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THE GENETIC BASIS OF GERMAN COCKROACH BAIT AVERSION

JULES SILVERMAN
Department of Entomology, North Carolina State University,
Raleigh, North Carolina, USA

Abstract Behavior is modulated by both learned and innate factors, and the heritability of behavior has been documented in several arthropod taxa. Certain behaviors have evolved following selection with toxicants. One such behavior that is adaptive to the German cockroach is glucose aversion, which is controlled by a single major gene. German cockroaches with this trait survive in the presence of baits containing glucose. I will provide a general overview of the genetics of taste in arthropods within the framework of plant-herbivore coevolution in an effort to understand current bait aversion issues as well as anticipate how others may arise.
Key Words Behavioral resistance, glucose aversion, baits, genetics

INTRODUCTION

The first documented case of bait aversion in *Blattella germanica* arose due to one or more mutations that were selected for in the presence of glucose and a toxicant (Silverman and Bieman, 1993). While this phenomenon has been generally referred to as behavioral resistance (Silverman and Ross, 1994), I regard this terminology as being too broad and not entirely accurate. That is, while the overt response of the cockroach is that of "avoiding" baits with glucose and thereby "resisting" the consequences of toxicant intake, a complex series of behavioral events may not be invoked. In the case of glucose aversion at least, the trait is controlled by a single major gene (Silverman and Bieman, 1993; Ross and Silverman, 1995a, b), therefore, it is unlikely that the mutation affects a sequence of behaviors, but rather a single site within a taste receptor or signaling pathway. However, single mutations may not explain all instances of *B. germanica* bait aversion. For instance, Wang et al. (2004) identified a German cockroach strain that was poorly controlled by two commercial baits that differed both in active ingredient (AI) composition and presumably inert ingredients. This Cincy strain displayed both moderate levels of resistance to each of the AI's and rejected several normally phagostimulatory sugars, at least one of which was probably a bait component. While the contact chemosensory system of *B. germanica* has been poorly studied, many sugars stimulate feeding in cockroaches (Tsuji, 1965), and sensilla on the maxillary palps of *Periplaneta americana* contain sugar-binding sites (Becker and Peters, 1989). Unless there is a general sugar receptor in *B. germanica*, Wang et al.'s (2004) discovery of aversion to glucose, fructose, sucrose and maltose points to independent mutations occurring in several distinct sensory receptors almost simultaneously. This seems unlikely. Instead, one of two alternate processes may be operating that are consistent with the explanation for the origin of glucose aversion (Silverman and Bieman, 1993). 1) The mutation is in a sensory receptor that normally binds deterrent molecules and instead the sugars act as ligands. Plant secondary compounds such as glycosides and glucosinolates deter several herbivore taxa and these compounds contain a glucose moiety. The disaccharides maltose and sucrose contain glucose, which may bind to the mutant receptor thereby exciting a deterrent pathway, which is subsequently expressed as avoidance behavior. The aversion to fructose, however, is not consistent with this explanation. 2) Sugar-receptor binding is normal; however, a mutation occurs within the CNS such that the information follows an inhibitory rather than stimulatory pathway. This explanation both incorporates the response of Cincy to fructose and may suggest a similar mechanism for Cincy and the glucose-averse strains. However, this explanation does not consider that the strains reported by Silverman and Ross (1994) were stimulated by fructose, sucrose and maltose. Therefore, a single mechanism for German cockroach bait aversion across collection sites may not apply.

Strain-dependent sugar aversion in *B. germanica* is clearly distinct from prior descriptions of attenuated responses to sugars, whereby mutant *Drosophila melanogaster* strains were identified which fed less and/or displayed a loss of electrical response in taste receptors to several sugars (Rodrigues and Siddiqi, 1981; Singh, 1997). Therefore, these unique sugar-averse strains provide excellent starting material for further studies in sensory neurobiology.

Should we expect bait aversion to be an obstacle to German cockroach management for the foreseeable future? Despite the efforts of manufacturers to remove offending ingredients from their bait products, the German cockroach has demonstrated an impressive level of adaptability in the face of a considerable arsenal directed at it. There is ample precedence for the bait aversion phenomenon coming from the evolutionary arms race between plant and herbivore. Polyphagous insects are more or less insensitive to the deterrent secondary chemicals produced by their host plants, and it has been postulated that they evolved from monophagous ancestors (Bernays, 1998). Moreover, the genetic basis of this host plant shift has been documented in several insect herbivores including *Bombyx mori* (Asaoka, 2000) where mutant gustatory receptors no longer respond to deterrent allelochemicals. While *B. germanica* is regarded as an omnivorous scavenger rather than a herbivore, it presumably evolved from a phytophagous orthopteroid ancestor and therefore is probably adapted to modify food choice in the face of environmental constraints.

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