

A Genetic Analysis of Phototactic Behavior in *Drosophila melanogaster*. II. Hybridization of Divergent Populations¹

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*Artificial selection has produced populations of *Drosophila melanogaster* which show either positive or negative phototactic behavior. Selection was carried out in the presence of various marked multiple inversions used to suppress genetic recombination. Reciprocal hybridizations between photopositive and photonegative populations of flies have revealed the X chromosome of *D. melanogaster* to be important in phototactic behavior regardless of conditions which restricted genetic recombination during selection.*

KEY WORDS: phototaxis maze; selection; recombination; sex linkage.

INTRODUCTION

Phototactic behavior in *Drosophila* may be measured using a multiple unit classification maze (Hadler, 1964a). The genetic basis for the phototactic behavior of *Drosophila* in the maze appears to be polygenic, and populations of flies respond rapidly to selection for positive and negative phototactic behavior (Hadler, 1964a,b; Dobzhansky and Spassky, 1967, 1969).

In *Drosophila melanogaster*, the effectiveness of selection for negative and positive phototaxis has been examined in the presence of marked multiple inversions which restricted genetic recombination in each of the

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three major chromosomes and in their various combinations (Markow, 1974). At least some degree of response to selection was observed under all conditions of recombination, but certain combinations of inversions rather drastically reduced the effectiveness of selection for either positive or negative phototactic behavior. In populations of flies in which recombination was restricted in chromosome 1, 2, or 3 alone, selection was nearly as effective as in populations in which recombination was not restricted. However, simultaneously restricting crossing over in chromosomes 1 and 3 interfered with selection for positive phototaxis but had no effect on selection for negative phototactic behavior. On the other hand, restriction of recombination in chromosomes 1 and 2 or in chromosomes 2 and 3 reduced the effectiveness of selection for negative phototaxis but not for positive phototaxis. The reduced effectiveness of selection under conditions restricting genetic recombination is felt to be a property of the organization of the genes influencing the photomaze behavior of this species. It was suggested that reducing new genetic variation by restricting genetic recombination would interfere with the effectiveness of selection if the particular chromosomes contained genes influencing phototaxis.

Hybridization of selected populations provides a further means of analyzing the genetic systems which control divergent phenotypes. Previous studies of reciprocal hybridizations of selected, wild-type phototactic strains of *D. melanogaster* are inconclusive about the relative contributions of the X chromosome and autosomes to phototactic behavior (Hadler, 1964*b*). The present paper reports the results of extensive reciprocal hybridizations between photopositive and photonegative populations of flies created by selection in the presence of various multiple inversions. The data are discussed in relation to the effectiveness of selection in the populations hybridized.

MATERIALS AND METHODS

Flies were raised in half-pint culture bottles containing standard cornmeal-molasses-agar medium. Hybridizations were carried out by placing 15 pairs of flies in each of five culture bottles. After 3 days, the flies were transferred to five new bottles containing fresh medium. Two or three replications were made of each hybridization and backcross.

Reciprocal hybridizations were carried out between the photopositive and photonegative populations of five different strains of flies. The strains were designated by the members of their chromosome sets heterozygous for genetically marked multiple inversions. The inversions used were FM6, Sm1, and TM3 (see Lindsley and Grell, 1968). The synthesis of these strains is described in an earlier paper. Strain 0 carried no inversions, and

genetic recombination occurred freely between homologous chromosomes in the females of this strain. The females of strains 1, 2, 3, and 23 were heterozygous for multiple inversions in the first, second, third, and second and third chromosomes, respectively. The males of each strain carried no inversions and were phenotypically wild type. Since crossing over does not occur in *Drosophila* males, recombination could be selectively reduced by the inversions in females. All strains had average photoscores ranging from 6.5 to 7.5 prior to selection. After 20 generations of selection, each strain had diverged to a different degree. Photoscores of males and females of each strain at generation 20 will be shown in the tables presenting the results of the hybridizations.

The phototaxis mazes (Hadler, 1964a) used in this investigation consist of a series of 15 consecutive Y-units. Each Y has a light and a dark arm. An individual fly passing through the maze makes 15 light/dark choices before emerging in one of 16 collecting tubes at the end of the maze. Flies making 15 light choices will appear in tube No. 16. Tube No. 1 will contain flies making 15 dark choices. Photoscores are based on the tube number in which flies emerge. A photoneutral population of flies will have a mean photoscore of 8.5.

RESULTS

Reciprocal hybridizations were made between the positive and negative lines of strains 0, 1, 2, 3, and 23 at generation 20 of selection.

Results of the reciprocal hybridizations between the positive and negative lines of strain 0 are shown in Table I. The F_1 progeny of photopositive females and photonegative males are intermediate between the two parental photoscores. While the F_1 females from the reciprocal cross are also intermediate between the parental populations, the F_1 sons are photonegative like their mothers. The results indicate a major role for the X chromosome in the negative phototactic behavior of Strain 0. Males from the F_2 and F_3 are consistently more negative than their sisters. The increased variance of the F_2 over the F_1 supports a polygenic mode of inheritance for phototactic behavior. Backcross data are given in Table II. As expected, whenever flies are homozygous or hemizygous for factors on the X chromosome selected for photonegative behavior, photonegative behavior is observed. Males nearly always appear to be significantly more photonegative than their sisters (Table III).

A similar series of hybridizations with strains 1, 2, 3, and 23 was carried out to determine the consistency of the sex linkage for photonegative behavior. These crosses were also aimed at uncovering any sex linkage for photopositive behavior in other strains. The results are shown in Table IV.

Table I. P₁, F₁, F₂, and F₃ Photoscores from the Reciprocal Hybridizations Between the Photopositive and Photonegative Populations of Strain 0 at Generation 20 of Selection

Generation	Females				Males				
	r	$\bar{X} \pm SE$	s ²	n	r	$\bar{X} \pm SE$	s ²	n	
		Strain 0(+) ♀ (11.01 ± 0.14) × strain 0(-) ♂ (3.51 ± 0.13)							
F ₁	1	6.24 ± 0.18	9.04	295	1	6.06 ± 0.18	9.88	293	
	2	7.28 ± 0.19	11.36	317	2	6.62 ± 0.23	14.19	259	
	3	6.58 ± 0.18	8.68	259	3	6.42 ± 0.18	9.05	271	
	Pooled	6.71 ± 0.11	9.33	871	Pooled	6.32 ± 0.12	10.79	823	
F ₂	1	8.23 ± 0.18	12.38	399	1	7.11 ± 0.24	15.44	261	
	2	8.46 ± 0.19	10.71	285	2	7.15 ± 0.20	11.80	286	
	Pooled	8.32 ± 0.13	11.68	684	Pooled	7.13 ± 0.16	13.49	547	
F ₃	1	8.49 ± 0.21	9.03	279	1	7.05 ± 0.19	9.88	279	
	2	8.48 ± 0.21	10.53	244	2	6.96 ± 0.23	10.68	203	
	Pooled	8.48 ± 0.21	9.94	453	Pooled	7.01 ± 0.15	10.06	482	
		Strain 0(-) ♀ (4.35 ± 0.19) × strain 0(+) ♂ (10.78 ± 0.14)							
F ₁	1	6.26 ± 0.15	9.29	438	1	4.04 ± 0.13	5.76	352	
	2	6.37 ± 0.14	7.81	429	2	4.32 ± 0.16	7.70	291	
	3	7.01 ± 0.26	15.71	241	3	4.32 ± 0.22	13.10	271	
	Pooled	6.46 ± 0.10	10.15	1108	Pooled	4.21 ± 0.10	8.56	914	
F ₂	1	7.24 ± 0.19	14.48	381	1	6.79 ± 0.22	15.39	307	
	2	7.46 ± 0.18	10.57	331	2	7.30 ± 0.21	15.21	372	
	Pooled	7.35 ± 0.13	12.66	712	Pooled	7.03 ± 0.16	15.34	579	
F ₃	1	6.70 ± 0.23	10.90	213	1	4.94 ± 0.23	8.64	169	
	2	8.04 ± 0.16	9.54	363	2	6.76 ± 0.19	12.44	335	
	Pooled	7.54 ± 0.14	10.48	576	Pooled	6.05 ± 0.15	11.47	504	

Table II. Photoscores of Strain 0 Backcross Progeny

Generation	Females				Males				
	<i>r</i>	$\bar{X} \pm SE$	<i>s</i> ²	<i>n</i>	<i>r</i>	$\bar{X} \pm SE$	<i>s</i> ²	<i>n</i>	
BS(1)		F ₁ 0(+) ₀ (-) ♀ ♀ (6.71 ± 0.11) × P ₁ 0(-) ♂ ♂ (3.51 ± 0.13)							
	1	4.96 ± 0.17	8.29	287	1	5.05 ± 0.16	8.24	298	
	2	5.54 ± 0.16	8.47	325	2	5.05 ± 0.16	7.65	304	
	3	5.96 ± 0.16	10.52	386	3	5.62 ± 0.22	12.78	263	
	Pooled	5.48 ± 0.10	9.50	998	Pooled	5.22 ± 0.10	9.46	865	
BC(2)		F ₁ 0(+) ₀ (-) ♀ ♀ (6.71 ± 0.11) × P ₁ 0(+) ₀ ♂ ♂ (10.78 ± 0.14)							
	1	9.95 ± 0.17	8.64	284	1	7.92 ± 0.19	11.33	312	
	2	10.28 ± 0.16	9.61	385	2	9.61 ± 0.21	15.07	352	
	3	9.90 ± 0.18	8.10	261	3	8.52 ± 0.22	11.56	249	
	Pooled	10.07 ± 0.10	8.90	930	Pooled	8.74 ± 0.12	13.34	913	
BC(3)		P ₁ 0(-) ♀ ♀ (4.35 ± 0.19) × F ₁ 0(+) ₀ (-) ♂ ♂ (6.32 ± 0.12)							
	1	5.91 ± 0.18	9.89	324	1	4.84 ± 0.16	9.36	359	
	2	7.10 ± 0.19	11.47	307	2	5.08 ± 0.19	10.22	274	
	3	7.98 ± 0.26	16.78	256	3	5.90 ± 0.24	15.34	261	
	Pooled	6.99 ± 0.12	13.10	887	Pooled	5.20 ± 0.11	11.48	894	
BC(4)		P ₁ 0(+) ₀ ♀ ♀ (11.01 ± 0.14) × F ₁ 0(+) ₀ (-) ♂ ♂ (6.32 ± 0.12)							
	1	9.86 ± 0.18	8.05	262	1	8.89 ± 0.18	10.07	309	
	2	10.71 ± 0.16	9.04	343	2	9.56 ± 0.21	12.58	296	
	3	10.52 ± 0.17	8.81	310	3	9.52 ± 0.18	10.89	318	
	Pooled	10.40 ± 0.10	8.78	925	Pooled	9.32 ± 0.11	11.21	923	

Table II. Continued

Generation	Females				Males				
	<i>r</i>	$\bar{X} \pm SE$	s^2	<i>n</i>	<i>r</i>	$\bar{X} \pm SE$	s^2	<i>n</i>	
BC(5)		$F_10(-)0(+)\varphi \varphi$ (6.46 ± 0.10) × $F_10(-)\sigma^2\sigma^2$ (3.51 ± 0.13)							
	1	4.97 ± 0.18	7.56	230	1	5.41 ± 0.16	8.22	338	
	2	5.95 ± 0.20	12.12	292	2	6.11 ± 0.20	14.01	365	
	3	5.24 ± 0.17	7.95	207	3	5.15 ± 0.18	9.87	299	
	Pooled	5.41 ± 0.11	9.45	789	Pooled	5.57 ± 0.10	10.92	1002	
BC(6)		$F_10(-)0(+)\varphi \varphi$ (6.46 ± 0.10) × $F_10(+)\sigma^2\sigma^2$ (10.78 ± 0.14)							
	1	9.60 ± 0.17	10.04	335	1	8.33 ± 0.17	9.94	349	
	2	9.98 ± 0.17	9.66	320	2	9.00 ± 0.18	10.54	328	
	3	10.60 ± 0.17	9.25	306	3	7.93 ± 0.22	12.42	260	
	Pooled	9.98 ± 0.10	9.53	961	Pooled	8.44 ± 0.11	11.00	937	
BC(7)		$F_10(-)\varphi \varphi$ (4.35 ± 0.19) × $F_10(-)0(+)\sigma^2\sigma^2$ (4.21 ± 0.10)							
	1	5.09 ± 0.17	9.23	313	1	3.85 ± 0.13	5.25	310	
	2	6.56 ± 0.18	10.73	338	2	6.02 ± 0.20	12.11	298	
	3	5.10 ± 0.20	9.07	221	3	4.69 ± 0.21	8.39	188	
	Pooled	5.66 ± 0.11	10.26	872	Pooled	4.84 ± 0.11	9.37	796	
BC(8)		$F_10(+)\varphi \varphi$ (11.01 ± 0.14) × $F_10(+)\sigma^2\sigma^2$ (6.32 ± 0.12)							
	1	9.03 ± 0.18	12.66	397	1	8.87 ± 0.19	11.87	338	
	2	10.23 ± 0.16	10.65	409	2	10.32 ± 0.17	12.43	406	
	3	9.12 ± 0.17	9.25	311	3	9.50 ± 0.21	13.80	305	
	Pooled	9.33 ± 0.10	11.18	1117	Pooled	9.61 ± 0.11	13.00	1049	

Table III. Comparison of Pooled Photoscores of Males and Females from F₁, F₂, F₃, and Backcross Generations of Strain 0^a

Generation	Females			Males			H ^b	P ^c	df
	$\bar{X} \pm SE$	s ²	n	$\bar{X} \pm SE$	s ²	n			
F ₁ 0(+)-0(-)	6.71 ± 0.12	9.93	865	6.32 ± 0.12	10.79	819	6.4179	0.05 >	P > 0.01
F ₁ 0(-)-0(+)	6.40 ± 0.16	10.15	1107	4.21 ± 0.10	8.56	913	271.9521		P < 0.01
F ₂ 0(+)-0(-)	8.32 ± 0.13	11.68	684	7.13 ± 0.16	13.49	547	34.3412		P < 0.01
F ₂ 0(-)-0(+)	7.35 ± 0.13	12.66	712	7.03 ± 0.16	15.34	579	3.4938	0.10 >	P > 0.05
F ₃ 0(+)-0(-)	8.48 ± 0.15	9.94	457	7.10 ± 0.15	10.06	472	38.4200		P < 0.01
F ₃ 0(-)-0(+)	7.54 ± 0.14	10.48	576	6.05 ± 0.15	11.47	502	51.6241		P < 0.01
BC (1)	5.48 ± 0.10	9.50	1011	5.22 ± 0.10	9.46	865	4.2149	0.05 >	P > 0.01
BC (2)	10.07 ± 0.10	8.90	930	8.74 ± 0.12	13.34	913	62.2556		P < 0.01
BC (3)	6.99 ± 0.12	13.10	887	5.20 ± 0.11	11.48	895	111.5357		P < 0.01
BC (4)	10.40 ± 0.10	8.78	925	9.32 ± 0.11	11.21	923	44.50		P < 0.01
BC (5)	5.41 ± 0.11	9.45	789	5.57 ± 0.10	10.92	1002	0.3255	0.70 >	P > 0.05
BC (6)	9.98 ± 0.10	9.53	961	8.44 ± 0.11	11.00	937	99.2700		P < 0.01
BC (7)	5.66 ± 0.11	10.26	872	4.84 ± 0.11	9.37	796	30.9982		P < 0.01
BC (8)	9.33 ± 0.10	11.18	1117	9.61 ± 0.11	13.00	1049	4.6215	0.05 >	P > 0.02

^a Sign in first parentheses represents direction of phototaxis for maternal strain, that in second parentheses represents paternal direction.

^b The Kruskal-Wallis H is a nonparametric group comparison test which does not assume normal distributions or homogeneous variances.

^c A χ^2 table is used to determine probability values (Woolf, 1968).

Table IV. Reciprocal Hybridizations Between the Photopositive and Photonegative Populations of Strains 1, 2, 3, and 23 at Generation 20 of Selection

Generation	Females				Males			
	r	$\bar{X} \pm SE$	s^2	n	r	$\bar{X} \pm SE$	s^2	n
		Strain 1(+) ♀ (9.53 ± 0.14) × strain 1(-) ♂ (4.31 ± 0.25)						
F ₁	1	6.98 ± 0.20	10.50	252	1	7.25 ± 0.23	12.42	232
	2	7.73 ± 0.20	7.04	170	2	7.85 ± 0.22	14.66	289
	Pooled	7.28 ± 0.15	9.22	422	Pooled	7.58 ± 0.16	13.73	521
		Strain 1(-) ♀ (5.05 ± 0.22) × strain 1(+) ♂ (10.60 ± 0.15)						
F ₁	1	8.29 ± 0.20	8.85	232	1	7.11 ± 0.22	13.02	263
	2	7.90 ± 0.20	10.59	258	2	5.85 ± 0.20	8.70	225
	3	6.50 ± 0.22	9.73	202	3	5.88 ± 0.24	12.64	211
	Pooled	7.62 ± 0.12	10.27	690	Pooled	6.33 ± 0.13	11.88	699
		Strain 2(+) ♀ (11.20 ± 0.18) × strain 2(-) ♂ (3.91 ± 0.15)						
F ₁	1	8.06 ± 0.23	11.62	216	1	8.43 ± 0.28	12.92	171
	2	9.14 ± 0.23	8.74	161	2	9.02 ± 0.23	9.17	179
	Pooled	8.52 ± 0.17	10.65	377	Pooled	8.54 ± 0.18	11.05	330

		Strain 2(-) ♀ ♀ (4.82 ± 0.17) × strain 2(+) σ^{σ} (11.82 ± 0.18)				
F ₁	1	8.32 ± 0.23	174	1	7.93 ± 0.23	11.66
	2	9.72 ± 0.19	240	2	7.88 ± 0.21	10.55
	Pooled	8.52 ± 0.15	404	Pooled	7.91 ± 0.15	11.08
		Strain 3(+) σ^{σ} ♀ ♀ (9.42 ± 0.18) × strain 3(-) σ^{σ} (4.05 ± 0.14)				
F ₁	1	7.51 ± 0.26	180	1	7.85 ± 0.27	15.37
	2	6.97 ± 0.22	185	2	6.60 ± 0.25	9.98
	Pooled	7.23 ± 0.17	365	Pooled	7.31 ± 0.19	13.38
		Strain 3(-) σ^{σ} ♀ ♀ (4.76 ± 0.22) × strain 3(+) σ^{σ} (9.70 ± 0.13)				
F ₁	1	7.36 ± 0.22	188	1	5.41 ± 0.20	6.97
	2	6.96 ± 0.22	194	2	5.09 ± 0.24	9.41
	Pooled	7.16 ± 0.15	382	Pooled	5.16 ± 0.16	8.22
		Strain 23(+) σ^{σ} ♀ ♀ (8.97 ± 0.28) × strain 23(-) σ^{σ} (6.39 ± 0.28)				
F ₁	1	9.72 ± 0.19	290	1	9.05 ± 0.23	11.37
		Strain 23(-) σ^{σ} ♀ ♀ (7.71 ± 0.24) × strain 23(+) σ^{σ} (10.26 ± 0.27)				
F ₁	1	8.82 ± 0.20	278	1	7.79 ± 0.25	13.68
	2	9.05 ± 0.23	184	2	7.26 ± 0.30	9.29
	Pooled	8.92 ± 0.15	462	Pooled	7.62 ± 0.19	12.33

Table V. Pooled Photoscores of F₁ Hybrids of Strains 1, 2, 3, and 23^a

Strain	F ₁ females			F ₁ males			H	P	df	
	$\bar{X} \pm SE$	s ²	n	$\bar{X} \pm SE$	s ²	n				
1(+)(-)	7.28 ± 0.15	9.22	422	7.58 ± 0.16	13.73	521	2.1590	0.20 >	P > 0.10	1
1(-)(+)	7.62 ± 0.12	10.27	690	6.33 ± 0.13	11.88	697	50.07	0.50 >	P < 0.01	1
2(+)(-)	8.52 ± 0.17	10.65	377	8.54 ± 0.18	11.05	330	0.7278	0.975 >	P > 0.30	1
2(-)(+)	8.52 ± 0.15	9.61	405	7.91 ± 0.19	11.08	473	7.2410	0.05 >	P < 0.01	1
3(+)(-)	7.23 ± 0.17	10.98	364	7.31 ± 0.19	11.38	366	0.0032	0.05 >	P > 0.90	1
3(-)(+)	7.15 ± 0.15	7.16	382	5.16 ± 0.16	8.22	338	74.5646	0.05 >	P < 0.01	1
23(+)(-)	9.72 ± 0.19	8.90	240	9.05 ± 0.23	11.37	217	4.4944	0.05 >	P > 0.025	1
23(-)(+)	8.92 ± 0.19	10.34	462	7.62 ± 0.19	12.33	327	27.9894	0.05 >	P < 0.01	1

^a Maternal phototaxis in first parentheses, paternal phototaxis in second parentheses.

The data reveal sex linkage for photonegative behavior in every strain (Table V). It appears that genes influencing photopositive behavior are largely autosomal and therefore nonallelic to genes controlling negative phototaxis.

DISCUSSION

Involvement of the X chromosome in the phototactic behavior of *D. melanogaster* was first suggested by Hadler (1964b). The present study shows the X chromosome to be important in photonegative behavior regardless of experimental conditions which reduced genetic recombination during selection for negative phototaxis.

The discovery of sex linkage for negative phototaxis in strain 1 shows that recombination within the X chromosome was not necessary for selection to be effective. It might have been expected that in strain 1 selection would have utilized more autosomal variation to bring about response in the negative direction. Since in strain 1 genetic recombination in the X chromosome was restricted, it is assumed that chromosomal segregation provided the major source of variation for the first chromosome in this strain. Therefore, in strain 1 selection for negative phototaxis must have been operating largely at the chromosomal level. A particular X chromosome or chromosomes having an influence on negative phototaxis may have been present in the original population and subsequently favored by selection. It would be interesting to know how many different wild-type X chromosomes remain in strain 1 (-) as opposed to strain 1 (+), where genes affecting positive phototaxis appear to be mostly autosomal.

Reciprocal hybridization in strain 23, which did not respond significantly to selection for photonegative behavior, still revealed some degree of sex linkage for negative phototaxis. Restriction of new autosomal recombination may have prevented strain 23 from responding to selection, thus indicating the existence of autosomal as well as sex-linked factors capable of influencing negative phototaxis. This would be consistent with a polygenic mode of inheritance (Lerner, 1958) as postulated for phototactic behavior in *Drosophila* (Dobzhansky and Spassky, 1969; Woolf, 1972; Markow, 1974).

Hybridization of photonegative and photopositive strains of *D. pseudoobscura* failed to reveal any influence of the X chromosome on phototactic behavior (Woolf, 1972). *D. pseudoobscura* has a metacentric X chromosome, of which one arm is homologous to the left arm of the *D. melanogaster* third chromosome and the other arm is homologous to the acrocentric X chromosome of *D. melanogaster*. The repeated finding of sex linkage for negative phototaxis in *D. melanogaster* and not in *D. pseudoob-*

scura suggests that the genetic systems controlling phototactic behavior in these two species may not be completely homologous. It would be interesting from an evolutionary standpoint to undertake similar selection and hybridization experiments in other *Drosophila* species having either metacentric or acrocentric X chromosomes.

The results reported here do not preclude the possibility that the sex linkage observed for negative phototaxis is attributable to a single region or a major-effect locus within the X chromosome. Walton (1970) reported that negative phototaxis in *D. melanogaster* was dominant as well as sex linked. His findings would be compatible with a sex-linked gene having more than one allele. The X chromosome of this species is currently being analyzed to determine the number and location of regions influencing negative phototactic behavior.

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