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Artificial and Natural Selection for Phototactic Behavior in *Drosophila melanogaster*

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초파리의 走光性行動에 대한 人爲淘汰와 自然淘汰

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摘 要

1974年 安養에서 採集한 초파리의 走光性行動에 대한 人爲淘汰實驗을 행하였다. 淘汰의 結果, 第10世代까지의 走光性 및 避光性系統의 遺傳率은 每世代當 2~4%로 나타났다.

淘汰系統間의 相對交配實驗의 結果, 避光性行動을 나타내는 遺傳子가 走光性遺傳子에 대하여 部分的 優性의 効果가 있음을 알았고, 그 効果는 淘汰의 後期世代에서 더욱 뚜렷하였다.

淘汰15世代後, 走光性과 避光性系統에 대하여 人爲淘汰를 中止하고 自然淘汰에 의한 遺傳子의 行動을 調査하였다. 實驗結果, 數世代以內에 最初集團의 走光性指數로 환원되었다. 이러한 현상은 自然淘汰에 의한 遺傳的複元性의 一例라고 생각된다.

INTRODUCTION

Working with *Drosophila melanogaster*, Hirsch and his colleagues (Hirsch, 1959; Hirsch and Erlenmyer-Kimling, 1961; Erlenmyer-Kimling *et al.*, 1962) studied on geotactic behavior by using a vertical classification maze. They selected the flies showing either positive or negative geotaxis over 65 generations, and concluded that the geotactic behavior was controlled by polygenic systems located on the chromosomes of X and both autosomes. Several investigators reported the similar results showing two traits of the behaviors for geo- or phototaxis (Dobzhansky and

Spassky, 1962; Dobzhansky *et al.*, 1967; Hadler, 1964; Walton, 1968; Choo, 1965a, b; Choo and Oshima, 1974).

Genetic changes correlated with behavioral selection were reported by many authors (del Solao, 1966; Pasteur, 1969; Choo and Oshima, 1974; Choo, 1975b). Choo (1976) selected the populations of *D. melanogaster* toward positive and negative phototaxis. After 10th and 15th generations, the frequency of lethal heterozygotes on the second chromosomes estimated to be 27% for the unselected population and those for positive and negative populations were 40% and 18%, respectively. Choo (1976) suggested that this correlated response to phototactic selection was closely linked between genes for positive phototaxis to lethal heterozygotes on the chromosome, and that the deleterious genes were concurrently accumulated by the long term selection.

In natural populations of *Drosophila*, genotypes of phototactic behavior are probably maintained by a balanced state between genes manifesting positive and negative phototaxis. The balanced state of genotypes for phototactic behavior would be biased by the directional selection. The experiment reported in this paper is to analyse the mechanism involved in changing of the genetic architecture controlling the phototactic behavior in *Drosophila melanogaster*.

MATERIALS AND METHODS

1. Experimental Population:

Several hundred flies of *Drosophila melanogaster* were collected by net at graperies in Anyang city, Gyunggi province in 1975. About 600 females already inseminated in natural population and 600 males were sampled from collected flies. They were divided into two experimental groups, I and II, and about 300 females and 300 males were used for the initial population of each experimental group.

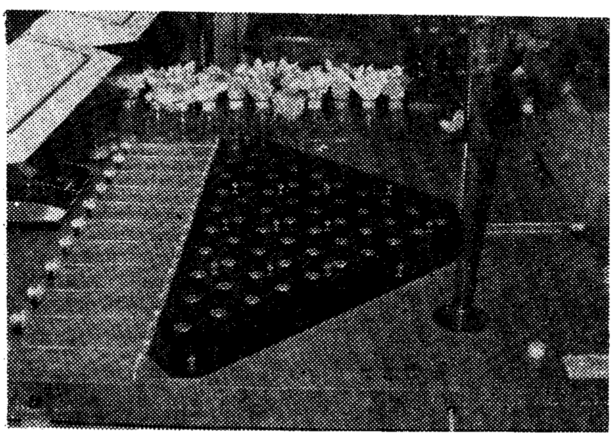

Fig. 1. A classification maze for selection of phototaxis. The flies are introduced into the tube on the right, and assort themselves into the 11 tubes on the left.

2. Maze Appratus:

The classification maze for analysis of the phototaxis was the modified from Hirsch (1959) but it was made by wood and has 11 terminal tubes (Fig. 1). The fluorescent white lamp (40 W) was equipped horizontally

30 cm above from terminal tubes of the maze.

About 300 females and 300 males were introduced separately into the starting tube of the maze. Flies allowed to choose either light (positive phototaxis) or dark (negative phototaxis) pathway. Finally, most flies were emerged into 11 terminal tubes, numbered 1 to 11 after about three hours.

The phototactic score was calculated by the formular $\Sigma ap/N$, where a means the number of flies in each terminal tube, p means the terminal tube number and N means the total number of flies collected in 11 terminal tubes. For example, a score of 6.0 means the phototactic neutrality, and the highest positive or the highest negative scores are 1 or 11, respectively. The experiment was run in the constant room temperature at 25°C.

3. Artificial Selection:

The initial population was classified into three, according to the result of the first running through the maze, positive, negative and neutral populations. In every generation, 20 females and 20 males which showed the most positive phototaxis were bred in a milk bottle containing cornmeal-yeast medium as the photo-positive population. The photo-negative and photo-neutral populations were established with 20 pairs of flies showing the most negative or neutral responses. Approximately 300 virgin females and 300 males, aged 2~3 days, were taken from each population in every generation and run separately through the maze. Such artificial selection was repeated for 15 generations.

4. Natural Selection:

After 15 generations of artificial selection, the photo-positive and photo-negative populations were relaxed in the following seven generations. In every generation, 300 virgin females and 300 males were randomly sampled from the total emerged flies, and were cultured for the next generation. Newly hatched virgin females and males, aged 2~3 days, were introduced separately into the maze in order to test for their photo response.

5, Hybridization Analysis:

At generations 10 and 15, all possible hybridizations were examined among selected populations for positive, negative and neutral phototaxis. Parental flies for the hybrid crosses were simultaneously taken from the same terminal tubes from which flies were taken for each selection line. For example, hybrid flies between positive and negative populations were made by parental flies for positive population which taken from the tube 1 and those for negative ones which taken from the tube 11. F_1 virgin females (about 300 flies of each sex) emerged from the six crosses including three reciprocal crosses at each generation were run separately into the maze and their mean photoscores were measured.

RESULTS

1. Artificial Selection:

Mean photoscores of the populations for positive, negative and neutral selections during 15 generations of experiments I and II are shown in Fig. 2. Average mean photoscores of both sexes in the initial populations of experiments I and II are found to be 6.0 and 5.9, and the scores are almost neutral in reaction to light. The selections responded graduallly in each generation. After 15 generations of selection, the mean photoscores of experiment I and II of photo-positive populations were 8.4 and 8.0, and those for photo-negative populations were 5.4 and 4.0, respectively. However, no significant difference of the mean score in both experimental groups was detected. The mean photoscores of the stabilizing selection toward neutrality did not change significantly from the neutral level.

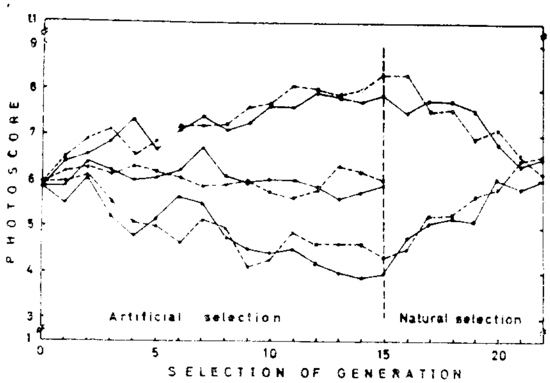

Fig. 2. Results of artificial and natural selections for phototaxis. Broken and solid lines show the experiments I and II. Upper, negative; middle, neutral; lower, positive populations.

The realized heritability recommended by Falconer (1964) is an effective estimation for heritability in selection process. This is computed by the average ratio of the selection response to the selection differential as described in the previous paper (Choo, 1975 a). The results are shown in Fig. 3 and Table 1. Average heritability was fairly low as about 2 to 4% in both directions to phototaxis, and no significant difference was detected between populations. However, standard error of the heritability of males was slightly higher than those for females.

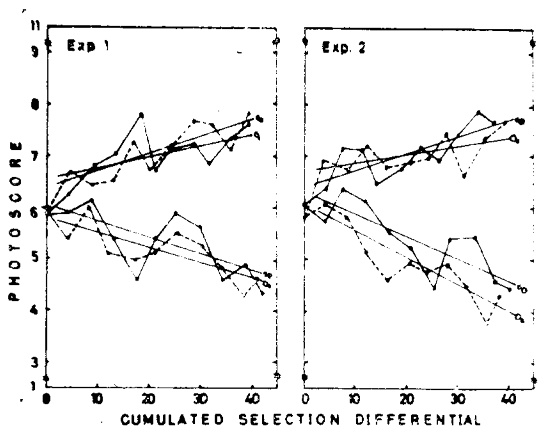

Fig. 3. Realized heritability for the first 10 generations. Upper, negative; lower, positive populations.

2. Natural Selection:

The populations selected for positive and negative phototaxis were relaxed

Table 1. Realized heritabilities for the first 10 generations of positive and negative phototactic strains.

		Positive	Negative
Exp I	Female	0.0285±0.0095	0.0343±0.0082
	Male	0.0332±0.0132	0.0230±0.0123
Exp II	Female	0.0495±0.0109	0.0156±0.0055
	Male	0.0428±0.0120	0.0327±0.0099

after 15th generation. Figure of changes in the photoscore in the following seven generations was shown in Fig. 1. The behavioral diversity produced by directional selection was rapidly extinguished by the relaxation of the selection. Their photoscores returned to the neutral level for a half time of the forward selection. However, the speed of return of the photo-positive population was slightly faster than that of the photo-negative one.

3. Hybridization Analysis:

To examine the degree of dominance of the phototactic genes, the behavior of the hybrid flies between selected populations were tested and compared with the corresponding parental populations.

Table 2. Differences between the mid-parent and hybrid values from the results of diallel crosses among selected populations.

		Differences from mid-parent value	
		Generation 10	Generation 15
P♀×U♂	F	−0.12	−0.45
	M	−0.03	−1.03
P♀×P♂	F	0.10	−0.41
	M	−0.49	−1.03
P♀×N♂	F	−0.61	−1.06
	M	0.05	0.02
N♀×P♂	F	−0.03	−0.34
	M	−0.17	−0.15
N♀×U♂	F	0.08	−1.36
	M	−0.06	−1.12
U♀×N♂	F	0.36	−0.31
	M	−0.43	−0.52

*Symbols of P, U and N mean the positive, neutral and negative strains, and F and M mean female and male, respectively.

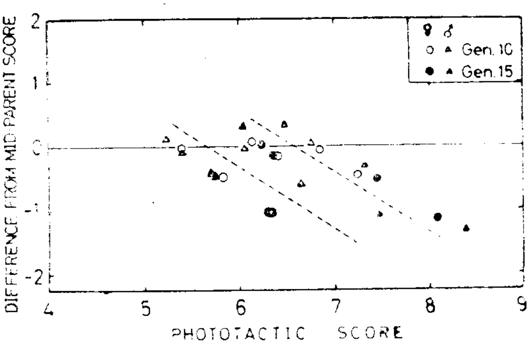

Fig. 4. Results of hybridization analysis among populations selected for phototaxis. Left, middle and right mean the hybrid points between positive-neutral, positive-negative and neutral-negative populations, respectively.

Differences between the hybrid values and the mid-parent values (Table 2) were plotted against the mid-parent values as shown in Fig. 4. In this figure, left one is the hybrid between positive and neutral, middle one is the hybrid between positive and negative, and right one is the hybrid between neutral and negative populations. If no dominant effect existed between the behavioral polygenes of the selected populations, the points in the figure should be distributed around the zero level. At generation 15, however, the distribution of the points was significantly deviated to the negative side ($P<0.01$). It can be said that the phototactic behavior was controlled by polygenes, but the negative phototactic genes are partially dominant over genes manifesting positive photataxis, and their dominant effect became more obvious in the later generations.

DISCUSSION

Phototactic behavior of *Drosophila melanogaster* is obviously controlled by polygenic system. The initial population responded neutrally to light, but the behavioral character of the population was steadily changed to either positive or negative direction by the artificial selection. Dobzhansky *et al.* (1967, 1969) and Dobzhansky and Spassky (1962) observed the similar results in the phototactic selection of *D. pseudoobscura*. However, Erlenmyer-Kimling *et al.* (1962) and Choo (1975 a) reported an asymmetrical response to selection in *D. melanogaster*. They reported that the selection for positive geotaxis or negative phototaxis responded continuously comparing to their opposite direction. Spassky and Dobzhansky (1967) reported the variability of geo- or phototactic scores in many natural populations of *D. pseudoobscura* and *D. persimilis*. It can be said that the gene contents which manifesting geo- or phototaxis are different from different populations and the response to selection is limited by the contents in the initial populations.

It is conceivable from the analysis of diallel crosses that some polygenes manifesting negative phototaxis were partially dominant. Similar results were observed in the previous experiments using the populations at Ohinawa and Katsunuma, Japan, in the same species (Choo 1975a, b). Erlenmyer-Kimling *et al.* (1962) suggested a partial dominance of positive geotaxis from the result of hybridization analysis. Walton (1968) reported the same hypothesis on the geotaxis. However, the present experiment of diallel crosses was not definitive, and dominant effect was not always unidirectional. Significant partial dominance appeared strongly in the later generation (Table 2 and Fig. 4). This suggests that the dominant effects of polygenes might appear after a certain accumulation of negative phototactic polygenes.

The phototactic neutrality of the initial population could be diverged toward both positive and negative phototaxis by the directional selection. If the selection was relaxed, the diversity of the population could be returned to the original state. Erlenmyer-Kimling *et al.* (1962) observed the similar phenomena in the geotactic behavior of *D. melanogaster*. These results can be explained by a generalized theory of the genetic homeostasis (Lerner, 1954). A balanced state of the gene pool of the population having no experience in selection would be biased by the directional selection. Even in the unbalanced state, a fairly large amount of heterozygotes would be restored in the population by their adaptive advantages. Therefore, if the population was relaxed, the balanced state would be rapidly recovered by the decrease in the number of homozygotes having disadvantages under the natural selection.

SUMMARY

Several hundred flies of *Drosophila melanogaster* collected in Anyang City were selected for positive, negative and neutral directions during 15 generations. The population responded effectively to the artificial selection. The realized heritability estimated for the first 10 generations was 2∼4% per generation in the positive and negative phototaxis.

The results of diallel crosses among selected populations indicated that some polygenes showing a negative phototaxis were partially dominant over polygenes controlled the positive phototaxis, and the dominant effect became greater in later generations.

The populations selected for positive and negative phototaxis were relaxed after 15 generations of selection, and their phototactic responses were completely returned to their original states. Such phenomena would be explained by the genetic homeostasis resulted from an action of natural selection. It seems reasonable to assume that the phototactic neutrality of a natural population was maintained as an adaptive trait under natural environment.

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