SELECTION FOR TEMPERATURE SENSITIVITY IN SCUTE DROSOPHILA

BERENICE KINDRED

C.S.I.R.O., Division of Animal Genetics, Delhi Road, North Ryde, New South Wales, Australia

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THE concept of canalisation as a system by which potential variation is channelled during development into a fairly uniform phenotype was put forward by WADDINGTON (1942). The term canalisation will here be used to mean a developmental buffering system by which potential variability is reduced and a relatively invariant phenotype is produced. If the canalisation system is upset by environmental shock or genetic mutants, this variability may be expressed. Selection on such exposed variability has demonstrated canalisation for wing-vein pattern (WADDINGTON 1953, 1955) and scutellar bristle number (RENDEL 1959) in *Drosophila*.

This system should itself be under genetic control and so should manifest genetic variability making it possible to select for good or poor canalisation (i.e. more or less effective reduction of variability) for a particular character. RENDEL and SHELDON (1960) have shown that, in the scute mutant, which has a reduced number of scutellar bristles, selection for low variance around a mean of two bristles produces increased canalisation at that number. There was a reduction in temperature sensitivity as well as the reduction in variance. WADDINGTON (1960) has selected for temperature insensitivity of several mutants as a means of canalising selection, but he did not select for temperature sensitivity (i.e. for poor canalisation). The aim of the present work is to compare the two methods of canalising selection, to see if reduction in temperature sensitivity is accompanied by reduction in variance and in sensitivity to other environmental variables, and if there are changes in sensitivity of other characters.

MATERIALS AND METHODS

The *sc bl* stock used by RENDEL and SHELDON (1960) as the basis of their canalisation selection lines has been maintained as an unselected stock, and flies from this were used in the present experiment.

The number of scutellar bristles was scored for at least ten males and ten females from each bottle. Forty single-pair matings were set up in each line, allowed to lay for three days in one set of bottles and then transferred to a second set of bottles for three days. The first set was raised at 28°C, later changed to 27°C to increase viability, and the others were raised at 19°C. The criterion for selection was the difference between means at the two temperatures. Ten bottles were selected from each line to provide parents for the next generation, four males and four females being taken from each bottle without regard for individual phenotype. The males were mated to females from four other bottles, and similarly, the females were mated to males from four other bottles. The line selected for greater difference was called the high response line (HR) and that selected for least difference, the low response line (LR). Several different ovens and

refrigerators were used and there were small differences in temperature, but as both lines were always treated together this should not have had any effect on ranking.

The first laid eggs were reared at the higher temperature purely for convenience, but this might have had some effect on the experimental results, so a check was made using a third set of eggs which were also raised at 27°C. Little difference in ranking was found if these, rather than the first set, were used for calculating differences, so the order of treatments was not important. Every fifth generation a third set of flies was raised at 25°C to measure the within-culture variance at an optimum temperature, thus, it was hoped, avoiding complications due to difference in mean. As the scale used ranges from 0 to 4 bristles, a high or low mean will lead to differences in variance owing simply to inadequacy of the scale in not scoring above 4 or below 0. For variance calculations at least 40 males and 40 females were scored from each bottle.

RESULTS

Selection has resulted in a clear difference between the high and low lines (Figure 1). The dashed lines indicate generations when for various reasons sufficient data could not be obtained. In Generations 18, 21, 24 and 25, less than ten bottles in the low line produced enough flies at 28°C. Originally both lines had come through well at 28°C, but the low lines became steadily poorer until at Generation 26 the temperature was reduced to 27°C and there was no further trouble. 28°C is not an unduly high temperature for *Drosophila* and the reason for failure is being investigated. At Generation 32 far fewer bristles were produced by the high line at 19°C, but no explanation can be offered.

The response to selection does not depend on symmetrical changes in the temperature effects (Figure 2). The greatest effect occurred at 19°C, and was larger in LR than in HR. At the higher temperature there was an early increase in the bristle counts of LR, but there has been no subsequent improvement and in HR there has also been an increase in bristle numbers in spite of selection which would favor lower numbers.

FIGURE 1.—The differences in response to selection between the high and low response lines. Females: solid line. Males: dotted line.

FIGURE 2.—Mean bristle scores of males (below) and females (above) for both selection lines at each 19°C and 27°C.

If general canalisation of scutellar bristle numbers has been increased by selection for low temperature sensitivity, there should be a difference between the selection lines in the variance of scutellar number measured at 25°C. The variances are shown in Table 1. On the whole the variance in LR is lower, but there is no indication of change with selection except perhaps in LR males. However, there has been a decrease in the mean (also measured at 25°C) great enough to account for this change (Figure 3). No attempt was made to control

TABLE 1
Mean within-bottle variance measured at 25°C

Generation	High response line		Low response line	
	Female	Male	Female	Male
5	0.51	0.64	0.41	0.59
10	0.41	0.59	0.44	0.61
15	0.48	0.60	0.40	0.53
22	0.49	0.61	0.48	0.35
27	0.44	0.60	0.40	0.46
32	0.47	0.69	0.41	0.41

Note: It was intended to measure variance at 25°C every five generations but owing to the laboratory moving to new premises Generation 20 could not be scored.

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FIGURE 3.—Mean bristle scores of males and females for both selection lines at 25°C.

the mean at 25°C, and as the mean dropped the number of flies with no bristles increased, thus reducing the variance.

The probit distance of a bristle class can be used as a measure of the canalisation at that class (RENDEL 1959); the greater the probit distance, the greater the degree of canalisation. As it seems likely that canalisation is associated with bilateral symmetry, there was a possibility that the low response line would tend to canalise around two bristles. This did not occur (Table 2).

Since a change in temperature sensitivity of scutellar bristles has been produced, a similar change in the sensitivity of other bristles might be expected. Counts were made of head, thoracic and fifth abdominal segment bristles. The head bristles counted were orbital, ocellar, vertical and postvertical and the thoracics were humeral presutural, notopleural, supraalar, postalar and dorso-central. Selection on temperature sensitivity of scutellars has produced no temperature effect on these bristles.

Asymmetry can be considered as an expression of poor canalisation. In this study, an animal was considered asymmetrical only if it had two bristles on one side of the scutellum and none on the other. This means that only flies with two bristles have been considered for asymmetry. There is no increase in the percentage of such flies in HR nor are they more frequent than in LR.

Abnormal bristles might also be an indication of poor canalisation. Certain

TABLE 2

Probit distance of the 2-bristle class measured at 25°C

Generation	High response line		Low response line	
	Female	Male	Female	Male
5	1.65	1.45	1.78	1.66
10	1.95	1.45	1.75	1.72
15	1.88	1.46	2.04	1.64
22	1.76	1.51	2.12	*
27	1.80	1.63	2.14	1.73
32	1.88	1.58	2.06	1.68

* Couldn't be measured—incomplete class.

TABLE 3

Bristle scores of flies treated with LiCl₂ and control

Line		Control			LiCl ₂		
		No. scored	Mean	Variance	No. scored	Mean	Variance
High response	Female	325	2.23	0.63	353	1.67	0.62
	Male	355	1.40	0.74	364	0.94	0.88
Low response	Female	352	1.68	0.63	304	1.22	0.54
	Male	354	0.55	0.43	334	0.45	0.43

bristle abnormalities occur in these lines: markedly curved bristles, bristles with a right angled bend, and an unusual pattern in which two bristles grow close together instead of having the normal spacing. The latter are a little more common in HR but are not increasing; the others, as well as abnormalities of the legs and wings, are evenly distributed in the lines. To see if response to other environmental factors might have changed, LiCl₂, CaCl₂ and urea were added to the food of the larvae. These were chosen from a wider range of chemicals used by DR. PAMELA PENNYCUIK (personal communication) as being the most likely to affect scutellar bristle number. LiCl₂ was the only one which did affect the number of scutellars and the effect was simply proportional to the number of bristles (Table 3). The food for these larvae was made up using a 0.1% solution of LiCl₂ instead of water, and they were raised at 25°C.

DISCUSSION

That a difference in temperature sensitivity has been produced cannot be denied although the response has been almost entirely in LR. In fact some LR matings even produced offspring with more bristles at 27°C than at 19°C. However, this large difference in sensitivity to temperature has not changed the scutellar bristle canalisation as measured by probit distance nor has there been any correlated change in other bristles, asymmetry or abnormalities. Since most of the effect has been at 19°C, it seems probable that it is the number of bristles produced under these conditions that has been altered. Current studies are aimed at elucidating how the change was brought about. WADDINGTON (1955) defined canalising selection: "—selection will tend to remove those alleles which render the developing animal sensitive to the potentially disturbing effects of environmental stresses and will build up genotypes which produce the optimum phenotype even under suboptimal or unusual environmental situations". In the present work there is no evidence that any effect other than a difference in response to a particular environmental variable, temperature, has been produced and even then the effect is only on the development of one group of bristles. These results are exactly comparable with those of WADDINGTON (1955) who found a response to temperature insensitivity without effects on variance or asymmetry. He interpreted this as canalising selection, but as the variance of the characters did not decrease it seems that response to temperature only was involved, and not re-

sponse to other environmental situations. On the other hand, RENDEL and SHELDON (1960) by selecting for low variance (at 25°C) produced a decrease in variance accompanied by an increase in the probit distance of the class they were measuring and a decrease in temperature sensitivity. Thus selection for low variance does seem to have increased stability of development while selection for insensitivity to temperature has affected only temperature effects.

ROBERTSON (1964) has reported that there are at least two components in the canalisation of body size in *Drosophila* and a similar situation may be in operation here. However, RENDEL and SHELDON affected response to temperature without directly selecting for it and it seems likely that selection for temperature response has produced a superficial effect of canalisation without changing developmental stability.

SUMMARY

Selection for temperature sensitivity and insensitivity during development has been carried out in an attempt to alter the canalisation of scutellar bristles in *Drosophila melanogaster*. This is similar to the canalising selection practised by WADDINGTON (1960) and differs from that used by RENDEL and SHELDON (1960); a comparison of the two techniques thus seemed desirable. A scute stock was used because the number of scutellar bristles varies with the temperature at which these are raised. The selection produced a difference in temperature sensitivity between the lines, but did not change within-bottle variance, probit distance of the bristle classes, or asymmetry.

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