VARIATION OF SCUTELLAR BRISTLES IN *DROSOPHILA*

II. EFFECTS OF TEMPERATURE

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Summary

Three strains (70, 71, and 73) of *D. melanogaster*, wild type for the scute locus, were exposed to temperatures of 16, 20, 25, and 30°C during larval development. They were found to vary in their temperature response; strain 70 showed a maximum development of additional bristles at the anterior site at 16°C, additional bristles were most frequent at the interstitial site between 20 and 25°C, and extra bristles at the posterior site rose to a maximum at 30°C; in strain 71 only the maximum for the anterior site at 16°C was observed; strain 73 had very few additional bristles at any site over the entire temperature range. Modification of the size of the flies by growing them under crowded conditions or by enriching the medium had no effect on the pattern of the temperature response.

I. INTRODUCTION

The number of scutellar bristles in *Drosophila* is affected by temperature during development (Child 1934*a*; Ives 1939; Rendel and Sheldon 1960). Child (1935*a*) found in scute flies exposed to temperatures ranging from 16 to 31°C that the numbers at the anterior site reached a maximum at 24·5°C, whilst those at the posterior site reached a maximum at 14°C. Rendel and Sheldon (1960) found, also in scute flies, that the number of bristles at the anterior site increased with decrease of temperature. Rendel and Sheldon (1960) also examined the effect of temperature on the number of extra scutellar bristles in wild-type flies of the Oregon strain. They found little effect of temperature except in cultures kept at 30°C, in which one or two small bristles appeared between the posterior bristles in a high percentage of flies. They infer that the scute gene interferes with one genetic system controlling the addition and subtraction of scutellar bristles at the normal and intermediate sites and that the small additional posteriors are a manifestation of the action of temperature on a second set of genes influencing scutellar bristle development in the wild-type fly.

Fraser (1963) found a correlation between the occurrence of these small posterior bristles and the appearance of additional anterior bristles in wild-type lines selected for extra scutellars. Extra posterior bristles were extremely rare in the base populations, and selection was effectively centred on extra anteriors which occur in a small percentage of unselected wild-type females. This selection was effective, causing an increase in the frequency of extra anterior bristles, and in the later generations an increase occurred in several, but not all, of the selection lines in the frequency

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of extra posterior bristles. On the basis of this correlation Fraser (1963) suggested that there is a genetic relationship between anterior and posterior extra scutellars, which differs from the conclusion of Rendel and Sheldon (1960).

In this paper data will be presented of the effect of different temperatures on the occurrence of extra scutellars in three wild-type strains of *D. melanogaster*.

II. Material and Methods

Three strains, wild type for the scute locus, were used, which differed originally in the frequency of extra scutellars. These were formed by backcrossing w^h, w, and w^{col} onto an Oregon inbred stock for five generations, followed by maintenance as mass cultures. Fraser (1963) has shown that selection for extra scutellars in these lines is effective, demonstrating that they contain a considerable variability of genes controlling the number of scutellars. The lines are termed 70, 71, and 73, respectively. The percentages of extra scutellars in females of these lines were 37, 6·1, and 0·7% respectively. These differences could be due to the lines differing at the w locus, but Fraser (1963) in crosses between lines 70 and 71 found no association of scutellar leakage with segregation at the w locus.

A series of cultures of these lines were exposed to four temperatures (16, 20, 25, and 30°C). Cultures were set up at 25°C in the evening, by placing four pairs of flies in each bottle. Three days later, in the morning, the parents were removed and the bottles were placed at the experimental temperature. Six days later the 30°C bottles were transferred to 25°C. Two days later the 20°C bottles were transferred to 25°C, and two days later the 16°C cultures were transferred to 25°C. After removal to 25°C the bottles were examined every 2 days for emerging flies. Scoring was continued until the cultures were 19 days old (16°C), 17 days old (20°C), 17 days old (25°C), and 15 days old (30°C). These limits were set because preliminary experiments showed that counts for flies which emerged late were lower than those for flies which emerged early. This was shown to be due to the fact that flies which were slow in developing had not reached the temperature effective period (T.E.P.) of their development by the time the temperature treatments were completed. The T.E.P. for scutellar bristles at the anterior, interstitial and posterior sites in scute and in wild-type flies has been shown to be between 3–5 days after the eggs are laid (Child 1935*b*; Ives 1939; Rendel and Sheldon, personal communication). For the small additional posteriors preliminary experiments suggest that the T.E.P. extends from 3½ to 7 days.

Two other treatments were imposed on the temperature treatments. Twenty matings were set up in each bottle instead of four. The crowding resulting from this treatment produced a marked reduction of body size. Another set of cultures was set up on a standard medium fortified with dead yeast. Flies scored on this medium were up to 50% heavier than those raised on standard food (Sheldon 1963).

Extra scutellars were scored on the scheme described by Fraser (1963) which distinguishes between anterior (*a*), interstitial (*i*), and posterior (*p*) extra scutellars. The raw data for the control runs are shown in Table 1. In assessing the frequency of extra bristles at a specific location, the number of flies with extra bristles at this

TABLE 1

COUNTS FOR FLIES WITH EXTRA SCUTELLAR BRISTLES IN THE 70, 71, AND 73 LINES KEPT AT 16, 20, 25, AND 30°C

Strain	Sex	Temp. (°C)	Number of Bristles																						Others	Total
			3		4	5			6						7											
			a	*p*		*a*	*i*	*p*	*aa*	*ai*	*ap*	*ii*	*ip*	*pp*	*aaa*	*aai*	*aap*	*aii*	*aip*	*app*	*iii*	*iip*	*ipp*	*ppp*		
70	♀	16			290	112	30	11	40	3		1				1										488
		20			423	131	47	4	41	9		4	5	2	1	1	1									669
		25			363	72	85	14	10	10	3	14	2			2	1	1							1(*aaap*)	578
		30			133	30	28	45	4	5	5	3	9	55				1		3		1	13			335
	♂	16		1	403	59	14	1	3																	481
		20			654	64	15		12	4																749
		25			507	17	39	3	1	3		1														571
		30			266	4	22	53		1			2	18				1				1			1(*aaip*)	369
71	♀	16			258	40			7	1																306
		20	1		386	74	1			16																478
		25			440	25	1		3																	469
		30			255	5	1	3																		264
	♂	16			253	18			1																1(4⁻)	273
		20			426	24	1		2																1(4⁻)	454
		25			455	3																				458
		30	1	1	263	3																			2(4⁻)	270
73	♀	16			427	6		1																		434
		20			553	1			1																	555
		25			661	4	1																		3(4⁻)	669
		30			763	3		9		1																776
	♂	16			393	1		1																		395
		20			458																				2(4⁻)	460
		25			637																				1(4⁻)	638
		30	1		718	1	1																		1($2^{ap}5^{ii}$)	722

site were summed and expressed as a percentage of the total number of flies in the culture, irrespective of the total score for the site under consideration or the occurrence of bristles at other sites.

III. Results and Discussion

The frequencies of extra *a*, *i*, and *p* bristles are shown in Figure 1 for the cultures at standard density on standard media. All three lines show an increase in frequency of *a* bristles with decrease of temperature. The effect was more marked in lines 70 and 71 than in line 73, which is consistent with the difference between the lines at 25°C. The formation of extra *a* bristles has a negative temperature coefficient.

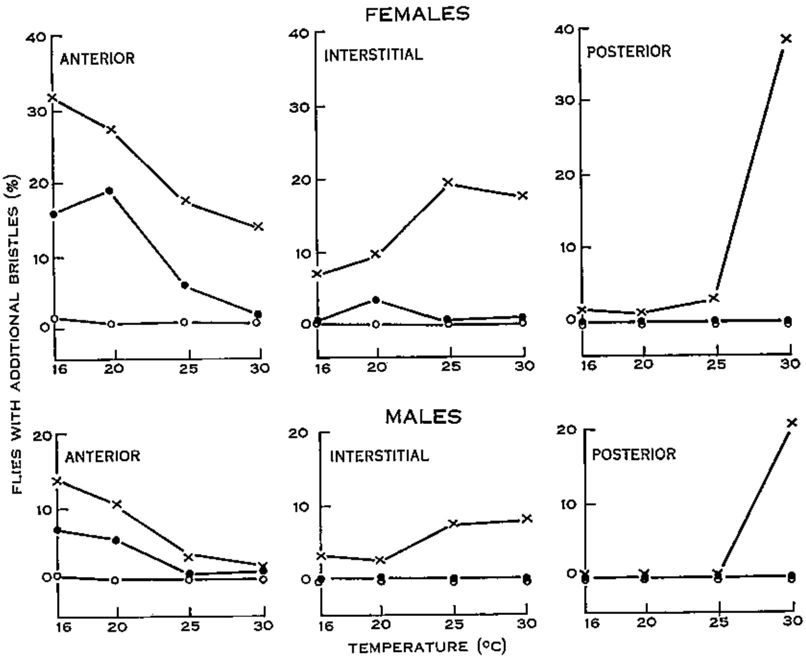

Fig. 1.—Frequency of occurrence of additional bristles at the anterior, interstitial,and posterior sites in three groups of male and female flies of strains 70 (×—×), 71 (●—●), and 73 (○—○) plotted against temperature.

At all experimental temperatures interstitial extra scutellars only occur as an odd rarity in line 73. This also is true for line 71 except at 20°C; cultures of this line at this temperature had an appreciable percentage of *i* bristles. In line 70 the frequency of *i* bristles is increased at the high temperatures. Clearly, the frequency of *i* bristles does not follow the same pattern of response to temperature as that of the *a* bristles. It is not certain whether the *i* bristles have a positive temperature coefficient, or whether there is a maximum at an intermediate temperature.

The *p* type of extra scutellar does not occur in line 73 at any temperature, and they are found in line 71 at 30°C only, and then only at a very low frequency. This is in marked contrast to line 70, where *p* bristles occur at a low frequency at 16, 20, and 25°C. At 30°C the frequency of *p* bristles is very markedly increased to nearly 40%. Green (personal communication) found in several strains that the frequency of *p* bristles was markedly increased at 28°C compared to the same strains at 25°C. It would appear that the temperature coefficient of *p* bristles is positive with a marked inflection between 25 and 28°C.

The results for the cultures kept on enriched media, and at high density, are shown in Figure 2. Although these treatments had a clear effect on body size, both the "crowded" and the "enriched" cultures had less extra bristles than the controls, showing that there is no simple correlation of scutellar leakage with body size. It

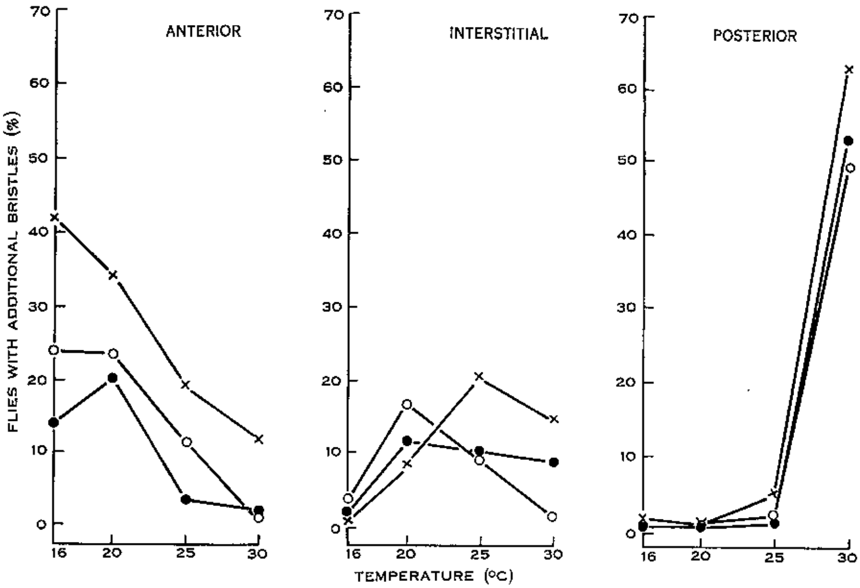

Fig. 2.—Frequency of occurrence of additional bristles at the anterior, interstitial, and posterior sites in three groups of female flies of strain 70 plotted against temperature. The three groups used were: controls (×—×), flies reared under crowded conditions (●—●), and flies reared on an enriched medium (○—○).

is possible that the reduced number of bristles in the flies on the enriched cultures may have been due to the speed with which they developed. Wattiaux (1962) has demonstrated that there is a correlation between the number of abdominal bristles and the speed of development.

The results for cultures at high density and on enriched media confirm in general the differences between the *a*, *i*, and *p* bristles in the pattern of their response to temperature. The *a* bristles increase in frequency with decrease of temperature; the *i* bristles appear to be at a maximum at temperatures in the range 20–25°C, and the *p* bristles are markedly increased in frequency at high temperatures.

The main conclusion which can be drawn from these data is that for one line of flies (70) with high numbers of additional bristles the three types of extra scutellars differ in their reaction to temperature. The results differ from those of Child (1935*a*) but this author was using scute flies and the additional bristles at the posterior site which he found at 14°C may not be comparable with the additional bristles found on the posterior scutellum of wild-type flies of strain 70 at 30°C. The results for the *a* and *p* sites are similar to those of Rendel and Sheldon (1960) for scute and wild-type flies respectively.

These differences in reactions to temperature could indicate an independence of the genetic systems controlling the appearance of additional bristles at the three sites (cf. Rendel and Sheldon 1960). It is also possible that the results could be explained by a shift of the zone of action of the "scutellar genes" with temperature.

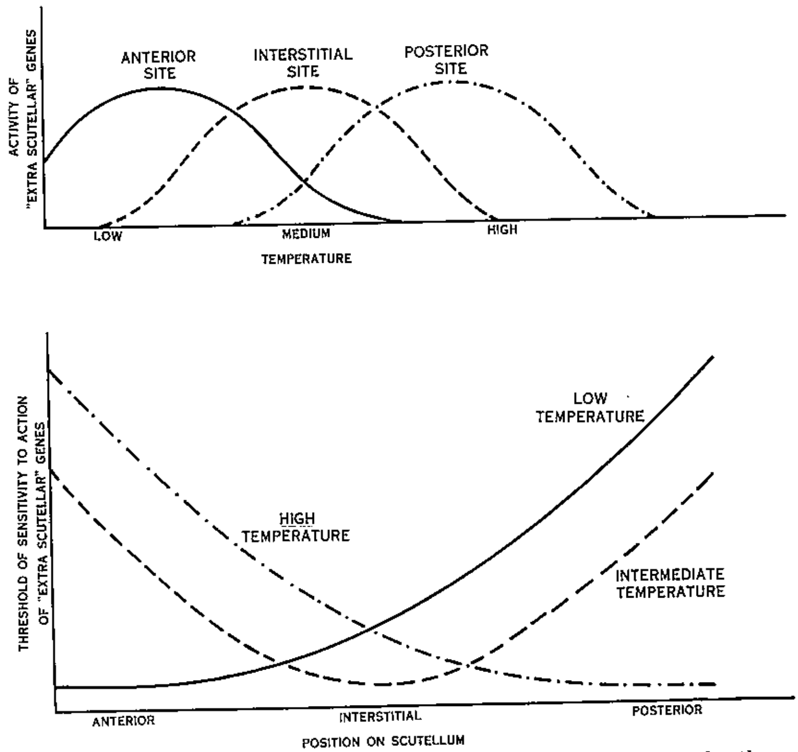

Fig. 3.—Two possible modes of action of extra scutellar genes at the three sites on the scutellum under different temperature conditions.

At low temperatures this can be envisaged as anterior; at intermediate temperatures it could be more median in location, and at high temperatures it could be more posterior in action. This is illustrated in Figure 3. Another possibility is that there are separate *a*, *i*, and *p* scutellar genes whose expression is conditional on a threshold which is affected by temperature. This is also illustrated in Figure 3.

At present there is very little evidence to support any of these hypotheses. It is possible that all three may operate under different circumstances. Further work on the isolation of the different components of the genetic system controlling scutellar numbers is clearly needed.

IV. Acknowledgments

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