The Homeotic Gene *spineless-aristapedia* Affects Geotaxis in *Drosophila melanogaster*

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The homeotic mutation *spineless-aristapedia* (ss\(^a\)) transforms the aristae into second tarsi. Flies with a ss\(^a\) phenotype also show extremely positive geotaxis as measured in a Hirsch-type geotaxis maze. Other antennal mutants and flies with their aristae amputated do not show such extreme positive geotaxis. Deletion analysis has comapped the geotaxis effect with ss\(^a\) in band 89C on the third chromosome. Finally, a biometrical analysis has detected additional genes on the X chromosome that also affects geotaxis.

**KEY WORDS:** *Drosophila*; biometrical analysis; behavior genetics; genetic analysis; ss\(^a\); deletion mapping.

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**INTRODUCTION**

Geotaxis, was apparently one of the first behaviors to be analyzed genetically in *Drosophila melanogaster* (Hirsch and Tryon, 1956). Several researchers have attempted genetic analyses of the differences between lines of flies selected for positive and negative geotaxis by hybrid analyses (Erlenmeyer-Kimling *et al*., 1962) or chromosome analyses (Ksander, 1966; Pyle, 1978). These analyses were often incomplete but all researchers claimed that geotaxis was polygenic and that there were genes on all three major chromosomes. Markow and Merriam (1977) tested 10...
strains that had been isolated in Benzer’s (1967) countercurrent distribution device for geotaxis and phototaxis. Eight of ten mutants showed mean geotaxis scores that differed from the parental Canton Special strain. No correlation was found between phototaxis and geotaxis scores. This suggested that single-gene mutations may have strong effects on a polygenic trait such as geotaxis. Unfortunately, these genes were not mapped, and the strains are no longer available, so it cannot be proven that only one gene in each strain was responsible for the behavioral effects observed.

There are two approaches to finding single gene mutations that affect behavior. One approach is to develop a mass screening procedure, mutate flies, and isolate flies that show a shift in mean behavioral response. The second way is to look for preexisting mutants that affect the sensory or neural systems that you are interested in studying. Both of these approaches have been used for learning. For example, Quinn and his coworkers (Aceves-Pina et al., 1983) isolated several learning and memory mutants including dunce, rutabaga, cabbage, and turnip. Livingstone and Tempel (1983) showed that the preexisting dopa decarboxylase (Ddc) mutation (Wright, 1977) also affected learning. We hypothesized that mutations which affect the morphology of structures putatively involved in gravity sensing may also cause changes in geotaxis. Insects sense gravity with proprioceptive gravity receptor (PGR) systems (Horn, 1985). PGR systems are located in the head and neck, where they respond to relative motion of the head, and in the legs, where they respond to displacement of the entire body. It has been suggested (Schwartzkopff, 1974) that resting flies sense gravity with their antennae.

Many mutations are known to affect antenna morphology in Drosophila. Since surgical manipulations of the antennae affect geotaxis in other insects (Horn, 1985), we hypothesized that antennal mutants might show similar effects. We screened several antennal mutants in modified Hirsch-type geotaxis mazes. The homeotic mutation spineless-aristapedia had the largest effect. This mutation transforms the arista and third antennal segment into a tarsus. In this paper we show that spineless-aristapedia flies are significantly geopositive and that this effect is not due to trivial antennal defects. Other alleles of spineless have the same effect. Finally, we comap the geotaxis effect and the antennal transformation by deletion mapping. A biometrical analysis corroborates the deletion analysis, at least in part, and we detected genes on the X chromosome that affect geotaxis.