VIABILITY OF HETEROZYGOTES FOR INDUCED MUTATIONS IN *DROSOPHILA MELANOGASTER*.

II. MEAN EFFECTS IN IRRADIATED AUTOSOMES

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THE purpose of these studies was to obtain an estimate of the effect of an unselected sample of irradiated chromosomes on viability. The viability of the heterozygotes for irradiated chromosomes was examined in relation to the viability of the homozygotes and the effects on the population were estimated.

In the first paper of this series (FALK, RAHAT and BEN-ZEEV 1965), we studied the effects of irradiation on the X chromosome. It was concluded that a dose of about 3000r induced, besides lethal mutations, many semilethals and subvitals. These effects had a dominance of 5 to 15%. In addition to mutations that could be detected directly, irradiation induced less severe mutations which reduced the mean viability in the normal range by about 2%, both in hemizygotes and in heterozygotes for irradiated chromosomes. Although this effect was not statistically significant, it indicated that the majority of the induced mutations (even those with slight detrimental effects) were deleterious to the heterozygotes. There were also indications that the less deleterious mutations penetrate in heterozygotes to a greater extent than the more deleterious ones. If there were "heterotic" mutations, or even "heterotic" combinations, that might have been deleterious in other combinations, they were in the minority in the sample of unselected new mutations.

The X-ray dose of 3000r used by us induced many aberrations. Experiments with the X chromosome may not be representative, owing to the possible specific reactions of this chromosome. There were also some technical difficulties in those experiments, which might have biased the results. It was decided to extend these studies to the second chromosome of *Drosophila* and to study the effects of irradiated chromosomes on viability under different environmental conditions. The present paper presents the first results of these experiments and gives the effects on the mean viability of a random sample of irradiated autosomes in a variety of environments.

MATERIALS AND METHODS

We studied the genetic changes affecting viability that were induced by irradiation in the second chromosome of *D. melanogaster*. For this purpose a stock was constructed which had three differently marked second chromosomes ("mixed stock"): (1) *In Cy.05 pr cn*²—referred to as

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All cultures were scored three times: on the 9th or 10th day after mating, on the 14th day after mating, and on the 17th day after mating.

From some chromosomes, F_4 flies were used to start population cages. This part of the experiments will be described in a separate paper.

The details for the four experiments described here are:

Experiment 1. Half the F_2 matings were made in bottles, and after three days the flies were transferred to vials for another three days. In the other half, the order was reversed. The F_3 analysis was carried on, in vials, for only a part of the chromosomes.

Experiment 2. The F_2 matings were made only in bottles. Analysis of F_3 in vials, was carried on with part of the chromosomes.

Experiments 3 and 4. In the F_2 , five repetitions in vials were made for each chromosome in the following manner: The individual F_1 males were mated for 3 days to ten females each. The inseminated females were distributed, three to a vial, and the males were mated for another 3 days to another group of ten females, after which the females were again distributed three to a vial. The first five F_2 vials that gave any progeny were scored. All chromosomes were also analysed in F_3 . Five matings were made for obtaining each of the irradiated and each of the unirradiated homozygotes, and two more were similar to those of the F_1 .

RESULTS

If we assign to the viability of unirradiated flies a value of unity, we may calculate a coefficient which would estimate the magnitude of the deviation in viability of heterozygotes for irradiated chromosomes.

Suppose that from a mating of unirradiated flies one gets A progeny of the genotype $Cy\ pr/pr$ and B progeny $Cy\ pr/b$. If, however, the b chromosome was irradiated and a mutation effecting viability was induced, we would get Bh flies of the $Cy\ pr/b$ genotype. If the pr chromosome was irradiated we would get Ah of the $Cy\ pr/pr$ genotype, thus:

	$Cy\ pr/pr$	$Cy\ pr/b$
Unirradiated	A	B
b irradiated	A	Bh
pr irradiated	Ah	B

The mutations induced in the pr chromosome would not be identical to those induced in the b chromosome, neither must their effect be identical. We are interested in the coefficient $\bar{h}$ for the *mean* effect of the irradiation on the viability of heterozygotes in a sample of chromosomes:

$$\bar{h} = \sqrt{\frac{\Sigma Ah \times \Sigma Bh}{\Sigma B \times \Sigma A}}$$

Here one half of the experiment serves as a control for the second half and *vice versa*, so the need for separate large scale unirradiated control experiments is obviated (CROW, as cited by FRIEDMAN 1964). Since each experiment was carried out in a number of samples, it is possible to test the significance of the calculated values of $\bar{h}$ and their confidence limits by the "jack-knife" transformation method (LEVENE *et al.* 1965).

Experiments 1 and 2: In the three repeated tests for estimating the viability of the heterozygotes (Table 1) there was a reduction of 0.4% in the bottles in F_2 (0.9958 ± 0.0062), a reduction of 1.2% in the vials in F_2 (0.9878 ± 0.0104) and

an increase of 0.5% in the vials in F_3 (1.0049 ± 0.0106). These deviations from unity are not statistically significant. In the various samples there was an increase in viability of up to 6.3% (sample d in Table 1-C) and a reduction of up to 8.6% (sample k in Table 1-A). In this narrow range around unity viability, environmental fluctuations had much more pronounced effects on the variability of individual results than the slight genotypic determinants, and there was only a low correlation between the results of the samples in the different tests (e.g., correlation coefficient 0.12 for h from Table 1-A and 1-B). The viability estimates of all samples can therefore be looked at as independent viability determinations of a random sample of heterozygotes for chromosomes irradiated with 2000r in a sample of environments. Twenty-seven samples had $\bar{h}$ values below unity and 17 had $\bar{h}$ values above unity. The weighted mean for all samples was $\bar{h} = 0.9946$, i.e. a viability reduction of 0.54%, or 2.663×10^{-6} lethal equivalents per roentgen (see FRIEDMAN 1964). Considering the fluctuations between samples and runs no effect of induced mutations in heterozygous condition could be proved.

The viability of homozygotes for 560 of the irradiated chromosomes and 571 of the unirradiated chromosomes was studied (Table 2). The frequency of irradiated chromosomes with lethal mutations was 12%. Only one or two semi-lethals were induced, and the distribution of viabilities below the mean control viability among the irradiated chromosomes appears to be rather similar to that among the nonirradiated chromosomes. When lethals were excluded from the distribution of viabilities of homozygotes, some increase in the frequency of minus-deviation groups, and a decrease in all but the most extreme plus-deviation groups, amounting to 6.8%, was observed. (The group limit 0.297 was taken as mean control, although the mean for the controls was actually 0.3001). Evidently, in addition to lethals that were induced in a random manner among all chromosomes, also slight detrimental mutations were induced, adding to the frequency of subnormals and minus-deviations that proportion by which they were depleted by removing chromosomes to the lethal group.

The effect of radiation induced mutations on the viability of homozygotes is obtained either from the ratio of the weighted proportion of non-Cy flies in the irradiation and control experiments, or from the ratio of the unweighted proportions (Table 3). Both estimates may be biased when the induced mutations are not completely recessive (GOLDSCHMIDT and FALK 1959). The weighted mean viability of the homozygotes increased by only 10% when the lethals—amounting to 12% of all chromosomes—were excluded. This could be due to the incomplete recessivity of the lethals; which is probably also the reason for the weighted mean to be higher than the unweighted mean. From the unweighted mean the total load in homozygotes was estimated as 0.142 lethal equivalents, of which 0.027 lethal equivalents were due to nonlethal detrimental mutations (D in the terminology of GREENBERG and CROW 1960) and 0.115 to lethals, giving a $D:L$ ratio of 0.237.

In Table 4 the mean viability of heterozygotes is given in relation to the via-

TABLE 2
Frequency distribution of viabilities of homozygotes for unirradiated and irradiated chromosomes

	Proportion of non-Cy flies																Total	
	0	3.3	6.6	9.9	13.2	16.5	19.8	23.1	26.4	29.7	33.0	36.3	39.6	42.9	46.2	49.5		52.8
<i>Unirradiated</i>																		
<i>chromosome purple</i>																		
Exp. 1	.	.	.	.	2	1	5	19	17	37	39	30	21	14	6	3	.	195*
Exp. 2	.	.	.	.	2	1	2	2	11	16	19	20	10	4	2	.	.	89
<i>chromosome black</i>																		
Exp. 1	1	.	.	1	3	9	10	25	36	26	33	28	11	7	4	2	1	197
Exp. 2	.	.	.	.	.	4	2	8	14	12	23	13	9	3	1	.	1	90
Total	1	.	.	1	7	15	19	54	78	91	114	91	51	28	13	5	2	571*
Percent	0.18	.	.	0.18	1.23	2.62	3.33	9.46	13.66	15.94	19.96	15.94	8.99	4.90	2.28	0.88	0.35	
<i>Irradiated</i>																		
<i>chromosome purple</i>																		
Exp. 1	20	.	.	.	2	4	1	19	19	37	38	17	17	6	4	4	.	189†
Exp. 2	8	1	.	.	.	1	4	2	10	15	25	11	4	3	1	1	.	87‡
<i>chromosome black</i>																		
Exp. 1	27	.	.	1	2	8	12	19	29	38	24	14	11	4	2	2	1	194
Exp. 2	12	.	.	.	2	1	3	9	8	16	14	14	7	3	.	.	1	90
Total	67	1	1	1	6	14	20	49	66	106	101	56	39	16	7	7	2	560†‡
Percent	11.96	0.18	0.18	0.18	1.07	2.50	3.57	8.75	11.79	18.93	18.04	10.00	6.96	2.86	1.25	1.25	0.36	
Percent— lethals excluded	.	0.20	0.20	0.20	1.22	2.84	4.07	9.94	13.39	21.50	20.49	11.36	7.91	3.26	1.42	1.42	0.41	

* One chromosome with viability 62.7 to 66.0 not marked.

† One chromosome with viability 66.0 to 69.3 not marked.

‡ One chromosome with viability 59.4 to 62.7 not marked.

TABLE 3

Viability of homozygotes for irradiated and unirradiated chromosomes

	Total number of flies		Weighted mean effect on viability	Unweighted mean effect on viability
	Irradiation	Controls		
Experiments 1 and 2				
<i>purple</i>				
Exp. 1	12560	13483	0.8891	0.8529
Exp. 2	6748	7542	0.8894	0.8935
<i>black</i>				
Exp. 1	10235	12815	0.8724	0.8501
Exp. 2	6844	6677	0.8803	0.8497
Totals	36387	40517	0.8858	0.8577
Totals—lethals excluded	33609	40484	0.9877	0.9727
Experiments 3 and 4				
<i>purple</i>				
Exp. 3	54065	54570	0.9121	0.8991
Exp. 4	58188	69314	0.7888	0.7864
<i>brown</i>				
Exp. 3	52676	51088	0.8296	0.8255
Exp. 4	59496	58932	0.7677	0.7777
Totals	224425	233904	0.8241	0.8196
Totals—lethals excluded	198059	233904	0.9632	0.9585

bility of homozygotes for irradiated chromosomes in the different experimental runs, as well as in the pooled experiments. Not all chromosomes tested in heterozygotes were also tested in homozygotes; the mean viability in those tested was somewhat over unity. The heterozygotes for lethals had a mean deleterious effect of only 1%. Compared with the results in the literature, this is low. In the remaining viability groups the fluctuations were considerable and inconsistent. In the lower part of Table 4, all minus-deviations from the mean control value—taken here as 0.297—both including lethals and excluding lethals, were pooled, as were the plus-deviations. There is a tendency for a correlation between the viability of homozygotes and heterozygotes, as the heterozygotes of the minus-deviations are less viable than those of the plus-deviations; this is so even when lethals were excluded.

Experiments 3 and 4: The results of Experiments 3 and 4 are now given in a similar manner to those of Experiments 1 and 2, so that they can serve as further tests of the consistency of the findings from the early experiments. For each chromosome, the calculations are from the sum of the replicates.

The effect of the radiation on the viability of heterozygotes for irradiated chromosomes (Table 5) was too small to be significantly different from unity (1.0072 ± 0.0070 in F_2 vials and 0.9882 ± 0.0108 in F_3 vials). When we consider all chromosomes and all environments there was no reduction in viability ($\bar{h} = 0.9997 \pm 0.0040$).

Classifying the chromosomes according to the viability of the homozygotes (Table 6) reveals that lethal mutations were induced in 14.7% of the chromo-

TABLE 4
*The viability of heterozygotes for irradiated chromosomes, according to the
 viability of their homozygotes*

Viability of homozygotes	F ₂ in bottles			F ₂ in vials			F ₃ in vials			Pooled		
	No. chrom. <i>pr</i>	<i>b</i>	Viability $\bar{h}$	No. chrom. <i>pr</i>	<i>b</i>	Viability $\bar{h}$	No. chrom. <i>pr</i>	<i>b</i>	Viability $\bar{h}$	No. chrom. <i>pr</i>	<i>b</i>	Viability $\bar{h}$
0-3.3	27	39	1.0122	20	27	0.9713	24	36	0.9475	71	102	0.9894
3.3-13.2	3	5	1.0144	2	3	1.0496	3	4	0.9495	8	12	0.9923
13.2-19.8	10	24	0.9995	4	20	1.1519	10	21	0.9800	24	65	1.0189
19.8-23.1	20	27	1.0245	18	18	0.9723	16	26	1.0338	54	72	1.0082
23.1-26.4	29	37	1.0036	19	28	0.9136	28	31	0.9760	76	96	0.9712
26.4-29.7	52	54	1.0052	37	38	0.9867	49	52	1.0458	138	144	1.0065
29.7-33.0	64	38	0.9819	38	23	0.9900	60	34	1.0080	162	95	0.9898
33.0-36.3	25	28	1.0033	15	14	1.0762	25	24	1.0080	65	66	1.0198
36.3-39.6	20	18	1.0135	17	11	1.0571	20	16	1.0162	57	45	1.0265
39.6 >	21	13	0.9849	15	9	1.0461	18	10	1.0685	54	32	1.0123
Total	271	283	1.0033	185	191	0.9955	253	255	1.0044	709	729	1.0017
minus-deviations	141	186	1.0117	100	134	0.9752	130	171	0.9983	371	491	0.9993
minus-deviations, lethals excluded	114	147	1.0107	80	107	0.9760	106	135	1.0103	300	389	1.0030
plus-deviations	130	97	0.9898	85	57	1.0302	123	84	1.0146	338	238	1.0098

TABLE 5

Viability of heterozygotes for irradiated chromosomes—according to samples and experimental runs

Sample	A. F ₂ in vials				Viability <i>h</i>	B. F ₃ in vials				Viability <i>h</i>
	No. <i>brown</i> chrom.	No. flies	No. <i>purple</i> chrom.	No. flies		No. <i>brown</i> chrom.	No. flies	No. <i>purple</i> chrom.	No. flies	
Experiment 3										
a	20	16705	20	18884	1.0055	20	7116	20	7632	0.9875
b	20	14980	20	15261	1.0290	20	6268	20	6124	0.9906
c	20	15028	20	12546	0.9809	20	7724	20	8305	1.0162
Experiment 4										
d	20	15829	18	13655	1.0197	20	8937	18	7346	0.9834
e	25	14345	22	13378	0.9893	23	7862	22	7881	1.0094
f	25	14122	24	13554	0.9967	25	10226	24	10130	0.9550
Total	130	91009	124	87278	1.0072	128	48133	124	47418	0.9882

TABLE 6

Frequency distribution of viabilities of homozygotes for unirradiated and irradiated chromosomes in Experiments 3 and 4

	Proportion of non-Cy flies											Total
	0	3.3	6.6	9.9	13.2	16.5	19.8	23.1	26.4	29.7	33.0	
Unirradiated												
<i>chromosome purple</i>												
Exp. 3	..	..	..	..	..	..	11	28	13	1	..	59
Exp. 4	..	..	..	..	..	2	26	29	11	1	..	69
<i>chromosome brown</i>												
Exp. 3	..	..	..	..	..	1	11	32	14	1	..	59
Exp. 4	..	..	..	..	4	16	23	19	1	..	..	63
Total	..	..	..	..	4	19	71	108	45	3	..	250
Percent	..	..	..	..	1.60	7.60	28.40	43.20	18.00	1.20	..	..
Irradiated												
<i>chromosome purple</i>												
Exp. 3	7	..	..	..	..	..	5	28	16	3	..	59
Exp. 4	10	1	..	2	2	5	19	20	4	1	..	64
<i>chromosome brown</i>												
Exp. 3	6	2	..	3	..	2	14	21	10	1	..	59
Exp. 4	14	..	..	3	5	9	22	14	2	..	..	69
Total	37	3	..	8	7	16	60	83	32	5	..	251
Percent	14.74	1.20	..	3.19	2.79	6.37	23.90	33.07	12.75	1.99	..	..
Percent, lethals excluded	..	..	..	3.79	3.32	7.58	28.44	39.34	15.17	2.37	..	..

somes. There were few induced semilethals and there was some increase in the frequency of subvitals and minus-deviations.

The mean effect of the induced mutations on the viability of homozygotes for irradiated chromosomes are given in the lower part of Table 3. In spite of the general shift in the viability of the unirradiated homozygotes as compared with

the first two experiments, the mean number of lethal equivalents did not change much: a detrimental load of 0.042 lethal equivalents, a lethal load of 0.139 lethal equivalents and $D:L$ ratio of 0.299.

In Table 7 the viability coefficients of heterozygotes for irradiated chromosomes that were tested also as homozygotes, were classified according to the viability of homozygotes. The heterozygotes for lethals were deleterious, though again the observed effect is low.

The frequency of chromosomes with the highest viability in homozygotes was increased in all irradiation experiments (Tables 2, 6) and the viability of the heterozygotes for these chromosomes was lower than that of less extreme plus-deviation chromosomes (Table 7; also Table 4). These must be chromosomes with completely dominant deleterious mutations.

In the tests of heterozygotes of four chromosomes in the "purple" set (two in Experiment 1, one each in Experiments 2 and 3) there were only *Cy pr/b* (or *Cy pr/bw*) females, and *Cy pr/pr* and *pr/b* (or *pr/bw*) males. These must have been cases of Y-2 translocations. If we estimate that there were about five times as many undetected major aberrations involving chromosome 2, and even if we add deletions and other detectable aberrations, there were not more than 50 aberrations among the 1350 tested chromosomes. These 3 to 4% chromosomes with aberrations could be responsible for only a small part of the effect observed in homozygotes for irradiated chromosomes.

We may now compare the effects of the radiation, found in this study, with those found by FRIEDMAN (1964) and in our previous study (FALK, RAHAT and BEN-ZEEV 1965)—see Table 8. The frequency of lethal equivalents per roentgen

TABLE 7

The viability of heterozygotes for irradiated chromosomes in Experiments 3 and 4 classified according to their viability in homozygotes

Viability of homozygotes	F_2 in vials			F_3 in vials			Pooled		
	no. chrom. <i>pr</i>	<i>bw</i>	viability $\bar{h}$	no. chrom. <i>pr</i>	<i>bw</i>	viability $\bar{h}$	no. chrom. <i>pr</i>	<i>bw</i>	viability $\bar{h}$
0-3.3	17	20	1.0118	17	19	0.9648	34	39	0.9955
3.3-13.2	3	8	1.0001	3	8	0.9346	6	16	0.9736
13.2-16.5	2	5	1.0643	2	5	0.9900	4	10	1.0408
16.5-19.8	5	11	1.0216	5	11	0.9731	10	22	1.0026
19.8-23.1	24	36	1.0157	24	36	0.9887	48	72	1.0053
23.1-26.4	39	36	1.0040	49	36	1.0017	88	72	1.0033
26.4-29.7	19	11	0.9975	19	11	1.0574	38	22	1.0125
29.7-33.0	4	1	0.9739	4	1	0.9016	8	2	0.9520
Total	113	128	1.0065	123	127	0.9941	236	255	1.0005
minus-devn.	51	80	1.0173	51	79	0.9739	102	159	1.0012
minus-devn., lethals excluded	34	60	1.0180	34	60	0.9778	68	120	1.0026
plus-devn.	62	48	1.0014	72	48	1.0076	134	96	1.0033

TABLE 8

Mean lethal equivalents per roentgen due to lethals (L), nonlethal detrimental (D), and total effect (T)

Homozygotes	Present study		FALK, RAHAT AND BEN-ZEEV (1965)		Friedman (1964)
	Experiments 1 and 2	Experiments 3 and 4	Series 1	Series 2	
<i>D</i>	1.365×10^{-5}	2.025×10^{-5}	-0.188×10^{-5}	0.550×10^{-5}	0.35×10^{-5}
<i>L</i>	5.750×10^{-5}	6.995×10^{-5}	3.964×10^{-5}	3.489×10^{-5}	2.76×10^{-5}
<i>T</i>	7.115×10^{-5}	9.020×10^{-5}	3.777×10^{-5}	3.239×10^{-5}	3.12×10^{-5}
<i>D:L</i>	.237	.290	—0.047	.158	.125

induced in the second chromosome, in the present study, was roughly twice that induced in the X chromosome in the other two studies; this is the ratio expected from the relative length of the second and X chromosomes. The load due to non-lethal detrimental in the present study is, however, more than twice that in the other studies, and accordingly the *D:L* ratio is higher. As noted before, if detrimental were dominant their frequency was underestimated. We suspect, therefore, that more undetected dominant deleterious mutations were induced in the previous investigations than in the present one. Since the X-ray dose applied in those studies was higher than in the present one, we suggest that these were mainly small aberrations that had a dominant detrimental effect on viability.

DISCUSSION AND CONCLUSIONS

Many of the difficulties of the previous series of experiments (FALK, RAHAT and BEN-ZEEV 1965) have been overcome in the present experiments. If there was a specific reaction of the X chromosome to induced viability mutations, it was eliminated in the present experiment. We believe that factors which could bias the results were balanced out by the complementary design of the experiments. The pairs of irradiated chromosomes *pr* and *b* (and later *bw*) no doubt had different viabilities to start with, yet they were not as different as the *Q.A.* and *Binscty* chromosomes in the previous study. Since we were interested in the mean effect of irradiation on the viability we had here a much wider range of conditions: two chromosomes were tested in different genotypic combinations and each combination was tested repeatedly in different environments. As the fluctuations from one set of test conditions to the other were considerable, the pooled data for all chromosomes and tests should represent a random sample of irradiated chromosomes under a variety of environmental conditions.

It can be concluded that the dose of 2000r to the spermatozoa of *Drosophila* caused a reduction in the viability of homozygotes, 10 to 20% of which was due to nonlethal detrimental, and the rest was due to lethals. Detrimental mutations may have been produced throughout the whole normal range of viabilities, but apart from lethals there were few, if any, mutations more extreme than those in the range of unirradiated chromosomes. The proportion of severe detrimental to lethals was less than one to two. This is in contrast to our finding in the previous.

studies with the X chromosome (FALK, RAHAT and BEN-ZEEV 1965), but is in accord with that of other recent studies (KÄFER 1953; BONNIER and JONSSON 1957; GREENBERG and CROW 1960; FRIEDMAN 1964).

In spite of the extensive deleterious effects induced in the irradiated chromosomes, the viability of heterozygotes for these chromosomes was not significantly effected. In our previous studies (FALK 1961; FALK, RAHAT and BEN-ZEEV 1965) there were indications for a deleterious effect on viability of heterozygotes for irradiated chromosomes. The present experiments were designed so as to improve on the earlier ones. Whatever reduction in viability that was detected could, however, be due to the induced lethals. The viability of flies heterozygous for lethals was reduced by approximately 1%. This is somewhat less than was found in other studies (see PROUT 1952; STERN, CARSON, KINST, NOVITSKI and UPHOFF 1952; HIRAIZUMI and CROW 1960; CROW and TEMIN 1964) but if we accept a dominance of 2 to 4% for lethals, as given in the literature, one would expect a reduction of 0.2 to 0.4% in the viability of heterozygotes for irradiated chromosomes. Induced mutations that were nonlethal had such a slight effect on the viability of homozygotes for irradiated chromosomes, that even if they were all completely dominant—or alternatively, exerted always a heterotic effect on viability—it would be hardly possible to detect their effect on the viability of heterozygotes for irradiated chromosomes. Actually, when lethals were excluded, the viability of heterozygotes for irradiated chromosomes may have been somewhat increased (Tables 5, 8). This is more in line with the results of WALLACE (1958, 1959) who observed an increase in the viability of flies heterozygous for irradiated chromosomes over that of flies homozygous for the unirradiated chromosomes, and to some extent also of flies heterozygous for unirradiated chromosomes. WALLACE irradiated the flies with only 500r, and accordingly induced fewer lethals and chromosomal aberrations than were induced in the present study.

The role of chromosomal aberrations in the induction of dominant mutations affecting viability was studied by repeating the procedure of these experiments with chromosomes irradiated in spermatogonia. The results will be reported in a later paper of this series.

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SUMMARY

The viability of flies heterozygous for unselected samples of irradiated second chromosomes was studied in repeated tests in different genotypic combinations. A dose of 2000r caused no significantly detectable reduction in the viability of heterozygotes for irradiated chromosomes. The slight effect suggested by the results could be due to induced lethals. Severe detrimental mutations were rare, and only 10 to 20% of the deleterious effect in homozygotes was due to nonlethals. It could not be decided whether their effect in heterozygous condition was too small or whether they had no effect at all.

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