

10. Paper electrophoresis with a 0.3M sodium phosphate buffer solution (pH 4.0) was used to characterize the radioactive compounds. Nonradioactive choline and acetylcholine were used as reference standards. The system was subjected to 26.3 v/cm for 2.5 hours. Acetylcholine moved 41.4 cm from the origin. The R_m of choline was 1.13.
 11. Paper chromatography with *n*-butanol-water (9:1 by volume) was used to characterize the radioactive compounds. Descending chromatography was conducted for 18 hours. Nonradioactive choline and acetylcholine were used as reference standards. The R_F of choline was 0.07 and the R_F of acetylcholine was 0.10.
 12. Supported by grants from the NIH (NB-04553 and 5T1-GM-153).
- * Predoctoral trainee under PHS pharmacology training grant 5T1-GM-153.

1 June 1964

"Cytoplasmic" Sterility in *Drosophila paulistorum* Which Is Ultimately Dependent on Nuclear Genes

Abstract. *A case of hybrid sterility in Drosophila paulistorum is due to an incompatibility of the Y chromosome of certain strains with the cytoplasm of other strains. The constitution of the cytoplasm responsible for the sterility is not, however, independent of the chromosomal genes. After seven backcrosses of the hybrid females to males of the same strain, fertile male progenies are finally obtained.*

At least three different kinds of hybrid sterility occur within the super-species *Drosophila paulistorum*. This superspecies consists of six races or incipient species; hybrids between the races are fertile as females but sterile as males (1). The hybrid females can be backcrossed to males of the parental races, and the backcross progenies consist again of fertile daughters and sterile sons. The sterility of the backcross males depends upon the genetic constitution of their mothers; all the sons of a female carrying any mixture of the chromosomes of the parental races are sterile, even if some of these sons themselves carry only the chromosomes of a single race (2). This is, then, an instance of a genic sterility operating through a maternal effect, the genes responsible being distributed in all three pairs of the chromosomes which the species possesses. Evidently, the sterility of the F_1 males is due to a different mechanism, since F_1 hybrids are descendants of pure rather than hybrid mothers.

A third kind of sterility has been reported (3), so far in only a single cross, between strains from Mesitas and those from Santa Marta, Colombia.

Both the Mesitas and Santa Marta strains belong to the Transitional race of *D. paulistorum*. The cross Mesitas female \times Santa Marta male gives fertile hybrids of both sexes, but the male progeny of the reciprocal cross is sterile. The hybrid females can be backcrossed to males of either parental strain; the male progenies of these backcrosses are sterile if they carry the Y chromosome of Mesitas in the Santa Marta cytoplasm, or the Y chromosome of Santa Marta in Mesitas cytoplasm. Genetic analysis consequently suggests that the sterility is caused by an interaction of the Y chromosome of the Santa Marta strain with the cytoplasm of Mesitas. This inference was based on a study of four backcross generations to both parental strains. Males with cytoplasm of Mesitas origin and a Santa Marta Y chromosome were sterile even when about 97 percent of their genome (other than the Y chromosome) were of Santa Marta origin. Since the earlier report (3) was published, additional backcrosses have been made to test the possibility that the cytoplasmic difference may eventually be overcome by the nuclear genes (4).

Fifteen new strains of *D. paulistorum* were obtained (5) from Mesitas, Colombia. These strains behaved like the old Mesitas strain (6), and were pooled into three stocks. All the experiments crossing Mesitas with Santa Marta were, therefore, made in triplicate; the results were uniform and can be described jointly. Mesitas females were crossed to Santa Marta males and the hybrid females were backcrossed repeatedly to Santa Marta males. The male progenies of the first four backcross generations were, as before, sterile. By the fifth or sixth backcross generation some motile spermatozoa were seen in the sperm-storing organs of the females with which the hybrid males were tested, but still none of the eggs deposited by these females hatched. The male progeny of the seventh backcross generation is, however, entirely fertile.

A similar situation was observed in the crosses with the Santa Marta cytoplasm. Six backcrosses to Mesitas males yielded sterile male hybrids, but the seventh backcross generation gave at least some fertile males. The progeny of the seventh backcross is expected to have more than 99 percent of the genes of the recurrent parent. Thus, by repeated backcrosses the origin of the

cytoplasm is finally overcome by the chromosomal genes. If the properties of the cytoplasm were transmitted independently of the nuclear genes, the sterility of the backcross males would have to be retained irrespective of the number of the backcrosses made, as it was after some 60 generations in the experiments of Laven (7) on a cytoplasmic sterility in crosses between certain mosquitoes. This is, however, not the case in *Drosophila paulistorum*. Finally, the male progeny of the seventh backcross generation of (Santa Marta female \times Mesitas male) \times Mesitas male was crossed to pure Santa Marta females. All the hybrid males thus obtained were sterile, just as the initial Santa Marta female \times Mesitas male F_1 males.

LEE EHRLMAN

*The Rockefeller Institute,
New York 10021*

References and Notes

1. Th. Dobzhansky and B. Spassky, *Proc. Natl. Acad. Sci. U.S.* **45**, 419 (1959).
2. L. Ehrman, *Evolution* **14**, 2 (1960).
3. ———, *Proc. Natl. Acad. Sci. U.S.* **49**, 155 (1963).
4. Several colleagues, especially Ernst Caspari of Rochester University and Theodosius Dobzhansky of the Rockefeller Institute suggested that these backcrosses should be made.
5. Through the courtesy of A. S. Hunter, Universidad de los Andes, Bogota, Colombia.
6. Th. Dobzhansky, L. Ehrman, O. Pavlovsky, B. Spassky, *Proc. Natl. Acad. Sci. U.S.* **51**, 3 (1964).
7. H. Laven, in *Cold Spring Harbor Symp. Quant. Biol.* **24**, 166 (1959).
8. This work was carried out under contract No. AT-(30-1)-3096, U.S. Atomic Energy Commission.

20 April 1964

Lateral Geniculate Nucleus and Cerebral Cortex: Evidence for a Crossed Pathway

Abstract. *Lesions were placed in the lateral geniculate nucleus of cats, and degeneration was traced in the brains after survival times ranging from 5 to 21 days. Degenerated fibers could be seen in the corpus callosum and in the lateral and suprasylvian gyri of the opposite hemisphere. Results suggest the presence of a crossed geniculocortical pathway.*

A number of earlier authors (1) suggested the possibility of a tract connecting each lateral geniculate nucleus with the contralateral cortex by way of the corpus callosum. Such a pathway was proposed to account for the paradoxical sparing of the macular portion of the visual fields in man after massive