (FROM DOBZHANSKY[3]) AND NORMAL FLIES

EXPERIMENT	PER CENT CROSSING-OVER IN REGION							NO. INDI-VIDUALS
	1	2	3	4	5	6	7	
Homozygous translocation	29.1	21.2	0.8	49.9	0.9	2.8	33.2	5303
Heterozygous translocation	26.9	16.9	0.9	4.5	3.7	7.5	28.9	3185
Control	27.5	21.3	0.4	6.1	13.3	11.6	35.0	1019

flies carrying the translocation in homozygous form is reduced in the *cu-sr* interval from 13.3 to 0.9 and in the *sr-e^s* interval from 11.6 to 2.8 per cent. Other comparable regions show no differences. Crossing-over in flies heterozygous for the translocation is also decreased as compared with the controls in the *cu-sr* and *sr-e^s* intervals. This decrease has been explained by Dobzhansky[8] on the basis of decreased frequency of synapsis. The fourth chromosome to which a section of chromosome III is attached presumably exerts a mutual attraction with its free homolog. Likewise, the two sections of chromosome III and the homologous unbroken third chromosome are attracted together. These counter-forces working on the broken third chromosome would be expected to interfere with synapsis and presumably also with crossing-over. This explanation obviously cannot be applied to the homozygous translocation form. One must, therefore, seek another explanation of the decrease.

Crosses were made to test the possibility that the observed decrease in crossing-over might have been due to the presence of an extra fourth chromosome. It is known from Dobzhansky's cytological work[3] on the original stock of the homozygous translocation that an extra fourth chromosome is probably not necessary for the survival and fertility of flies homozygous for the translocation. Crosses of homozygous translocation flies with flies carrying dominant eyeless in one-fourth chromosome and minute-IV in the other gave only two classes, eyeless and minute-IV. A total of 22 flies homozygous for the translocation were so tested. Since two normal allelomorphs suppress minute-IV this test indicates that the homozygous translocation flies did not carry an extra fourth chromosome. Two normal allelomorphs also suppress dominant eyeless but since the extra fourth chromosome would have carried the recessive eyeless-2 gene this test may not be valid. Crosses of 11 homozygous translocation flies with haplo-IV gave normal and haplo-IV flies in varying ratios but in two cases these were such (215 to 161 and 105 to 116) that the translocation parent could hardly have carried an extra fourth chromosome. The fact that haplo-IV flies carrying the translocation survive

and are fertile shows that the fourth chromosome to which the section of chromosome III has been translocated does not carry a lethal. There is therefore no apparent reason why an extra fourth chromosome should be necessary to flies carrying the translocation in homozygous form. The above tests make it very improbable that the homozygous translocation stocks carried an extra fourth chromosome or a fragment of one which might have accounted for the observed decrease in crossing-over.
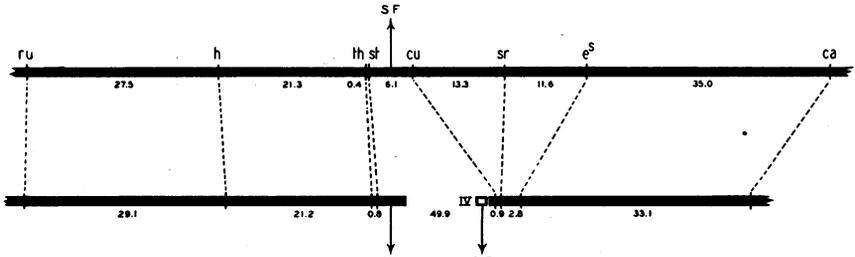

FIGURE 2

Comparison of crossing-over in control and in homozygous translocation-*c*. Figures represent observed percentages of crossing-over. S F refers to spindle fibres. The fourth chromosome is designated IV.

The above data indicate that the decrease in crossing-over in the *cu-sr* and *sr-e^s* intervals in the translocation stock is due to these intervals being closer to the spindle fibre (of the fourth chromosome) than in the control by a distance equal approximately to one-fourth the length (cytologically) of the right limb of chromosome III.

On the basis of the hypothesis of crossing-over recently presented by Sax[9] the spindle fibre should reduce crossing-over in its immediate neighborhood. If the opening out of chromatids at diplotene is determined in the reductional plane at the spindle fibre then interference with crossing-over for a distance on both sides of the spindle fibre would be expected. On the basis of the crossing-over hypothesis put forward by Janssens[10] and recently supported by Darlington[11] or on the scheme of Belling[12] there is no apparent reason why the spindle fibre should interfere with crossing-over.

Coincidence values across the break in chromosome III have been calculated. They are as follows:

REGIONS	COINCIDENCE
1–6	0.76
2–6	0.90
1–7	0.94
2–7	1.01

As might have been expected there is no significant interference of crossing-over between the two independent sections of chromosome III.

Summary.—Crossing-over data from a homozygous III–IV translocation in *Drosphila melanogaster* indicate that the spindle fibre interferes with crossing-over in its immediate neighborhood.

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AN EXPANSION OF MEROMORPHIC FUNCTIONS

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It is the primary object of this note to exhibit a development in series of an arbitrary meromorphic function, a development which represents the function throughout its entire domain of definition, and which can be chosen in an infinite variety of ways.

THEOREM I. *If $f(z)$ is a meromorphic function of z (that is, analytic except possibly for poles, at every finite point of the plane), if all the poles of $f(z)$ belong to the sequence α_1, α_2, α_3, $\ldots \longrightarrow \infty$, where every pole occurs a number of times at least corresponding to its multiplicity, and if the numbers β_1, β_2, β_3, $\ldots$ are distinct from the α_n and uniformly limited, then there exists a unique expansion*

$$f(z) = a_0 + a_1 \frac{z - \beta_1}{z - \alpha_1} + a_2 \frac{(z - \beta_1)(z - \beta_2)}{(z - \alpha_1)(z - \alpha_2)} + \ldots \quad (1)$$

valid for all finite values of z other than the points α_i. The series (1) converges absolutely for all values of z other than the α_i and uniformly in any