KOREAN JOURNAL OF ZOOLOGY
Vol. 18, No. 1, 1—8 (1975)

Studies on the Effects of Deleterious Genes on the Strains Selected for Phototaxis in *Drosophila melanogaster*

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초파리에 있어서 走光性行動의 選拔에 關한 有害遺傳子의 影響*

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(Received September 14, 1974)

摘 要

Multiple-unit classification maze를 使用하여 走光性行動에 關한 positive와 negative의 directional selection을 15世代동안 행하였다. 方向性 選拔에 의해 얻어진 兩系統의 遺傳的 構造를 알기위해 第2 染色體上에 위치한 致死遺傳子의 頻度를 調査하고 이들 有害遺傳子와 走光性行動과의 相關關係를 考察했다.

走光性에 對한 positive와 negative의 選拔效果는 初期부터 反應이 나타나 選拔後 第10世代동안의 realized heritability는 positive系統과 negative系統이 각각 3.08%와 2.86%로 算定되었다.

第2 染色體의 有害遺傳子(lethal and semi-lethal)는 positive(43%)系統이 negative(18%)系統보다 훨씬 높은 빈도였다. 한편 無選拔 系統(27%)은 兩選拔 系統의 중간빈도였다.

positive走光性 遺傳子와 有害遺傳子의 相關關係는 각 選拔系統에서 축출한 2量劣性 致死遺傳子(l_i/l_j)에서도 확인하였다.

본 實驗의 결과로 走光性行動의 選拔에 의해 얻어진 positive polygene과 有害遺傳子 polygene과에 어떤 linkage의 相關關係가 존재한다고 사료된다.

INTRODUCTION

Using the multiple classification maze which constructed by Hirsch (1959), several investigators have studied the two behavioral traits on light (phototaxis) and gravity (geotaxis) (Erlenmyer-Kimling *et al.*, 1962; Dobzhansky *et al.*, 1967, 1969; Hadler, 1964). They have shown that the geotactic or phototactic behavior was controlled by additive polygenic system. Dobzhansky and Spassky(1962) selected for geotaxis in populations of monomorphic and polymorphic gene arrangements in *D. pseudoobscura*. They obtained that chromosomal composition was changed by

* The present work was carried out at the National Institute of Genetics, Japan when the author was a visiting researcher at the Institute.

artificial selection. Correlated response to behavioral selection using the maze apparatus have been reported in some quantitative or qualitative characters (Pasteur 1969, Choo, 1974; Choo and Oshima, 1974). There are several causes carring the artificial selection, one of which is linkage relationship-genes by selection may be associated with chromosomes, and the other is pleiotrophism-genes affecting directional selection may have manifold effects.

Natural wild flies are probably maintained by balanced state between variants of genes for plus and minus phototactic behaviors which were genetically controlled. Selection to positive and negative directions was highly divergent in their phototactic scores, and some components of fitness characters would be changed by such artificial selection. The experiments reported in this paper is designed to study the effects of deleterious genes on the second chromosome in the strains selected for positive and negative phototaxis.

MATERILAS AND METHODS

1) Selection for positive and negative phototaxis.

The experimental population of *D. melanogaster* was derived from flies collected at Katsunuma, Japan, about ten years ago, which cage population was kept in regular mass culture in a constant temperature room at 25°C. Photographs and plane structure of the maze apparatus used in this experiment have previously been described (Oshima *et al.*, 1972; Choo, 1974a, b).

About 300 females and 300 males taken from the cage population were run separately through maze. Flies introduced into the starting tube of the maze were choices either light or dark pathway, and they finally arrived at eleven terminal tubes. Flies reached in terminal tube No. 1 or No. 11 are making 10 light or 10 dark choices. Equal number of light or dark choices lead to the tube No. 6.

In every generation, twenty pairs of flies showed the most positive phototaxis were bred in a milk bottle containing corn meal agar medium as the photopositive strain. The photonegative strain was established by the same method from the most twenty pairs of negative phototaxis. Such selections to both positive and negative directions were repeated for fifteen generations.

2) Estimation of homozygous viability of selected strains for phototaxis and unselected strain.

Many second chromosomes were randomly sampled from the total flies of strains selected for phototaxis and unselected strain at generation 10. Unselected strain was maintained by 20 pairs of flies in every generation and had no experience in the phototactic selection. Individual male fly isolated from each strain was crossed to three *Cy/Pm* females (*Cy*, Curly wing; *Pm*, Plum eye). A single F_1 male, *Cy*/+ (+, wild second chromosome) was crossed again with three *Cy/Pm* females. Three

pairs of F_2 *Cy*/+ flies from each cross were mated. At generation 3, a second chromosome was duplicated homozygously and the deleterious effects of genes on it were revealed. If a second chromosome isolated from above strains has a deleterious gene, the proportion of wild type flies in the F_3 generation should be lower than 0.33 (normal viability). If non-*Cy* flies could not emerged, the chromosome was classified as lethal, and emerged less than 16.8%, 25.0 and over 25.0, the chromosome was classified as semilethal, subvital and normal genes, respectively.

3) Allelism of lethal genes.

Lethal genes isolated from the experimental strains are maintained as balanced strain with *Cy* chromosome. These lethal strains were crossed with each other to get the frequency of allelism. The value was obtained by percentage of allelic crosses among the half diallel crosses.

4) Phototactic response to lethal genes.

If a lethal gene has not allelic to another one from the results of allelism test, the hybrid flies are segregated to *Cy* and non-*Cy* flies. These non-*Cy* flies were heterozygous for non allelic lethal (l_i/l_j). Non-*Cy* flies were gathered from all crosses and their phototactic response were examined.

RESULTS

1) Selection for positive and negative phototaxis.

Mean photoscores and their variances in the positive and negative strains for

Table 1. Photoscores and their variances in strains selected for positive and negative phototaxis.

Generation of selection	Positive				Negative			
	Male		Female		Male		Female	
	$\bar{X}$	σ^2	$\bar{X}$	σ^2	$\bar{X}$	σ^2	$\bar{X}$	σ^2
0	5.84	7.36	5.81	7.27	5.84	7.36	5.81	7.27
1	5.97	7.88	5.39	7.32	6.21	7.96	6.65	8.16
2	6.11	5.90	6.07	6.25	6.79	7.24	6.44	6.83
3	5.43	7.57	5.17	7.75	7.03	7.01	6.53	6.94
4	4.59	6.63	5.02	7.09	7.86	6.27	7.27	6.06
5	5.41	8.02	5.18	7.92	6.69	9.16	6.79	8.05
6	5.91	8.54	5.53	9.34	7.10	8.69	7.15	7.68
7	5.72	9.47	5.37	8.69	7.20	8.39	7.64	6.09
8	4.65	10.15	4.82	9.77	6.75	10.20	7.59	7.60
9	4.90	8.28	4.30	8.30	7.38	8.62	7.11	9.64
10	4.37	9.36	4.63	10.36	7.65	7.53	7.75	7.43
11	4.44	9.23	4.77	10.26	7.57	9.01	7.59	8.66
12	4.21	7.96	4.20	8.90	8.01	7.03	7.54	7.72
13	3.79	7.76	4.25	8.79	7.79	7.20	7.77	6.87
14	4.20	8.21	3.91	8.16	7.57	7.68	7.73	8.19
15	4.09	9.20	4.09	9.47	7.75	9.47	7.55	9.67

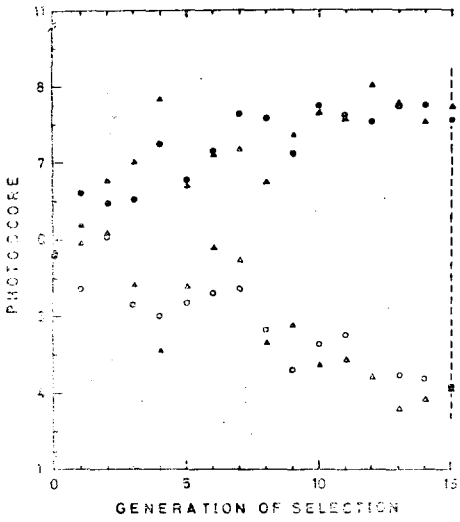

Fig. 1. Results of directional selections to positive and negative phototactic behavior. Under, positive strain; upper, negative strain. Circles and triangles show female and male, respectively.

fifteen generations are presented in Table 1, and shown graphically in Fig. 1. The foundation population was neutral to light on the average which mean score and variance were 5.84 and 7.36 for males, and 5.81 and 7.27 for females, respectively. The effects on directional selection to positive and negative phototaxis were clearly divergent in the selection proceeded. After 15 generations of selection the mean score of males and females for photopositive strain was 4.09 (same score in both sexes), and that of photonegative strain was 7.75 and 7.55, respectively. The observed variances of the positive and negative strains were equally large in all generations, and it did not decrease during the selection. Differences of mean scores between both sexes are not found.

Realized heritability for the first ten generations was computed by the average of the selection response to the selection differencial as explained in preliminary paper (Choo, 1974a). The results of heritabilies for females and males of photopositive strain were computed as 2.85% and 3.32, % and thoss for photonegative strain were calculated to be 3.43% and 2.30%, respectively. The heritability due to additive polygenes was fairly low. No difference between positive and negative strains was detected.

2) Estimation of homozygous viability of selected strains for phototaxis and unselected strain.

The distribution of viabilities of homozygous flies for second chromosomes isolated from phototactically selected and unselected strains are summarized in Table 2, and graphically shown in Fig. 2. The frequencies of the deleterious chromosomes

Table 2. Frequencies of deleterious and normal second chromosmes in strains selected for phototaxis and unselected strain.

Viability \ Strain	Positive	Negative	Unselected
Number of tested chromosomes	145	125	137
Lethal (%)	48(33.10)	18(14.40)	33(24.49)
Semilethal (%)	15(10.34)	4(3.20)	4(2.92)
Subvital (%)	23(15.86)	11(8.80)	2(1.46)
Normal (%)	59(40.68)	92(73.70)	98(71.53)
L+Sl (%)	63(43.44)	22(17.60)	37(27.00)

(lethal and semilethal chromosomes) of the photopositively selected strain and those for the photonegatively selected strain were 43.4% and 17.6%, respectively. On the other hand, the frequency of deleterious chromosomes in the unselected strain(27%) was obtained from the intermediate between both selected strains. In natural populations of Kofu and Katsunuma, Japan, the average frequency of deleterious chromosomes from 1965 to 1968 was 21.5% (Watanabe, 1969). In the results of experiment the lethal and semilethal chromosomes in the positively selected strain were very high frequency than that of negatively selected one as over 60 percent.

3) Allelism of lethal genes.

Table 3 presented the results of allelism tests in the phototaically selected and unselected strains. In the within strain the percentage of allelic chromosomes between lethals in each strain was very high, and they were similar proportion comparing to their lethal frequencies. On the other hand, the frequency of allelic crosses between strains selected for positive and negative phototaxis was very low (3.8%), and

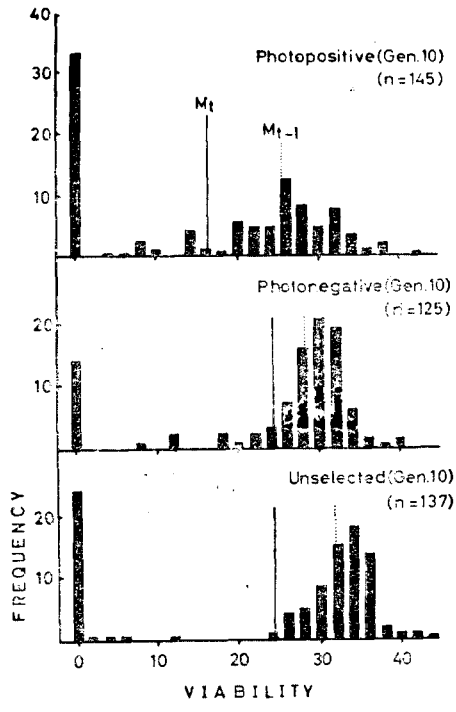

Fig. 2. Frequency distributions of viability of homozygotes for second chromosomes isolated from strains selected for positive and negative phototaxis and unselected strain. *Mt* means viability of total homozygotes; *Mt-1*, means viability of homozygotes except lethals.

Table 3. Allelism of lethal genes isolated from strains selected for positive and negative phototaxis and unselected strain.

	Within strain		
	Positive	Negative	Unselected
No. of lethal chromosomes	48	18	33
No. of crosses	1176	171	561
No. of allelic crosses	257	16	78
Frequency of allelism (%)	21.85	9.36	13.90
	Between strain		
	Posi.×Nega.	Posi.×Un.	Nega.×Un.
No. of lethal chromosomes	48×14	48×33	18×33
No. of crosses	864	1584	594
No. of allelic crosses	33	0	0
Frequency of allelism (%)	3.82	0	0

Table 4. Photoscores and their variances of lethal heterozygotes (l_i/l_i) isolated from strains selected for positive and negative phototaxis and unselected strain.

Strain	Total tested flies	Male		Female	
		$\bar{X}$	σ^2	$\bar{X}$	σ^2
Positive	9.29	4.49	6.69	5.04	8.44
Negative	11.54	5.70	7.69	5.66	9.15
Unselected	8.97	5.45	8.75	5.47	8.16

allelic chromosome did not found in the crosses with lethal chromosomes isolated from unselected strain.

4) Phototactic respones to lethal genes.

The results of mean photoscores and their variances of non-*Cy* flies extracted from strains selected for phototaxis and unselected strain are presented in Table 4. The mean photoscore of non-*Cy* flies derived from positive strain was 4.49 for males and 5.04 for females which scores were significantly tended to photopositivity from the theoretical neutrality ($\bar{X}$=6.0). The mean score of non-*Cy* flies derived from negative and unselected strains were also slightly shifted to photopositive side.

DISCUSSION

Response to phototactic selection in *Drosophila melanogaster* is under genetic control. The foundation population was phototactic neutral on the average, and highly diverged to artificial selection for positive and negative phototaxis. Dobzhansky and Spassky (1962) selected for geotaxis in populations of monomorphic and polymorphic gene arrangements of *D. pseudoobscura*. They obtained that the positive and negative geotactic behaviors were divergent in the early generations of selection, and relaxation of selected strains gave almost complete return to the original state. Similar results obtained in selection for phototaxis of *D. melanogaster* in the present experiment.

Frequency of deleterious genes in Japanese natural populations have been observed by several investigators (Oshima and Kitagawa, 1961; Watanabe, 1969; Oshima and Choo, 1972 and others). In natural populations of Kofu and Katsunuma, frequency of deleterious genes ($L+Sl$) from 1965 to 1968 was 21.5% on the average, and that of allelic rate of lethals was 3.48% (Watanabe, 1969). The presence of recessive lethals in natural populations of *Drosophila* is interest at the point of genetic control of fitness. In general, the viability of lethal heterozygotes was lesser than that of normal heterozygotes. The present experiments revealed the accumulation of deleterious genes in the populations selected for positive and negative phototaxis. Artificial selection toward different traits will affect the frequencies of alleles of polygenic system. There are several genetic mechanisms underlying such correlated response to selection. Mather and Harison (1949) detected the sterility

in the lines selected for high and low bristle number in *D. melanogaster*. They concluded that the sterility was due to linkage relationship with increased number of bristle.

In phototactic selection, Pasteur (1969) selected for opposite geo-and phototaxis in *D. pseudoobscura*, and effects on morphological differences between strains could be recognized. In *D. virilis*, Choo and Oshima (1974) selected for phototaxis over 40 generations, and they obtained the effects on some quantitative or qualitative characters. They concluded that photopositivley selected flies were lesser fitness: fecundity, longevity, body weight, body size than that of photonegatively selected ones. Dobzhansky and Spassky (1962, 1967) obtained that selection for negative geotaxis favored the carriers of *RH* chromosomes, but that of positive geotaxis gives an advantage to the *AR/CH* heterokaryotype.

In the present experiments, the deleterious genes, namely recessive lethal gene, were more accumulated in the photopositive strain than the photonegative one. The correlated relationship between lethal genes and photopositive genes could be recognized by the results that the phototactic response of heterozygous flies for two different lethal chromosomes ($1_i/1_j$), which were isolated from the photopositive, photonegative and unselected strains, was more positive phototaxis than theoretical neutrality. It was difficult to explain the relation between phototaxis and deleterious genes. However, if several polygenes were closely linked with deleterious genes, they would be accumulated concurrently by the long term selection.

SUMMARY

The experiment has been analyzed for genetic architecture of behavioral trait in strains selected for positive and negative phototaxis in *Drosophila melanogaster*. Response to selection for two different directions was rapidly diverged in their phototactic scores.

Realized heritabilities for the first ten generations of selection in the positive and negative strains calculated to be 3.08% and 2.86%, respectively in both sexes.

The frequency of deleterious chromosomes (lethal and semilethal chromosomes) in the positively selected strain (43%) was higher than that of negatively selected one (18%). The unselected strain (27%) was intermediate frequency between both selected strains.

The correlated relationship between deleterious genes and photopositive polygenes was confirmed by the phototactic behavior of the lethal heterozygotes ($1_i/1_j$).

From the results, the deleterious genes induced by long term selection for phototaxis would be considered some linkage relationship with photopositive polygenes.

ACKNOWLEDGEMENT

The author is indebted to Dr. Chozo Oshima, National Institute of Genetics, Japan,

for his valuable suggestions and criticisms in the course of this investigation. This study was supported, in part, by the grant from Ministry of Education, Japan to Dr. C. Oshima.

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