Lucchesi, J. C., S. Mills and R. Rosenbleeth. University of Oregon. Relative frequencies of induced TM and RA compound X chromosomes in D. melanogaster females.

Lindsley (1958) has proposed that in males pairing and subsequent (spontaneous) exchange involving X and Y heterochromatin "are conditioned by non-homologous but heterochromatin-specific forces." On the other hand, Lucchesi (1964) has offered arguments supporting the view that in females pairing and subsequent (induced) exchange involving an attached-X and Y chromosomes are conditioned by homology. The present experiment was undertaken to further investigate pairing affinities of X and Y heterochromatin.

Females of the following constitution were obtained:

Ia. $X{\cdot}Y^{L}$, $In(1)sc^{8L}$, EN^{R}, y^{+} f cv $y{\cdot}Y^{L}/X\ Y^{S}{\cdot}Y^{L}$, y $Y^{S}{\cdot}Y^{L}$ B^{S}

b. " $/X\ Y^{L}{\cdot}Y^{S}$, y $Y^{L}{\cdot}Y^{S}$ y^{+}

IIa. $Y^{S}X{\cdot}Y^{L}$, In(1)EN, Y^{S} B f v w $y{\cdot}Y^{L}$ $y^{+}/\ XY^{S}{\cdot}Y^{L}$, y $Y^{S}{\cdot}Y^{L}$ B^{S}

b. " $/\ XY^{L}{\cdot}Y^{S}$, y $Y^{L}{\cdot}Y^{S}$ y^{+}

These were treated with 3000r of X-irradiation, mated to suitable males, and brooded for five 3-day broods. TM chromosomes would result from breaks in the centric heterochromatin of each homologue; RAs would most likely involve a break in the distal X-heterochromatin (I) or in the Y^{S} arm (II) of the inverted chromosomes and a break in the centric region of their homologues (Novitski, 1954).

In order to determine the true number of compounds formed, corrections have to be effectuated that will take into account those compounds which were induced and then lost due to meiotic crossing over. The observed frequencies of TMs and RAs in broods 1 and 2 represent 13% and 15% of the actual number of compounds induced in oöcytes, respectively. In broods 3, 4, and 5, the observed frequencies of TMs and RAs represent 16% and 30% of the compounds actually induced in oögonia. These figures were calculated using the tetrad analyses of Novitski (1951) and Sandler (1954) for compounds and our own tetrad analyses for inversion heterozygote tetrads in which the events producing a compound were superimposed on crossing over. In addition, the assumptions that the tetrad distribution in the inversion heterozygotes and in the TMs is E_0=.05, E_1=.60, and E_2=.35, whereas in the RAs it is E_0=.44, E_1=.12, and E_2=.44, were made. The results of the experiment are given in the following table:

	P	TMs*	RAs*	N**	Freq. TMs	Freq. RAs	Ratio TMs/RAs
I	a.	21	74	109,100	192×10^{-6}	678×10^{-6}	.284
	b.	121	54	61,312	1973 "	880 "	2.241
II	a.	22	6	213,180	103 "	28 "	3.666
	b.	152	61	262,464	579 "	232 "	2.492

* corrected (see text)
** corrected (x4)

Fully realizing that an uncomfortable number of assumptions were made to obtain the tabulated figures, we maintain that some trends are still worthy of notice: (1) The frequency of TMs is greater in those cases where the non-inverted chromosome was $XY^{L}{\cdot}Y^{S}$ (Ib and IIb). This may indicate that Y^{L} of the inversion folds back and preferentially pairs with Y^{L} of the non-inverted chromosome and/or that Y^{S} of the non-inverted chromosome folds back and preferentially pairs with X-heterochromatin to the left of the centromere of the inverted chromosome. In the case of Ia and IIa, the same preferential pairing relationships would make the formation of TMs more difficult. (2) The frequency of RAs is greater when the distal heterochromatin on the inverted chromosome is that of sc^{8L}. This observation cannot readily be explained on the basis of homology and may reflect a greater breakability of X vs. Y-heterochromatin. (3) The higher frequency of RAs induced in IIb than in IIa may be a function of the longer heterochromatic segment available to the left of the centromere of the non-inverted chromosome in IIb. This physical difference apparently masks the fact that Y^{S} may have greater pairing affinity for Y^{S}, in the case of IIa, than it would have for Y^{L}, in the case of IIb. The same trend is seen in Ib vs. Ia. Here, the lessened degree of difference indicates that X-heterochromatin (of sc^{8L})

pairs more readily with Y^S than Y^S would with Y^S. This may not be as peculiar as it may seem if one considers that in normal situations, the X and Y are pairing partners.

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The influence of heterochromatin on crossing over in ring/rod heterozygotes of D. melanogaster.

The presence among the Eugene stocks of a large number of tandem metacentric (TM) lines, synthesized for other purposes by Drs. E. Novitski and W. J. Peacock, has afforded the opportunity to study the influence of pericentric heterochromatin on the crossing over properties of ring X-chromosomes. The TM lines had been obtained by irradiating females of the constitution XY, y^2su-$w^a w^a Y^S \cdot Y^L y^+$(Parker)/ XY^L, In(1)sc^4-sc^{8L}, EN^R, y f v(or m) cv $y \cdot Y^L y^+$. Two different inverted chromosomes, derived from two separate stocks of In(1)EN, had been used. TM's bearing one or the other of these inverted chromosomes will be referred to as (A) or (B) in the following presentation (series 17- and 19- of Novitski and Peacock).

Virgin females from each of 5 (A) and 9 (B) TM lines (all heterozygous for the markers y, cv, v (or m) and f) were crossed to males bearing the fertility tester Y-chromosomes of Brosseau; the fertility of ring-bearing sons with each of the various Y-testers determined the amount of Y heterochromatin present in a given TM (and, therefore, in the ring X-chromosomes derived from it), measured in terms of fertility factors. Using the representation for a normal Y + + + + + c + +, where the first five + signs indicate kl-5 through kl-1, c is the centromere and the next two + signs are ks-1 and ks-2, the following distribution was obtained: - - - - - c - - (3), - - - - + c - - (5), - + + - + c - - (1) and + + + + + c - - (5).

Ring chromosomes from each of the above four types were used in the following crosses: X^c(from TM (A) or (B)), y cv v (or m) / f x sc cv v f B / Y. Each cross consisted of 12 or 24 pair matings, brooded for three 3-day broods. Care was taken concerning uniformity in age of females and temperature. The results are presented in the following table:

Ring Type* (kl-1 tokl-5)	Rod ♂♂ c.o. / n.c.o.	Rod ♂♂ % c.o.	Ring ♂♂ c.o. / n.c.o.	Ring ♂♂ % c.o.	Pat. ♂♂	♀♀	Pat. ♂♂ / ♀♀
(A) - - - - -	87 / 1785	4.6	32 / 1340	2.3	77	3405	2.3
+ - - - -	187 / 1635	10.3	55 / 1300	4.1	85	3447	2.5
(B) - - - - -	169 / 1657	9.3	36 / 1302	2.7	87	3127	2.8
+ - + + -	124 / 910	12.0	20 / 590	3.3	70	1681	4.2
+ + + + +	94 / 883	9.6	24 / 612	3.8	67	1683	4.0

* Refers to the number of Y^L factors present in the pericentric heterochromatin of the ring chromosome.

The results of crosses involving rings derived from type (A) TM chromosomes suggest that an increase in pericentric heterochromatin results in an increase in the frequency of crossing over. Furthermore, this increase is of greatest magnitude in region IV which, significantly perhaps, is the region adjacent to heterochromatin in both the ring and the rod chromosomes. Rings derived from type (B) TM's show an increase in crossing over with added heterochromatin of a much lower level of magnitude. The following table presents recombination frequencies for each individual region studied; the rings containing no Y^L fertility factors are used as the reference base; the Table also includes a comparison of one of the (B) rings with the (A) series