

Lawrence Berkeley National Laboratory

Recent Work

Title

AGE DEPENDENCE OP THE LOCATIONS OF X-RAY-INDUCED SOMATIC CROSSING-OVER IN DROSOPHILA

Permalink

<https://escholarship.org/uc/item/1d62w7dp>

Authors

Tokunaga, Chiyoko
Anaheim, Norman

Publication Date

1966-03-01

University of California
Ernest O. Lawrence
Radiation Laboratory

AGE DEPENDENCE OF THE LOCATIONS OF
X-RAY-INDUCED SOMATIC CROSSING-OVER IN DROSOPHILA

TWO-WEEK LOAN COPY

*This is a Library Circulating Copy
which may be borrowed for two weeks.
For a personal retention copy, call
Tech. Info. Division, Ext. 5545*

DISCLAIMER

This document was prepared as an account of work sponsored by the United States Government. While this document is believed to contain correct information, neither the United States Government nor any agency thereof, nor the Regents of the University of California, nor any of their employees, makes any warranty, express or implied, or assumes any legal responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by its trade name, trademark, manufacturer, or otherwise, does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof, or the Regents of the University of California. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof or the Regents of the University of California.

Submitted to Genetics

UCRL-16687

UNIVERSITY OF CALIFORNIA

Lawrence Radiation Laboratory
Berkeley, California

AEC Contract No. W-7405-eng-48

AGE DEPENDENCE OF THE LOCATIONS OF
X-RAY-INDUCED SOMATIC CROSSING-OVER IN DROSOPHILA.

Chiyoko Tokunaga and Norman Arnheim, Jr.

March 1966

AGE DEPENDENCE OF THE LOCATIONS OF
X-RAY-INDUCED SOMATIC CROSSING-OVER IN *DROSOPHILA*.¹

Chiyoko Tokunaga and Norman Arnheim, Jr.

Lawrence Radiation Laboratory,
Department of Zoology and Department of Genetics
University of California, Berkeley, California

Communicated March 1966

INTRODUCTION

Somatic crossing-over was first demonstrated in *Drosophila melanogaster* by Stern (1936). Many factors are known to influence the frequency of somatic exchanges, including temperature (Brosseau 1957, Kaplan 1953, Stern and Rentschler 1936), X-irradiation (Becker 1957, Lefevre 1949), the presence of Minute genes (Stern 1936), the polygenic background (Weaver 1960), and the amount of heterochromatin (Walen 1964). In addition to these factors the frequency of somatic crossing-over has been found to vary from one body region to another (Abbadessa and Burdick 1963, Stern 1936), with the presence of heterologous inversions (Ronen 1964), and with maternal age, although the effect of this last factor is subject to controversy (Baker and Swatek 1965, Brown and Welshons 1955, Schwartz 1954). The frequency of somatic crossing-over events induced by temperature shock (Brosseau 1957) and X-irradiation (Becker 1956) has been found to vary, depending upon the time during ontogeny when the treatment is given. The experiments by Brosseau suggested that the position on the chromosome where the somatic exchange event occurs can be influenced by temperature treatments given at certain periods during ontogeny. The experiments to be reported here concern the effect on the location in the chromosome of somatic crossing-over events of X-irradiation delivered at different times during development.

While the junior author was investigating the developmental action of the dominant gene Tufted (Tft) located on the left arm of the second chromosome, he discovered that more of the somatic exchange events induced by X rays in young larvae occurred not between Tft and the kinetochore (i. e., to the right of Tft), but distal to the Tft locus (to the left of Tft) (Arnheim 1966). This was somewhat unexpected, since it is often assumed that somatic crossing-over occurs primarily in the region most proximal to the kinetochore. To investigate this phenomenon further, two experiments were planned. It was known that the scute⁸ inversion chromosome suppresses the recovery of X-ray-induced somatic crossovers in the X chromosome (Lefevre, 1949); therefore in our first experiment an inversion-carrying chromosome was used to reduce, if possible, the recovery of somatic crossovers to the left of Tft. The results of this experiment not only confirmed the original findings with respect to very young larval stages, but also suggested that as development proceeds there is a change in the ratio of X-ray-induced somatic crossing-over events occurring to the right and to the left of the Tft gene.

To test this suggestion we made extensive experiments using the gene Bristle.

Material and Methods

The Tufted gene is known to be located somewhere between the genes black (48.5) and purple (54.4) close to the kinetochore on the left arm of the second chromosome (Ritterhoff 1952). The Tft phenotype consists primarily of numerous supernumerary macrochaetae on the posterior half of the mesothorax, usually accompanied by a widening of the area, and often incomplete separation of the scutellum from the mesonotum. Somatic crossing-over to the right of Tft in a cell of a larva heterozygous for Tft (Tft/+) can result in the production of +/+ and Tft/Tft tissue areas which form a twin spot on the adult fly. The not-Tft spots (+/+) can, if they are in the posterior mesothorax region, be distinguished from the background tissues by the absence of supernumerary macrochaetae. The Tft/Tft segregants are not sufficiently different in phenotype from the Tft/+ background to be distinguishable from it. Crossovers to the left of Tft do not result in a change of the original heterozygous Tft/+ genotype. Such crossovers, however, can be identified by means of a marker located to the left of Tft, preferentially one that affects the coloration of the body surface and its bristles. In a method similar to that used in the work with the gene esc (extra sex combs) (Tokunaga and Stern 1965), this color marking was accomplished by the use of a mutant allele of the gene yellow (y) in the X chromosome and a wild-type allele of yellow (y⁺) inserted in the second chromosome to the left of Tft. [The scute¹⁹ⁱ insertion from the T(1;2)sc¹⁹ stock was used for this purpose.] Were it not for this y⁺ insertion such flies would have yellow body and bristle coloration. When a somatic crossing-over event occurs to the

right of Tft in such cells (see Fig. 1A) the resulting yellow area will also be homozygous for the Tft⁺ allele. When a cross-over event falls to the left of Tft, between it and the y⁺ insertion, the resulting yellow area retains its heterozygosity for Tft. In this way somatic crossing-over events to the left and to the right of the Tft gene can be distinguished from each other. Double somatic crossing-over results in a not-yellow and not-Tft tissue patch.

The same marking method was used in the experiment with Bristle (Bl, 2-54.8). This dominant gene is located to the right of Tft and very close to the kinetochore. It causes abnormal development of bristles, making them shorter and thicker than normal, with a blunt and beaded outline.

Figure 1A shows the genetic constitution of the flies examined for mosaicism in the original experiment (Arnheim 1966). The genotype of the flies studied in the present experiment with Tft is shown in Fig. 1B. Figure 1C presents the genetic constitution of the flies studied in the experiment with Bl.

Somatic crossing-over was induced by X-rays at various larval as well as late embryonic stages. In all but the original experiment, in which eggs were collected over a 24-hour period, the collections were at 5- or 10-hour intervals. After being aged for selected periods of time the larvae were irradiated with either 1000 r or 1500 r at a dose rate of 75 r per minute (140 kv, 4 ma, 1.5 mm Al inherent filtration plus 0.75 mm Al external filtration). For unknown reasons a slightly different dose rate of 84 r per minute occurred in series (b) of the Bl experiment.

The age of the individual at the time of irradiation is expressed in this paper in hours after egg depositions. The temperature in all experiments was maintained at $25 \pm 1^\circ\text{C}$. The adult flies were inspected for mosaicism on the mesothorax under a dissecting microscope with a magnification of at least $50\times$, and, when necessary, $160\times$.

In both the Tft and Bl experiments only mosaic areas that included one or more macrochaetae were used in the analysis of the data. The spots could be divided into two groups: one yellow and not-Tft (or not-Bl) resulting from somatic crossing-over occurring to the right of Tft (or Bl), and the other yellow and Tft (or Bl) resulting from somatic crossing-over to the left of Tft between it (or Bl) and the y⁺ insertion.

In both experiments a few mosaics resulting from double crossing-over events were found (not-yellow, not-Tft and not-yellow, not-Bl). There were, however, some mosaic specimens which could not be classified unambiguously as resulting from double somatic crossing-over. In the Bl experiment, for instance, the presence of some extra macrochaetae was frequently observed in both irradiated and not-irradiated groups. The origin of these extra bristles is not known, although possibly they may result from the presence of the sc¹⁹ⁱ insertion. In the original sc¹⁹ translocation stock, extra bristles were observed with low frequency in females. This situation does not interfere with the scoring of mosaics in the Bl experiment. In the Tft experiments, however, the frequency of double crossing-over events would be underestimated if extra bristles caused by the sc¹⁹ⁱ insertion were thought to be the result of the presence of the Tft gene. Another source of uncertainty is present in the Bl experiments. Here the

occurrence of bristles which were not yellow and not typically Bl but whose shape and length varied from Minute-like to normal made classification of double crossing-over events difficult. Because of the uncertainty of the real number of double crossovers the observed frequencies are not given.

The conclusion that the two types of mosaic patches result from somatic crossing-over in two different regions rests on several assumptions. One is that the genotype of a mosaic spot can reliably be inferred from its phenotype. It is possible to assume, for instance, that certain mosaic patches that lack the Tft gene because of its removal by somatic crossing-over early in development can differentiate nonautonomously--that is to say, can develop the Tft phenotype. This hypothesis, however, encounters the following objection: Those tissues that lose the Tft gene late in development as a result of late irradiation should be the most likely to form regions expressing the Tft phenotype. On the contrary, as will be shown, the mosaic patches derived from late somatic crossing-over events are found to exhibit predominantly the non-Tft phenotype. Similarly, in the Bl experiment, late somatic crossing-over events also exhibit mostly a not-Bl phenotype. Another underlying assumption is that no genetic changes other than the somatic crossing-over events are responsible for the production of the mosaic spots. The appearance, however, of a yellow tissue patch with the Tft or Bl phenotype could be the result of a loss of the y⁺ insertion or of a somatic mutation from y⁺ to y. The results of both phenomena would be included in the data as somatic crossovers. Such cases, however, would at most be very rare (see Lefevre 1949), and should not interfere with the interpretation of most mosaics as resulting from somatic

exchanges. Final proof that all the events observed are really results of somatic crossing-over would be based upon the observation of twin spots. None of the experiments reported here permits the detection of such spots.

Results

The original Tufted experiment (Fig. 1 A)

The data are given in Table 1, Experiment A. Among the two types of mosaics the majority (14 out of 20) appeared to be the result of somatic crossing-over to the left of Tft, between it and the y^+ insertion and not in the region to the right of Tft, which includes the proximal heterochromatin. The seven cases considered unclassifiable are discussed below.

An experiment with Tufted and an inversion (Fig. 1 B)

Here the chromosome carrying the inversion [In(2L)t] was used as a homologue to the chromosome carrying Tft and the y^+ insertion. This was done in the expectation that In(2L)t would reduce the recovery of somatic crossing-over events to the left of the Tft locus within the limits of the inversion--more specifically, within the segment from salivary band 34A to a region distal to the y^+ insertion that is located about one or two units to the right of dumpy (2-13.0, salivary band 25A).

Larvae between the ages of 45 and 50 hours were given a dose of 1500 r. In order to reduce the high mortality usually associated with a high dose of radiation given to very young larvae the 22- to 27-hour and 22- to 32-hour age groups were exposed to only 1000 r. Among the

mosaic flies obtained in this experiment, a considerable number had spots of such a size or in such a position that unambiguous classification as to the presence or the absence of the Tft phenotype was impossible. Also very rare local tissue interactions between Tft and not-Tft cells, resulting in a Tft phenotype of presumably not-Tft bristles at the border line, occasionally make classification of spots difficult. All such mosaics were designated as being unclassifiable. The results are shown in Table 1, Experiments B. (Among the mosaics listed as yellow and not-Tft in Table 1 B, there are two cases of females in which an extra macrochaeta was found between the dorsocentral bristles of one side. One of them, from the 22-27-hour age group, had a mosaic patch which included both scutellar, postalar, and dorsocentral bristles and the posterior supra alar bristle. Another mosaic from the 22-32-hour age group had a patch covering the two dorsocentral bristles and adjacent microchaetae on one side of the thorax. Were it not for the presence in each case of one extra bristle, these flies would have been classified without hesitation as having a not-Tft patch. Even in the presence of the extra bristle this classification is upheld, since the presence of the extra bristle is thought to be due either to tissue interaction with surrounding Tft areas or possible extra bristle formation unrelated to Tft, as is occasionally seen in wild strains of flies. The two cases therefore were recorded as indicative of somatic crossing-over to the right of the Tft locus.)

As in the original experiment (Table 1 A), there were more crossovers to the left than to the right of Tft in the 22-27-hour age group, the numbers being 6 and 4 respectively, giving a ratio of right/left crossovers which equals 0.67. In the 22-32-hour age group, there were equal numbers of the two types, namely 15:15, giving a ratio of 1.0.

The 45-50-hour age group showed a ratio ($26/6 = 4.3$) which is strikingly different from that observed in the younger groups. A homogeneity test between the crossover distribution in the younger groups (22-27-hour and 22-32-hour age groups) and in the older group (45-50-hour), using Yate's correction, gives a χ^2 value of 7.26. This is significant at less than the 1% level. These data suggest that with increasing age of the larvae there is an increase in the relative frequency of X-ray-induced somatic crossing-over events to the right of the Tft locus compared with the left in the same chromosome arm.

The effect of larval age on the position of somatic crossing-over, however, has not been unambiguously demonstrated. It is possible that in the presence of In(2L)t the difference in the ratios between the younger and older larval groups results from a difference in the dose of radiation given (1000 r and 1500 r respectively). Further experiments were therefore planned.

Experiment with the gene Bristle (Fig. 1C)

An extensive study with Bristle was undertaken to determine the relation between larval age and the position of somatic crossing-over. In these experiments individuals of different ages ranging from late embryos to larvae 66 hours after egg deposition were irradiated with either 1000 r or 1500 r. Two experimental series, (a) and (b), separated by a period of 3 months, were run in order that both young and old individuals would be exposed to each one of the doses used.

In the analysis of the data in this experiment only males were classified according to their mosaic type. This was decided because there was some difficulty in making an unambiguous classification of the bristle pigmentation in mosaic females. Analysis of 500 male and 500 female flies identical in genotype to the irradiated flies but not receiving the X-ray treatment showed the occasional presence of abnormally pigmented bristles in females only (14/500 females affected and 0/500 males). The exclusive use of males in the experimental analysis allowed the identification of mosaics to be uninfluenced by this sexual dimorphism in the frequency of abnormal bristle pigmentation. Those males in the experimental series which seemed to exhibit X-ray-induced abnormalities of bristle pigmentation or morphology, making classification of the B1 or not-B1 phenotype difficult (only two mosaic cases were involved in this category), were excluded from the data.

The data are given in Table 2 and summarized in Fig. 2. It can be seen that as development progresses, the effect of either a 1000 r or 1500 r dose of radiation is to increase the proportion of somatic crossing-over events occurring to the right of Bl. The significance of the differences between the age groups in the distribution of crossovers to the left and right of Bl are shown in Fig. 3A for the experiments with 1000 r and in Fig. 3B for the experiments with 1500 r. The figure shows that, as in the experiment with Tft, the change in the ratio of crossover types with age is significant.

Analysis of the data in Table 2 indicates that the total frequency of mosaics in the 22-32-hour age group is greater in the 1500 r than in the 1000 r experiment. The same is true for the 45-50-hour and 50-60-hour age groups. An unexpected finding, however, is that for any one of the above three age classes the ratio right/left crossovers is greater in the 1500 r than in the 1000 r group (Fig. 2). One possibility that can explain this phenomenon is that the actual ratio of the two types of crossover events is dependent upon some dose effect. Another possibility, however, is that the higher ratios observed with the 1500 r doses results from a lethal effect upon the younger larvae in any one age group. The experiments with 1000 r and 1500 r each showed that the younger the larvae, the more frequent are crossovers to the left of Bl among the total number of crossovers. If a 1500 r dose tended to kill more of the younger larvae in an age class than a 1000 r treatment, the effect would be to reduce the probability of recovering somatic exchanges to the left of Bl. This would in effect raise the ratio right/left crossovers. A comparison was made within each one of the three age groups of the distribution of crossover events

occurring to the left and right of Bl after irradiation with 1000 r and 1500 r. There were no significant differences for the 22-32-hour, and 50-60-hour age groups, but the difference was significant for the 45-50-hour age group ($\chi^2 = 5.48$, $P < 0.02$). This was the only age group given the 1000 r and 1500 r doses in the separate experimental series (a) and (b). It is not known why the 22-32-hour age group, which is composed of the youngest larvae and would therefore be expected to show the greatest difference when the 1000 r and 1500 r groups are compared, did not show a significant difference. One other possible explanation why the data from the 45-50-hour age group in the 1500 r experiment were significantly different from those in the 1000 r experiment might be that the dose rate delivered in the experimental (b) series (84 r per minute) was different from that used in the (a) series (75 r per minute). It is interesting to note in this respect that the 22-32-hour age groups at 1000 r and 1500 r, which were run with the same dose rate, did not yield a significant difference. This is also true for the 50-60-hour experiments. Whether the trend observed is indicative of an age-specific dose effect, an age-specific killing effect, or some other factors is not known.

From the data obtained here, what we can say is that the ratio of the somatic crossing-over events changes consistently according to the age of larvae in each of the experiments with Bl as well as Tft.

Discussion

In Drosophila melanogaster, Bridges found that the frequency of meiotic crossing-over in second and third chromosomes of oocytes varies according to the age of the female. Each chromosome section investigated showed its own age-dependent change in the frequency of crossing-over, different from the change in other marked sections (see review by Bridges 1929).

The increase in meiotic crossing-over following X-irradiation is also known to affect some regions of the chromosome more than others (Muller 1925). It is of special importance within the context of this paper that the region of the second chromosome most affected by irradiation in Muller's studies was that between black (48.5) and purple (54.5), the same region in which Tufted is located and near which lies Bristle (54.8).

A general finding in studies on somatic crossing-over is that the majority of the events occur in the proximal portions of the chromosomes, usually adjacent to or in the centromeric heterochromatin. Somatic exchange events do not necessarily take place in the most proximal part of a chromosome. On the contrary, crossing-over in the X-chromosome is restricted to the heterochromatin distal to the bobbed locus (66.0), of the left arm. It does not occur in the heterochromatin/proximal to bobbed (Stern 1936). The prevalence of somatic crossing-over in the region near the centromere is found for spontaneous cases as well as for events induced by temperature, Minute genes, and X-irradiation. In somatic crossing-over in the X-chromosome, Stern (1936) showed that events occurring early in ontogeny under the influence of the M(I)n gene (62.7) as judged by large-sized spots, were principally to the right of this locus. This conclusion was based on the fact that the majority of the exchanges to the left of M(I)n occurred in small patches of tissue, as would be expected from events

occurring late in ontogeny. With respect to spontaneous cases of somatic crossing-over, there seemed to be no difference between the time during development at which crossovers to the left and right of sn³ took place. The work of Brosseau (1957) on somatic crossing-over in the X chromosome induced by heat and cold shocks indicated that the early exchange events were principally to the right of the singed locus (22.0) and therefore presumably in or around the proximal heterochromatin. The later events were both to the left and right of the singed locus, and the ratio of these two types of events could be altered by various treatments. No obvious correlation between the temperature used and the position of the somatic exchange occurring during the later stages of development could be detected.

Experiments by Kaplan (1953) on Minute-induced somatic crossing-over in the second chromosome revealed that the majority of the somatic exchanges occurred in regions close to the kinetochore. The gene Minute (2)z (12.9) on the left arm of the second chromosome was shown to increase the frequency of somatic crossing-over events to the left and to the right of Bl. Among the crossovers induced, 72% occurred to the right of Bl. Our data indicate that with respect to the left arm of the second chromosome, irradiation in early developmental stages results in a greater proportion of somatic crossovers to the left of the Tft and Bl loci than to the right of them. Later in development, a greater proportion of the events occurs to the right than to the left. This would imply that at least two regions of the chromosomes studied differ with respect to each other in the time during ontogeny at which they are most sensitive to irradiation-induced somatic crossing-over.

ACKNOWLEDGMENT

The authors wish to gratefully acknowledge the assistance of Professor Curt Stern, who during the course of this investigation and during the preparation of the manuscript has made valuable comments and criticisms.

Summary

In Drosophila melanogaster, X-ray-induced somatic crossing-over was studied in the left arm of the second chromosome. In experiments with the genes Tufted (Tft, 48.5-54.5) or Bristle (Bl, 54.8) irradiation given early in development results in more somatic exchanges to the left of these loci than to the right of them. Later in development the opposite is true, with more crossing-over occurring to the right than to the left. It would appear that both the Bl and Tft loci lie between two chromosome regions, which differ in the time during ontogeny at which they are maximally sensitive to X-ray-induced somatic crossing-over.

Literature Cited

- Abbadessa, R., and A. B. Burdick, 1963 The effect of X-irradiation on somatic crossing over in *Drosophila melanogaster*. *Genetics* 48: 1345-1356.
- Arnheim, N., Jr., 1966 Regional bristle formation in *Drosophila* in mosaics for lethal⁹⁻⁷⁻¹ and Tufted. Ph.D. dissertation. University of California, Berkeley. 44 pp.
- Baker, W. K., and J. A. Swatek, 1965 A more critical test of hypotheses of crossing over which involve sister-strand exchange. *Genetics* 52:191-202.
- Becker, H. J., 1956 On X-ray-induced somatic crossing over. *Drosophila Inform. Serv.* 30:101-102, 1957 Über Röntgenmosaikflecken und Defektmutationen am Auge von *Drosophila* und die Entwicklungsphysiologie des Auges. *Z. Ind. Abst. Vererb.* 88: 333-373.
- Bridges, C. B., 1929 Variation in crossing over in relation to age of female in *Drosophila melanogaster*. *Carnegie Inst. Wash. Publ.* 399: 63-89.
- Brosseau, G. E., 1957 The environmental modification of somatic crossing over in *Drosophila melanogaster* with special reference to developmental phase. *J. Exptl. Zool.* 136: 567-593.
- Brown, S. W., and W. J. Welshons, 1955 Maternal aging and somatic crossing over of attached-X chromosomes. *Proc. Natl. Acad. Sci. U.S.* 41: 209-215.
- Kaplan, W. D., 1953 The influence of *Minutes* upon somatic crossing-over in *Drosophila melanogaster*. *Genetics* 38: 630-651.
- Lefevre, G., Jr., 1949 Mutation in Germinal and Somatic Tissue. *Drosophila Inform. Serv.* 23: 91-92.

- Muller, H. J., 1925 The regionally differential effect of X rays on crossing over in autosomes of Drosophila. Genetics 10: 470-507.
- Ritterhoff, , 1952 Report of Johns Hopkins University, Report of New Mutants (Tufted). Drosophila Inform. Serv. 26:68-69
- Ronen, A., 1964 Interchromosomal effects on somatic recombination in Drosophila melanogaster. Genetics 50:649-658.
- Schwartz, D., 1954 Studies on the mechanism of crossing over. Genetics 39: 692-700.
- Stern, C., 1936 Somatic crossing over and segregation in Drosophila melanogaster. Genetics 21: 625-730.
- Stern, C., and V. Rentschler, 1936 The effect of temperature on the frequency of somatic crossing over in Drosophila melanogaster. Proc. Natl. Acad. Sci. U.S. 22: 451-453.
- Tokunaga, C., and C. Stern, 1965 The developmental autonomy of extra sex combs in Drosophila melanogaster. Develop. Biol. 11: 50-81.
- Walen, K. H., 1964 Somatic crossing over in relationship to heterochromatin in Drosophila melanogaster. Genetics 49: 905-923.
- Weaver, E. C., 1960 Somatic crossing over and its genetic control in Drosophila. Genetics 45: 345-357.

Footnotes

1. This work was carried out under the auspices of the United States Atomic Energy Commission and supported in part by National Science Foundation grant G 18057 and a Postgraduate Training Program in Genetics (USPHS-GM367) Traineeship awarded to the junior author.

Table 1. Distribution of mosaics in the experiment with Tufted. A: Experiment without inversion In(2L)t. B: Experiment with inversion In(2L)t. The data include both males and females. The time of irradiation is given in hours after egg deposition.

Age at irradiation	Dose	Experiment	Number of flies	Number of mosaics resulting from somatic crossing over to the:			Ratio right/left crossovers
				left of <u>Tft</u> (y, <u>Tft</u>)	right of <u>Tft</u> (y, not- <u>Tft</u>)	unclassifiable	
24-48	1500	A	3370	14	6	7	0.43
22-27	1000	B	2630	6	4	2	0.67
22-32	1000	B	3522	15	15	11	1.00
45-50	1500	B	3536	6	26	10	4.33

Table 2. Distribution of mosaics in two series of experiments (a) and (b) with Bristle. The data are for males only. The time of irradiation is given in hours after egg deposition.

Age at irradiation	Dose r	Experimental series	Number of flies	Number of mosaics resulting from somatic crossing over to the:		Ratio right/left crossovers
				left of <u>B1</u> (y, <u>B1</u>)	Right of <u>B1</u> (y, not- <u>B1</u>)	
17-22	1000	(a)	806	3	0	0.24
		(b)	5379	22	6	
22-27	1000	(a)	5280	22	2	0.09
22-32	1000	(a)	4267	26	15	0.58
33-43	1000	(b)	3949	49	30	0.61
45-50	1000	(b)	3418	26	29	1.12
50-60	1000	(b)	3527	11	24	2.18
61-66	1000	(b)	3161	18	30	1.67
22-32	1500	(a)	3210	38	37	0.97
45-50	1500	(a)	3597	22	58	2.64
50-60	1500	(b)	3128	18	52	2.89

Figure Legends

Fig. 1. Genotypes of the flies used for the induction of mosaics by means of somatic crossing-over.

A: Genotypes in the original experiment with Tft.

B: Genotypes in the experiment with Tft and inversion In(2L)t.

C: Genotypes in the experiment with Bl.

I: Sex chromosome constitution.

II: Second chromosome constitution.

black part: X chromosome

white part: Second chromosome

cross-hatched: Y chromosome

In: Inversion In(2L)t.

Fig. 2. The effect of a 1000 r or 1500 r dose of irradiation on the ratio of crossovers occurring to the left and right of Bl in embryos or larvae of different ages. The age is expressed in hours after egg deposition, and represents the average age of the individuals collected over a 5- or 10-hour period.

● : Experimental series a.

○ : Experimental series b.

⊙ : Experimental series a and b.

Fig. 3. Graphic expression of the results of χ^2 analysis for different age groups of irradiated larvae in the B1 experiment. Lines of arbitrary equal lengths are placed so that nonoverlapping lines indicate that there is a significant difference between the two age groups, at least at the 5% level, in the distribution of somatic crossovers to the left and right of B1.

A: Groups exposed to 1000 r.

B: Groups exposed to 1500 r.

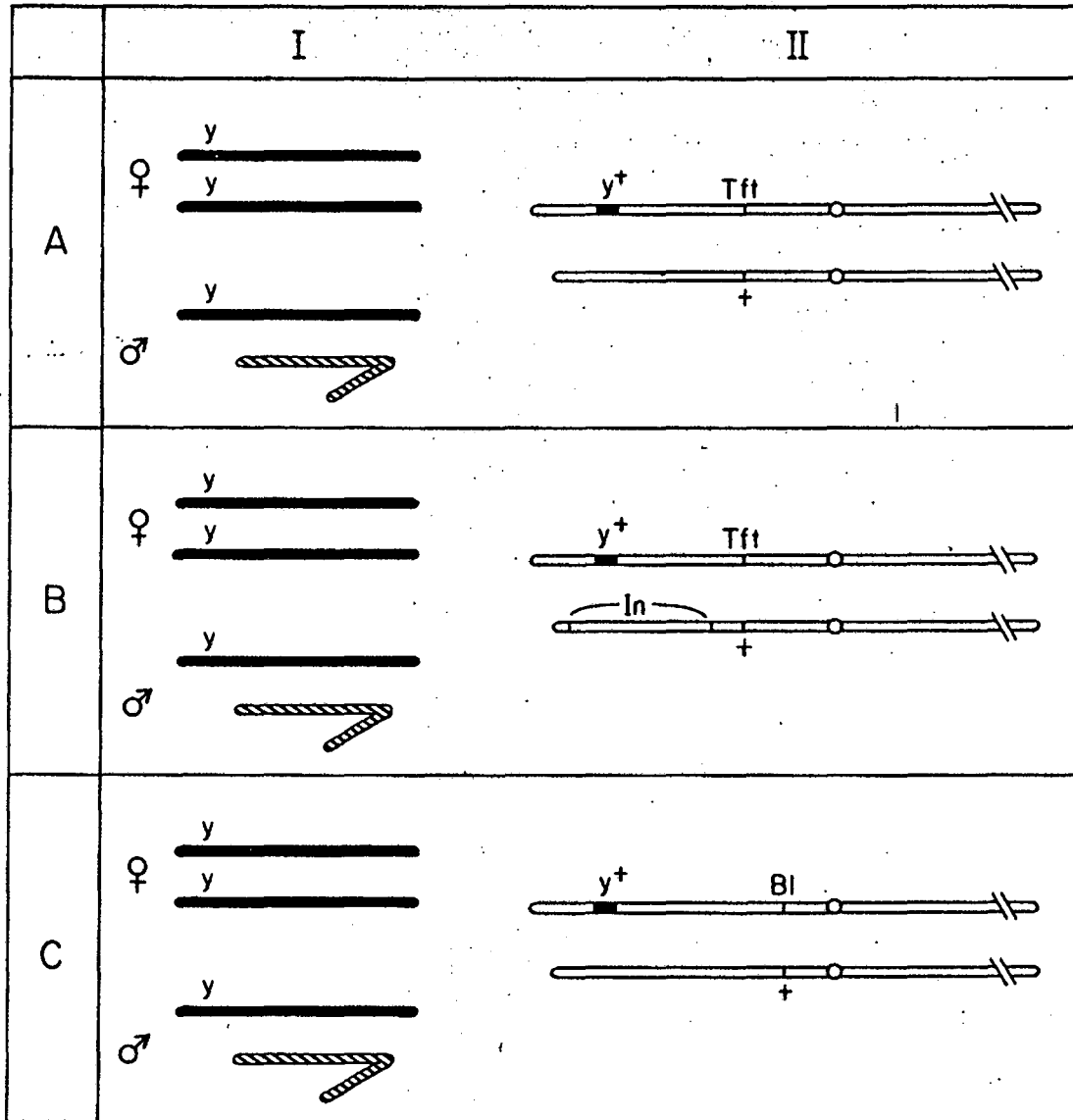


Fig. 1

MUB-9396

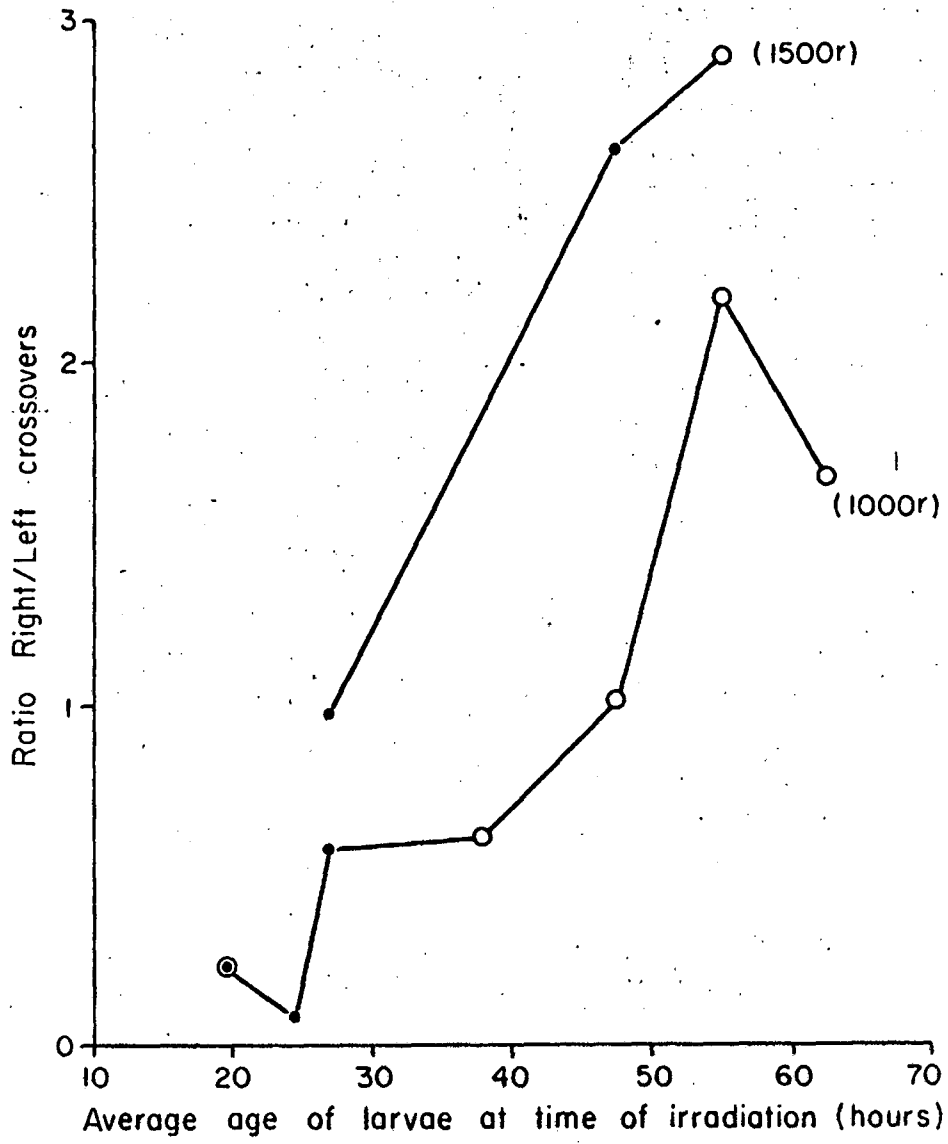


Fig. 2

MUB-9391

Figure 3A

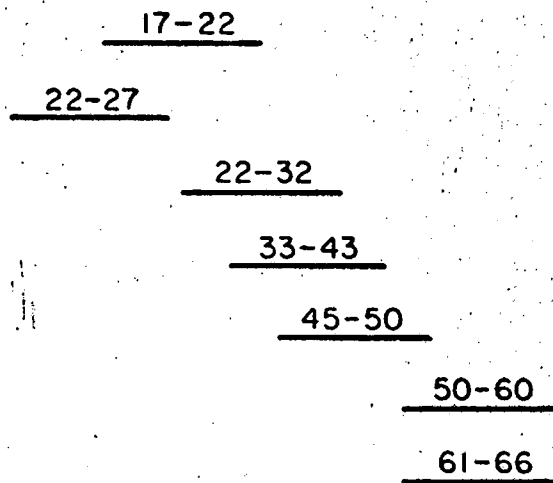


Figure 3B

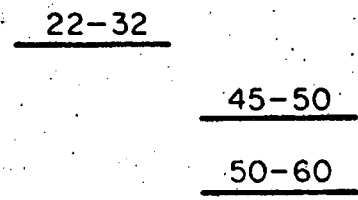


Fig. 3

This report was prepared as an account of Government sponsored work. Neither the United States, nor the Commission, nor any person acting on behalf of the Commission:

- A. Makes any warranty or representation, expressed or implied, with respect to the accuracy, completeness, or usefulness of the information contained in this report, or that the use of any information, apparatus, method, or process disclosed in this report may not infringe privately owned rights; or
- B. Assumes any liabilities with respect to the use of, or for damages resulting from the use of any information, apparatus, method, or process disclosed in this report.

As used in the above, "person acting on behalf of the Commission" includes any employee or contractor of the Commission, or employee of such contractor, to the extent that such employee or contractor of the Commission, or employee of such contractor prepares, disseminates, or provides access to, any information pursuant to his employment or contract with the Commission, or his employment with such contractor.