AN EFFECT OF X RAYS ON THE LINKAGE OF MENDELIAN CHARACTERS IN THE SECOND CHROMOSOME OF *DROSOPHILA* *MELANOGASTER*

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INTRODUCTION

In previous contributions it has been shown (MAVOR 1923 a, b) that X rays cause a decrease in crossing over between eosin eye color and miniature wing in the first or sex chromosome of *Drosophila melanogaster*. Since PLOUGH (1917) has shown that temperatures above or below normal cause an increase in crossing over in the black-to-curved region of the second chromosome in the same species it appears of interest to discover what, if any, effect X rays have on crossing over in the same region of the second chromosome. The investigation to be reported here had this in view.

When a normal wild-type fruit-fly (*Drosophila melanogaster*) is mated with a black-bodied, purple-eyed and curved-winged fly, the heterozygous offspring obtain the factors for the three mutant characters from one parent. If, now, the daughters of such a cross are back-crossed to black purple curved males, a majority of their offspring will be either wild-type or black purple curved, showing that these characters are linked (in this

case in the second chromosome). These two kinds of flies form the non-crossover classes. There will be also a number of offspring in which the characters are not associated in this way, namely, normal-bodied, purple-eyed and curved-winged, and black-bodied normal-eyed and normal-winged (crossing over between black and purple); normal-bodied, normal-eyed and curved-winged, and black-bodied, purple-eyed and normal-winged (crossing over between purple and curved); and normal-bodied, purple-eyed and normal-winged, and black-bodied, normal-eyed and curved-winged (double crossing over). The percentages of crossing over between the characters mentioned have been accurately determined independently by BRIDGES, MULLER and PLOUGH, and a summary of their results is given by BRIDGES and MORGAN (1919). They give as the weighted averages of all previous determinations for crossing over between black and purple, 6.2 percent, the determination having involved somewhat over 50,000 flies, and for crossing over between purple and curved, 19.9 percent, this determination having involved somewhat over 60,000 flies. It should be added that the determinations by the different investigators are in approximate agreement.

DESCRIPTION OF EXPERIMENTS

The investigation to be described in the present paper included two experiments. In the first of these, twenty sisters from the mating of a wild-type female with a black purple curved male were used. Eleven were kept as controls and nine were X-rayed for 3 minutes and 15 seconds at a distance of 23.5 cm from the tungsten target, the Coolidge tube being operated at 50,000 volts and .05 amperes. Previous experiments had shown that the temperature in the X-ray box in which the flies were exposed did not vary from that of the room by more than 1°C. On the day after the X-raying, all of the twenty females were mated to black purple curved males and placed in individual culture bottles. The pairs, control and X-rayed, were changed to new bottles every three days until the eighteenth day when they were killed. The offspring coming out in the bottles were counted daily until the seventeenth day after mating. The second experiment was performed in the same way with the following exceptions: the control contained eleven pairs and there were twenty-seven pairs in which the females were X-rayed. The X-ray treatment was the same, except that the time was shortened to 3 minutes. The females were mated immediately after being X-rayed and were transferred to new bottles every three days until the twelfth day, when they were killed. The flies coming out in the culture bottles were counted every three or

four days until the seventeenth day after mating. The bottles of both experiments were kept in an incubator set at 22°C, and during the whole time the temperature did not go below 20°C, or above 24°C.

First experiment

The results of the first of these experiments, our number 103, are shown in table 1. The data from which the percentages in this table were calculated are given in the appendix in table 5. The sterilizing effect of the X

TABLE 1

Experiment 103. Effect of X rays on crossing over in the second chromosome. The numbers in all of the columns except those headed $\frac{\text{Diff.}}{\text{P.E. diff.}}$ give percent of crossing over.

Black-to-purple region

BOTTLE	X-RAYED	CONTROL	DIFFERENCE	P. E. diff.	$\frac{\text{DIFF.}}{\text{P. E. diff.}}$
First.....		5.6			
Second.....	18.5	6.3	12.2	2.1	5.9
Third.....	24.4	4.4	20.0	1.0	19.1
Fourth.....	17.3	3.5	13.8	1.0	13.8
Fifth.....	9.5	3.3	6.2	1.1	5.8
Sixth.....	8.6	4.2	4.4	1.5	3.1

Purple-to-curved region

BOTTLE	X-RAYED	CONTROL	DIFFERENCE	P. E. diff.	$\frac{\text{DIFF.}}{\text{P. E. diff.}}$
First.....		17.2			
Second.....	26.2	14.7	11.5	3.0	3.8
Third.....	28.4	14.7	13.7	1.8	7.5
Fourth.....	16.2	16.2	0.0	2.0	0.0
Fifth.....	20.4	15.8	4.7	2.2	2.1
Sixth.....	14.0	16.1	-2.1	2.6	0.8

rays was so marked in the first bottles, only 12 offspring being produced, that an accurate crossover value cannot be obtained. In the second bottles there is a conspicuous difference in the case of the first crossover (that between black and purple). This difference 12.2, divided by the probable error, 2.07, is equal to 5.9. The difference divided by the probable error for the purple-to-curved crossover is 3.8. In the third bottles the greatest difference occurs. Here the crossover value has been increased from that of the control, 4.39 percent, to 24.36 percent, giving a difference of

FIGURE 1.—Graph of percent of crossing over between black (body color) and purple (eye color) in experiment 103. The X-rayed females were treated soon after emergence from the pupa (within two days). Both control and X-rayed females were mated on the day after the X-ray treatment was given. The pairs of flies, both in the X-rayed and control sets were transferred to new bottles every three days. In making the graph the percentages were determined from the total number of F_1 which emerged in the bottles within seventeen days from the time the parents were placed in the bottles. The number of F_1 which emerged in the first bottles of the X-rayed females was not sufficient to give a significant crossover value.

approximately 20 percent; this divided by the probable error gives 19.1. For the purple-to-curved region in the third bottles the difference between the X-rayed and control, divided by the probable error, is 7.5.

The statistical treatment of the data shows that there is a significant increase in crossing over in the X-rayed females for the black-to-purple crossover in each of the second, third, fourth and fifth bottles. In the case of the purple-to-curved crossover there is a significant increase in the second and third bottles and possibly the fourth. Since the purple-to-curved

FIGURE 2.—Graph of crossing over between black and purple in experiment 103 using the same data as in figure 1, but plotted to show the difference (continuous line) in percent of crossing over between the X-rayed and control females and the probable error of the difference (interrupted line).

region has normally the larger crossover value it is clear that X rays have more effect on crossing over in the black-to-purple than in the purple-to-curved region. The percent of crossing over of black-to-purple in this experiment is shown graphically in figure 1. In figure 2 the difference in percent of crossing over between the X-rayed and control females is shown, the probable error being indicated by the broken lines.

Second experiment

The results of the second of these experiments, our experiment number 404, are shown in table 2. The data from which the percentages in this table were calculated is given in the appendix in table 6. The X-ray dose in this experiment was somewhat less than in the previous one, having

TABLE 2

Experiment 404. Effect of X rays on crossing over in the second chromosome. The numbers in all of the columns except those headed $\frac{\text{Diff.}}{\text{P. E. diff.}}$ give percent of crossing over.

Black-to-purple region

BOTTLE	X-RAYED	CONTROL	DIFFERENCE	P. E. diff.	$\frac{\text{DIFF.}}{\text{P. E. diff.}}$
First.....	4.8	4.2	0.6	0.8	0.8
Second.....	7.0	2.9	4.1	0.7	6.6
Third.....	14.7	3.6	11.1	0.5	24.4
Fourth.....	10.8	4.2	6.6	0.5	14.3

Purple-to-curved region

BOTTLE	X-RAYED	CONTROL	DIFFERENCE	P. E. diff.	$\frac{\text{DIFF.}}{\text{P. E. diff.}}$
First.....	19.8	18.6	1.2	1.5	0.8
Second.....	17.6	12.3	5.3	1.0	4.8
Third.....	23.6	12.9	10.7	0.8	12.5
Fourth.....	17.8	14.7	3.1	0.8	3.8

lasted only 3 minutes as against 3 minutes and 15 seconds in the case of the first experiment. Also a greater number of females were X-rayed. For this reason the probable errors of the differences are considerably smaller. The results of this experiment confirm those of the first. The differences are smaller, however, corresponding to the smaller dose of X rays given to the females. Considering first the black-to-purple region, one sees that, as in experiment number 103, in the first bottles there is no sig-

nificant difference between the percent of crossing over in the X-rayed and control females, $\frac{\text{Diff.}}{\text{P.E.}_{\text{diff.}}} = 0.8$. In the second, third and fourth bottles there is a significant difference, the greatest difference being in the third bottles, where the difference, 11.1, is 24.4 times the probable error of the difference. In the case of the purple-to-curved region in the first bottles

FIGURE 3.—Graph of crossing over between black and purple in experiment 404. The conditions of this experiment were similar to those of experiment 103, figure 1, with the exception that the females were mated immediately after X-ray treatment, and the X-ray dose was less.

there is also no significant difference between the percent of crossing over in the X-rayed and control females. In the second and third bottles the difference for the purple-to-curved region is significant, being greatest in the third bottles, where the difference is 12.5 times the probable error.

The difference in the fourth bottles is not significant. Graphs for this experiment for the black-to-purple region, similar to those for the first experiment, are shown in figures 3 and 4. Similar graphs for crossing over in the purple-curved region for the second experiment, No. 404, are shown in figures 5 and 6.

FIGURE 4.—Graph of crossing over between black and purple in experiment 404, plotted according to the method used in figure 2.

The combined results of the two experiments

The results of the two experiments are combined in table 3. Here it is seen that when the experiments are considered together there is a significant difference between the crossover values of the control and X-rayed females for the black-to-purple region in the second, third and fourth bottles, and for the purple-to-curved region in the second and third bottles and possibly the fourth. A graph of the weighted values of the percent of crossing over between black and purple in experiments 103 and 404 for three-day intervals (each set of bottles) is shown in figure 7. In figure 8 is shown a similar graph for the difference in percent of crossing over between the control and X-rayed females, the interrupted lines indicating the corresponding probable errors. In figure 7 it is seen that the control, dotted line, varied from 4.78 percent to 3.25 percent, there being a slight decrease with age until the fifteenth day. This decrease in the crossover value with age has already been reported by BRIDGES (1915) and PLOUGH

(1917). The effect of the X rays on the crossover value (continuous line) becomes apparent in the counts of the offspring of the X-rayed females in the second bottles (the fourth to the seventh day after X-raying in the case of the first experiment and the third to the sixth day in the case of the

FIGURE 5.—Graph of crossing over between purple and curved in experiment 404, plotted as in figure 3.

FIGURE 6.—Graph of crossing over between purple and curved, plotted as in figure 4.

TABLE 3

Experiments 103 and 404 combined. Effect of X rays on crossing over in the second chromosome.

The numbers in all of the columns except those headed $\frac{\text{Diff.}}{\text{P. E. diff.}}$ give percent of crossing over.

Black-to-purple region

BOTTLE	X-RAYED	CONTROL	DIFFERENCE	P. E. diff.	$\frac{\text{DIFF.}}{\text{P. E. diff.}}$
First.....	4.7	4.8	-0.1	0.8	0.16
Second.....	8.0	4.5	3.5	0.6	6.11
Third.....	15.8	4.0	11.8	0.4	29.14
Fourth.....	11.2	3.8	7.4	0.4	20.78

Purple-to-curved region

BOTTLE	X-RAYED	CONTROL	DIFFERENCE	P. E. diff.	$\frac{\text{DIFF.}}{\text{P. E. diff.}}$
First.....	19.6	18.0	1.6	1.4	1.1
Second.....	18.4	13.5	4.9	1.0	5.2
Third.....	24.1	13.8	10.4	0.7	14.6
Fourth.....	17.7	15.5	2.2	0.7	3.3

second experiment). The effect of the X rays is greatest in the third bottles (seventh to tenth day after X-raying in the first experiment and sixth to ninth day after X-raying in the second experiment). The fourth, fifth and sixth bottles (ninth to eighteenth day) show a gradual recovery toward

FIGURE 7.—Graph of crossing over between black and purple, experiments 103 and 404 being combined. It should be noted that the graph starts with the time of mating in each of the experiments and that the X-ray treatment was given in one case (experiment 103) on the day before mating and in the other case (experiment 404) on the day of mating.

the crossover value of the control. The difference between the crossover value in the cultures of the X-rayed and control females divided by the probable error of the difference is for each of the six bottles 0.16, 6.11, 29.14, 20.78, 5.78 and 3.07, respectively.

The data obtained show that X rays have a similar effect on crossing over between purple and curved, although the increase in the crossover

value is relatively not so great as in the case of black to purple and recovery to the normal crossover value is more rapid. A graph showing the difference in percent of crossing over between purple and curved for experiments 103 and 404 (the values having been weighted) is shown in figure 9.

The values of the coincidence of crossing over between black to purple and purple to curved for the cultures of the X-rayed and control females

FIGURE 8.—Graph of crossing over between black and purple, experiments 103 and 404 being combined, plotted according to the method used in figure 2.

cannot be determined with a sufficiently small probable error to admit of an accurate comparison. The values found are shown in table 4. They show that there is no great increase or decrease in the coincidence due to the X-ray treatment.

TABLE 4

Experiment 404. Effect of X rays on coincidence of crossing over in the second chromosome, black to purple and purple to curved.

BOTTLE NUMBER.....	1	2	3	4
Coincidence, control...	149.6	180.5	114.3	91.5
Coincidence, X-rayed...	96.3	140.1	101.8	147.0

FIGURE 9.—Graph of crossing over between purple and curved, experiments 103 and 404 being combined, plotted according to the method of figure 2.

DISCUSSION

Viability

The experiments show that the crossover value, as determined from counts of the offspring, is greater in the case of females which were submitted to X-ray treatment than in the case of their sisters which did not receive the treatment but were otherwise reared under identical conditions. The question arises whether this increased crossover value found in the case of the X-rayed females is really an expression of an increased amount of crossing over in the eggs. That the X-ray treatment had an injurious effect on some of the eggs is shown by the lessened fertility of the X-rayed females. It is known, further, that the different mutant forms used in determining the crossover values have different viabilities. May it not be that the X-ray treatment merely accentuates the differences in viability between the crossover and non-crossover classes?

In considering this question it is to be noticed that the effect of the X

rays is to give an *increased* crossover value. It is clear that an increased crossover value which was due to greater differences in the viabilities of the classes of offspring could only be brought about by one of the three following conditions: (1) a relative decrease in the viability of one or more of the non-crossover classes; (2) an increase in the viability of one or more of the crossover classes; (3) a combination of these two conditions. BRIDGES and MORGAN (1919) have discussed the determination of the viabilities of the classes of offspring in experiments on crossing over. An accurate determination of the viabilities of the various crossover and non-crossover classes in the experiments now under consideration would require three additional experiments similar to either of those described but differing from them in having different groupings of the mutant genes in the chromosome. Thus, while in the experiments described, the females

had the formula $\frac{++}{b \ p_r \ c}$, to determine the viability of the different classes

experiments in which the females had the formulae, $\frac{b++}{+ \ p_r \ c}$, $\frac{b \ p_r +}{++ \ c}$, and $\frac{b+c}{+ \ p_r +}$, would be required. It is possible, however, from the data at

hand, to compare the viabilities of certain of the classes. Such a comparison is given in table 7, in which the numbers of offspring in the complementary classes are compared. Considering first the non-crossover classes it is seen that in both the cultures of the control and X-rayed females the number of offspring showing all three of the mutant characters is approximately equal to the number of normal offspring. Hence, if the increased crossover value shown by the X-rayed females, is to be attributed to a decreased viability of the non-crossover classes, the decrease must be the same whether the offspring are normal or contain the three mutant characters. The crossover classes may be considered next. In the case of crossover 1, that between black and purple, there is a noticeable difference between the viability of the $+ \ p_r \ c$ class and the $b++$ class, the $b++$ class being the more viable, and this difference is greater in the case of the offspring of the X-rayed females. It might be conceived therefore that the increased crossover value found for the X-rayed females for the black-to-purple region was due to a *relatively* increased viability of the $b++$ and $+ \ p_r \ c$ classes. It is necessary to include both of these classes, since, if the crossover value is found by taking only the $+ \ p_r \ c$ class (the smaller) with one of the non-crossover class (either one, since they are approximately equal), the value found is still much greater (approximately three times in experiment 404) in the case of the X-rayed females than in that

of the control. Turning to the crossover 2, that between purple and curved, it is seen that here also the two classes of offspring do not show equal viability, but that the class, $++c$, is more viable. However, the relative viability, as shown by the ratio, is approximately the same in the offspring of the control and X-rayed females, so that here again if the increased crossover value is due to differences in viability, both the classes of offspring of the X-rayed females must show increased viability. In the case of the classes of double crossovers the numbers are probably too small to give definite information as to the relative viabilities of the classes. However, it can be shown, as in the two previous cases, that, if the increase in the double crossing over is to be accounted for by an increase in the viability of the classes of double crossovers, then the viability of each class must have been increased. An examination of the numbers of offspring in the crossover classes leads to the conclusion that if the increased crossover value shown by the X-rayed females is due to a relatively increased viability of the offspring in the crossover classes, then the increased viability must affect each of the classes of crossovers. In other words, in all cases where crossing over occurs, the offspring have or acquire greater resistance to X-ray injury. The alternative to this conclusion is that the effect of the X rays is to actually increase the amount of crossing over in the eggs. Between these two the experimental data do not give the means to decide, although it is difficult to see how merely going through the process of crossing over should increase the resistance of an egg to the effects of X rays.

Comparison of the effects of X rays on the first and second chromosomes

The effect of X rays on crossing over in the second chromosome may be compared with the effect of X rays on crossing over in the first or sex chromosome already recorded by one of us (MAVOR 1923 a, b). Here it was found that X rays decrease the crossover value for eosin-eyed and miniature-winged, the effect increasing with the dose. After a dose approximately the same as that given in the first of the experiments on the second chromosome the crossover value for eosin and miniature was decreased from approximately 25 percent to less than 10 percent and the effect continued from the sixth to the twelfth day after the treatment. We see in the effects which X rays produce on crossing over in the first and second chromosomes of *Drosophila* a remarkable instance of opposite effects on the mechanism of heredity produced by the same treatment with the same physical agent.

Comparison of the effects of X rays and temperature on crossing over

It is of great interest to compare the effect which the experiments described show X rays to have on crossing over in the second chromosome with the effect which PLOUGH (1917) found temperature to have on crossing over. PLOUGH found, using the same characters, that submitting females to temperature either considerably above or below the normal rearing temperature (22°C) caused an increase in the crossover value. The X-ray experiments show that X rays also cause an increase in the crossover value when the flies are kept at a temperature of 22°C. Whereas PLOUGH found that the effect of temperature on crossing over became first apparent on the seventh to eighth day after the beginning of the heat treatment, the X-ray experiments show that the X-ray effect on crossing over becomes apparent on the fourth to seventh day (first experiment) or third to sixth day (second experiment).¹ It has already been stated that X rays cause the death of a considerable number of the eggs in the later stages of maturation. It is possible that eggs which are in the earlier stages of the crossing-over process and survive may be accelerated in maturation by the X rays and thus be laid at an earlier period. This may offer an explanation of the difference in the time of the beginning of the increase in the crossover value in the experiments of PLOUGH (1917) and the present experiment. It should be stated, however, that there is no evidence of such acceleration, e.g., earlier hatching out of offspring of X-rayed flies. A more striking difference is that, while the effect of temperature lasts for a time corresponding to the period of time treated and then disappears abruptly, the effect of an X-ray treatment which lasted only 3 minutes and 15 seconds starts on the third to sixth day, reaches a maximum on the sixth to ninth day, and then gradually falls off, the effect being still evident after fifteen days.

Do X rays directly affect the process of crossing over?

The question is raised as to whether X rays affect directly or only indirectly the process of crossing over. A further comparison of the results of the X-ray experiments with those of PLOUGH (1917) gives evidence on this point. If PLOUGH's figures 5 and 7 be compared with our figures 1 and 3 it will be noted that in the case of his figure 5 (p. 177) where the heat treatment was begun on the day of hatching and continued for seven days, the rise in the crossover value appears suddenly in the counts of the seventh to ninth days and disappears as suddenly in the counts of the

¹ In a third experiment recently completed, the X-ray effect does not appear until the sixth day.

fifteenth to seventeenth days and in the case of his figure 7 (p. 178) where the heat treatment lasted from the third to the eleventh day the rise in percent of crossing over begins somewhat gradually in the counts of the ninth to eleventh days, rises to maximum in the counts of the fifteenth to seventeenth days and disappears abruptly in the counts of the nineteenth to twenty-first days. The tables and curves given by PLOUGH bring out the following facts (p. 181):

“Exposure of a female to a temperature of 31.5°C for a given period results in a decided increase in the percentage of crossing over among her offspring for a period about as long as the exposure. In case she is exposed up to the time of hatching this increase shows among the offspring of the first seven or eight days after mating. If the adults are exposed, the effect begins to be noted at the seventh or eighth day after the adults first began to receive treatment. The increase is maintained for the definite period mentioned above only.”

PLOUGH believes that

“The facts admit of only one interpretation, namely, that the high or low temperature has an effect on the chromosomal mechanism at one point in the development of the eggs only, and that eggs which have already passed this particular point in their development when the new temperature is applied, or which do not reach that point during the period of exposure, register no higher percentage of crossing over than the controls.”

In contrast to these results are the results of the X-ray treatment. Here it may be said that an X-ray treatment given to females after hatching and before mating leads to an increase in the crossover value of the black-to-purple region beginning from three to six days after the treatment, rising to a maximum on the sixth to ninth day, and lasting until twelve to fifteen days after the treatment. Since we are dealing here with the time during which eggs were laid, the parents having been transferred to new bottles every three days, it is not possible to attribute the prolongation of the effect of the X-ray treatment on the crossover value to retarded development of the eggs.

One is therefore forced to conclude that X rays do not affect the “chromosomal mechanism at one point in the development of the eggs only.” The effect which X rays have in increasing the crossover values in the second chromosome is therefore seen to be due to some effect which they have either on the chromosomes or on some other part of the mechanism involved, which produces a condition which increases the amount of crossing over. X rays can not be said, therefore, to act directly on the process of crossing over in this case.

CONCLUSIONS

1. It has been shown that X-ray treatment of the female leads to an increase in the crossover values for black to purple and purple to curved.
2. The greatest effect for the same dose is produced in the black-to-purple region.
3. An X-ray treatment lasting for 3 minutes and 15 seconds causes an increase in the crossover value for the black-to-purple region lasting for at least twelve days.
4. A comparison of these results with those of PLOUGH (1917) leads to the conclusion that X rays do not directly affect the process of crossing over, but that they produce either in the chromosomes or some other part of the mechanism a condition which causes an increase in crossing over.

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APPENDIX—Tables 5 to 7

TABLE 5

Experiment 103. Effect of X rays on crossing over in the second chromosome. The columns give actual numbers of flies. The column headed 1 refers to the black-to-purple region, and the column headed 2, to the purple-to-curved region. The column headed 1-2 contains double crossovers.

BOTTLE		TOTAL	NON-CROSSOVER	1	2	1-2
First.....	Control	808	637	32	126	13
	X-rayed	12	11	—	1	—
Second.....	Control	1472	1192	63	188	29
	X-rayed	65	43	5	10	7
Third.....	Control	1299	1066	42	176	15
	X-rayed	201	110	34	42	15
Fourth.....	Control	1262	1027	31	191	13
	X-rayed	173	121	24	22	6
Fifth.....	Control	1199	981	29	179	10
	X-rayed	137	100	9	24	4
Sixth.....	Control	1556	1257	49	234	16
	X-rayed	93	73	7	12	1

TABLE 6

Experiment 404. Effect of X rays on crossing over in the second chromosome. The columns give actual numbers of flies. The column headed 1 refers to the black-to-purple region, the column headed 2 to the purple-to-curved region. The column headed 1-2 contains double crossovers.

BOTTLE		TOTAL	NON-CROSSOVER	1	2	1-2
First.....	Control	1030	807	31	180	12
	X-rayed	438	334	17	83	4
Second.....	Control	1411	1377	36	187	11
	X-rayed	671	516	37	108	10
Third.....	Control	1493	1254	46	185	8
	X-rayed	1505	982	168	302	53
Fourth.....	Control	1223	999	44	173	7
	X-rayed	2602	1912	227	408	55

TABLE 7

The comparative viability of the non-crossover and crossover classes in experiments 103 (second to sixth bottles) and 404 (second to fourth bottles). The figures are for black, purple and curved. + = wild character; - = mutant character.

	CLASS	EXPERIMENT 103		EXPERIMENT 404	
		Control	X-rayed	Control	X-rayed
Non-crossover.....	+++	1722	141	1875	1672
	---	1680	122	1755	1688
Ratio.....		1.02	1.16	1.07	0.99
Crossover in region 1	+- -	65	22	58	160
	-++	75	43	68	269
Ratio.....		0.87	0.51	0.85	0.60
Crossover in region 2	--+	238	28	201	305
	+- -	321	46	336	498
Ratio.....		0.74	0.61	0.60	0.61
Crossover in regions 1 and 2	-+-	32	25	12	79
	+- +	28	4	14	37
Ratio.....		1.14	6.3	0.86	2.1