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A note on the effects of temperature on the mutant characters "bent" in Drosophila virilis and Drosophila melanogaster.

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The character "bent" in *D. melanogaster* is a member of the "fourth linkage group" in that species.[1] The genes for this and the other two characters now known in this linkage group have been shown by Bridges[2] to be "carried" by the small, dot-like "fourth chromosome." Bent is characterized mainly by two variable modifications, one affecting the wings, the other the legs. The wings vary from "normal" through a series of modified shapes including spread wings, narrow wings, broad wings, swollen wings and most frequently wings that are bent sharply backward at a point near the base. The legs likewise vary from a "normal" condition through a series of stages in which progressive degrees of shortening and twisting is exhibited, beginning with the basal tarsal joint of the hind legs. The extent of the modification seems to be influenced considerably by environmental conditions.

Some time ago I found in *Drosophila virilis* a mutant character which bears considerable resemblance to this bent in *D. melanogaster* both in appearance and behavior. It exhibits much the same series of variable leg and wing modifications, except that those of the wings are less extreme and less frequent—the sharp bend being absent entirely. There are several lines of evidence pointing toward the conclusion that these characters in the two species are homologous, and that the gene for bent is in the small, dot-like chromosome in virilis as it is in melanogaster. Most of this evidence will be considered elsewhere, however. The present paper deals primarily with the effects of temperature on the two characters.

Since the characters show indications of homology and are

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1 Muller, H. J., *J. Exp. Zool.*, 1914, xvii, 325.

2 Bridges, C. B., *Proc. Nat. Ac. Sc.*, 1921, vii, 186.

both influenced by environmental conditions it is of interest to ascertain whether or not they react similarly to similar conditions. The experiments dealing with this problem are still in their preliminary stages, but certain general results have been indicated even by the relatively crude methods used at first. Other agents than temperature have been tried somewhat, but without any definite results thus far.

In the first experiment stock cultures of "bent" virilis were exposed to different degrees of temperature—one at about 9°-12° C., and others at approximately 16°, 23°, and 25° respectively. Each bottle was left at the one temperature during the development of the flies; *i. e.,* up to the time they began to hatch. The three higher temperatures had no observable influence on the bent character, the three lots of flies being essentially like those from ordinary stock bottles of this race. The lot raised in the cold, however, was markedly different. The most conspicuous difference was exhibited by the eyes. In ordinary bent stock of D. *virilis* the eyes are lightly speckled, due apparently to a disarrangement of the hairs between the facets, and occasionally to a slight disarrangement of the facets themselves. In flies reared in the cold the eyes were decidedly roughened—almost all of the facets being disarranged in some cases. In addition the posterior cross-vein was broken in some individuals, the scutellar bristles were disarranged in many, and other modifications were noted here and there. The wing and leg characteristics, however, showed no exaggeration whatever. In fact they seemed to be less marked than usual.

These results indicated that there was no correlation between the effects on the eyes and those on the legs and wings, and also that cold served to bring out several characteristics of bent that do not appear at ordinary temperatures. They also led, of course, to a similar experiment with the bent race of D. *melanogaster.* In the latter the eyes are ordinarily normal, not speckled. But when reared in the cold this race also showed the speckling of the eyes. The gene for bent in melanogaster, then, seems to have what may be called the potentiality for speckled eyes like that of virilis, but requires a different environment for producing the effect. In other respects, also, the case parallels the preceding. The legs and wings are, if anything, less extremely affected in the cold than at ordinary temperatures, and some of

the modifications revealed only by the cold in bent virilis are likewise revealed here. These will be noted more specifically below.

Another feature brought out by these experiments is that exposure to cold produces its effect at a fairly definite time in ontogeny. Space forbids going into the details of the experiments, but a few data may be cited. In one experiment a stock bottle (bent virilis) was put directly into the cold when made up and left there for forty seven days at a temperature varying from about 9° to 12° C. This is more than three times the ordinary developmental period in the incubator (23° C.), but the embryos were still in the larval stage when removed from the cold. None of the flies from this bottle showed any noticeable effect of the cold, which suggests that they were not treated at a late enough stage. Another similar experiment gave the same result.

In another experiment a bottle of bent virilis was kept in the incubator as usual for six days, then transferred to the cold for eighteen days, then kept constantly in the incubator. The eyes showed considerable effect in the early counts and then became more like those of ordinary bent in the later ones. In addition other modifications were observed as follows: (1) one or more scutellar bristles misplaced or absent (abbreviation sc); (2) one or more sternopleural bristles absent (stp); (3) apex of fifth vein thickened delta-like (del). Table 1 includes a record of the flies hatching from this bottle, together with the number of days elapsing between the time the bottle was removed from the cold and the time the flies were taken from the bottle. The eye modification, being difficult to classify accurately, is omitted from the table.

TABLE I.

Stock bottle "bent (virilis). Incubator 6 days; cold (approx 9-11°C.) 18 days; incubator remaining time. Pupæ present when removed from cold. The first column indicates the number of days after the bottle was removed from the cold.

Days after cold	del.	del. sc.	del. stp.	del. sc. stp.	sc.	sc. stp.	stp.	none
(7)	8	4	4	2	0	0	0	0
(10)	0	2	0	0	11	0	0	44
(16)	0	0	0	0	0	0	0	57
(17)	0	0	0	0	0	0	0	10
(23)	0	0	0	0	0	0	0	40

It is to be noted that large larvæ were present in the bottle when it was placed in the cold. These were presumably six days old and within twenty-four to forty-eight hours of pupation. When the bottle was removed from the cold a few pupae were present. Presumably these were the first to hatch and are included in the first count; and since all of the flies in this count are modified it may be inferred that these had not passed the critical stage when placed in the cold. This would place the critical stage near the end of the larval period or in the early pupal period. Experiments now under way ought to locate the time accurately. Another noticeable feature in the above experiment is that in the first count all of the eighteen flies are delta-like, whereas in the next count only two out of the thirteen modified flies show this characteristic. This suggests that the effect on the fifth vein is produced relatively later in ontogeny than that on the bristles, particularly the scutellar bristles.

Another bottle carried along with the one just considered, but left in the cold a shorter time gave very similar results. A third treated at a different time and left longer in the cold did likewise, except that only five delta-like flies appeared and these were in the second count instead of the first, although the other modifications appeared in the first.

It has been shown by Krafka[3] that in the bar-eye race of D. *melanogaster* temperature exerts an influence on the extent of reduction of the eye, and that it acts before pupation, during the third to fourth day of development (when the embryo is from 32%-45% developed). Likewise Hoge[4] has shown that temperature affects the manifestation of "reduplicated legs" in the same species. Here it is effective on the egg instead of the larva. The present results more nearly resemble those of Krafka, although the critical period may not come at exactly the same stage in the two cases. They also appear to agree in that the effect is produced before the organs concerned are laid down in the pupa.

The similarity of response to cold on the part of the bent race in *D. melanogaster* was shown by experiments similar to those outlined above. In one of these a lot of bent flies from stock[5]

[3] *J. Gen. Physiol.*, 1920, v, 433.

[4] *J. Exp. Zool.*, 1915, xviii, 241.

[5] I am indebted to Professor T. H. Morgan for this stock.

was put successively into seven vials, the entire lot being transferred from one vial to the next each time. After being made up the vials were kept in the incubator until after the final transfer, then all were put in the cold for thirty-six days (three times the ordinary developmental period in the incubator). In the first vial the pupae were nearly ready to hatch when placed in the cold and in the others the embryos were successively younger, those in the last being only one day old. From the first three vials many flies hatched while in the cold. From the last none hatched until six days after removal from the cold. No modified flies hatched from the first vial until near the end of the hatch, six days after removal from the cold; and these had normal eyes, (only the bristles affected). In the next vial modified flies appeared earlier and in larger numbers, and so on through the series until in the later vials modified flies appeared in the first counts and were absent from the final counts. The modifications noted were: (1) speckling or roughening of the eyes, (2) abnormal number of arrangement of sterno-pleural bristles, and (3) abnormal number or arrangement of scutellar bristles. The latter was less frequent than in virilis and the former bristle modification usually involved additional bristles instead of fewer as in virilis. Rarely the posterior cross-vein was affected also.

The effects of cold, then, on the bent race of melanogaster agreed with those on bent virilis in that they involved the eyes, the sternopleural bristles and the scutallar bristles. Likewise cold had no effect at all, unless it was an inhibiting effect, on the leg and wing modifications. The only effect of cold found in virilis and not thus far found in melanogaster is the thickening of the apex of the fifth vein. It is also to be noted that the effective period of the cold is localized in both species, although the exact developmental stage at which it comes has not yet been determined.

In conclusion it may be observed that in "normal" stocks of both species reared in the cold none of the above effects has been observed. Also matings of specimens of D. *virilis* showing the scutellar, sternopleural and delta-like modifications, without exposure to cold, have given only ordinary bent offspring. These facts, together with the nature of the results as a whole, are believed to eliminate the possibility of modifying factors or other genetic causes (rather than cold) being primarily responsible. It

seems safe to conclude that the cold simply reveals the "potentialities," so to speak, of the "bent" genes, and that these potentialities are similar in the two species.

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Localization of the vomiting center.

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1. Emesis was induced after destruction of the quadrigeminate bodies, after destruction of the cerebellum, and after section of the columns of Goll and Burdach in the cat, and after destruction of the area described as the vomiting center by Thumas[1] in the cat and in the dog.

2. Emesis could not be induced by any drug that we employed after destruction of the sensory nuclei of the vagi in the cat, nor could it be induced in any of three experiments in this animal in which the sensory nucleus of only one side had been destroyed, but vomiting did occur in one experiment in which an attempt to destroy the sensory nucleus of the right vagus may have been only partially successful.

3. Results of these experiments indicate that the sensory nuclei of the vagi are essential for the coordination of the vomiting reflex (that is, for vomiting however induced), and this is in harmony with our conception of the mechanism of emesis because: (a) It is well know that the vagus nerve is essential for emetic action of many drugs. (b) We have been unable to induce vomiting in the cat after destruction of the sensory nuclei of the vagi while taking especial care to avoid injury to the area described by Thumas as the vomiting center. (c) There are no nerve cells concerned so far as known, in the area described by Thumas.

4. We have shown elsewhere[2] that afferent emetic impulses from the heart pass by way of the sympathetic nerve, hence the conclusion is unavoidable that this nerve must make functional communication with the sensory nuclei of the vagi.

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[1] Thumas, L. J., *Arch. f. Anat. u. Phys.*, 1891, cxxiii, 44.

[2] Hatcher, R. A., and Weiss, Soma, *Arch. Int. Med.*, 1922, vol. xxix, 690.