Changes in Taste Neurons Support the Emergence of an Adaptive Behavior in Cockroaches

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In response to the anthropogenic assault of toxic baits, populations of the German cockroach have rapidly evolved an adaptive behavioral aversion to glucose (a phagostimulant component of baits). We hypothesized that changes in the peripheral gustatory system are responsible for glucose aversion. In both wild-type and glucose-averse (GA) cockroaches, D-fructose and D-glucose stimulated sugar–gustatory receptor neurons (GRNs), whereas the deterrent caffeine stimulated bitter-GRNs. In contrast, in GA cockroaches, D-glucose also stimulated bitter-GRNs and suppressed the responses of sugar-GRNs. Thus, D-glucose is processed as both a phagostimulant and deterrent in GA cockroaches, and this newly acquired peripheral taste sensitivity underlies glucose aversion in multiple GA populations. The rapid emergence of this highly adaptive behavior underscores the plasticity of the sensory system to adapt to rapid environmental change.

Sensory systems guide the assessment of food, habitat, and potential mates, and prominently govern intra- and interspecific interactions. Although great progress has been made in our understanding of chemosensory processing, especially in insects (1, 2), how chemosensory systems change in response to rapidly changing environments remains largely unknown. Cross-species divergence has been well investigated, particularly in olfactory processes (2–4). However, identifying the chemosensory mechanisms that underlie adaptive intraspecific polymorphisms has been challenging. Among the most important such polymorphisms are sensory adaptations that confer behavioral resistance to insecticides (5).

The German cockroach, Blattella germanica, offers a tractable system to explore mechanisms of sensory adaptation. Since the mid-1980s, control of this pest has increasingly shifted to baits that combine an insecticide with various phagostimulants, typically D-glucose (glucose henceforth) and D-fructose (fructose) (6). Within just several years, cockroach populations evolved a...
new behavioral trait—glucose aversion. Glucose-averse (GA) cockroaches avoid eating glucose-containing baits (movies S1 to 4 and fig. S1), resulting in failure of otherwise highly effective baits (7). The GA trait is heritable (7, 8), and the aversive response is robustly evoked by glucose alone (7, 9). Although growth and reproduction are slower in GA than in wild-type cockroaches (10), GA cockroaches outcompete wild-type cockroaches under the strong selection pressure of glucose-containing baits (7, 11).

We hypothesized that the GA trait could be encoded by changes in glucose detection. Tastant detection in insects occurs in peripheral gustatory receptor neurons (GRNs), which are housed within hairlike sensilla on the mouthparts (12, 13). The GRNs have modal taste specificity, so in Drosophila, for example, four GRNs encode four taste classes: sugar-, bitter-, water- and salt-sensitive GRNs (13, 14). Each GRN expresses multiple gustatory receptors (GRs) that recognize tastants and transduce information about their quality and strength into neuronal impulses that can be distinguished by their amplitude and duration (15, 16). As in other animals, tastants that activate sugar-GRNs elicit appetitive behavior (13, 17) and tastants that activate bitter-GRNs drive aversive behavior (13, 18).

The organization and functions of GRNs in the German cockroach are poorly understood (19). We concentrated on glucose-sensitive sensilla on the paraglossae (Fig. 1A) because the paraglossae alone can drive glucose acceptance in wild-type cockroaches and its rejection in GA cockroaches (9). Analysis of impulse waveforms [Fig. 1B; also see (20)] and cross-adaptation experiments (fig. S2) in wild-type cockroaches demonstrated that glucose-sensitive sensilla contain four distinct GRNs. Fructose and glucose selectively stimulated GRN1, whereas caffeine selectively stimulated GRN2.

The sugar- and bitter-GRN sensitivities of GA cockroaches (strain T164-BC) were considerably different from those of wild-type cockroaches. Glucose stimulated four rather than only three types of GRNs (Fig. 1B and fig. S2), corresponding to the sugar-GRN, bitter-GRN, GRN3, and GRN4 of wild-type cockroaches. Electrophysiological recordings from GA cockroaches with 10 tastants further demonstrated that the bitter-GRN...
responded to glucose and all the tastants that elicited aversive behavior (Fig. 1C and fig. S3). We therefore suggest that glucose and related compounds drive the aversive response in GA cockroaches by stimulating the bitter-GRN, the same GRN that is stimulated by caffeine in both cockroach strains (Fig. 1C). By contrast, GRN3 and GRN4 responded without any apparent discrimination among stimuli (Fig. 1C, fig. S4A, and table S1), suggesting that they do not contribute to the differential discrimination of appetitive and aversive tastants by the two cockroach strains.

We compared the sensitivities of the sugar- and bitter-GRNs in the wild-type and GA strains with dose-behavioral response studies with six tastants (Fig. 2A). The two cockroach strains showed similar behavioral and GRN responses to fructose and caffeine (Fig. 2, B and C), suggesting that wild-type and GA cockroaches have fundamentally similar gustatory neural networks for appetitive and aversive behaviors. However, glucose and two related compounds stimulated the bitter-GRN in GA cockroaches (Fig. 2, B and C), and 3-α-methyl-D-glucose, which was aversive to both strains, elicited significantly higher bitter-GRN responses in GA than in wild-type cockroaches.

The results suggest that in wild-type cockroaches, glucose and related compounds are discriminated structurally by narrowly tuned receptors on sugar-GRNs, eliciting appetitive behavior. In GA cockroaches, by contrast, the expression of a broadly tuned receptor or multiple narrowly tuned receptors may contribute to the broad acceptance of glucose and related compounds by bitter-GRNs, driving aversive behavior.

Sugar-GRNs in GA cockroaches also exhibited a significantly lower response to glucose than in wild-type cockroaches (Fig. 2C). We tested whether the sugar-GRNs of GA cockroaches are less sensitive to glucose, or if their responses are depressed by the activities of adjacent GRNs. Complementary behavioral assays and electrophysiological recordings with mixtures of phagostimulants and deterrents revealed that in GA cockroaches, both glucose and caffeine attenuated the appetitive response to fructose (Fig. 3A and table S2) and significantly depressed the sugar-GRN responses relative to fructose alone (Fig. 3B). By contrast, in wild-type cockroaches, combining glucose with fructose increased both the appetitive response and the electrophysiological responses of sugar-GRNs compared to fructose alone (Fig. 3B). These results demonstrate that GA cockroaches detect glucose as a genuine deterrent, which also suppresses sugar-GRN responses, as alkaloids and glucosides do in other insect species (21–23).

How prevalent is this mechanism in glucose-averse field populations? We screened the feeding responses of 19 field-collected populations and found seven populations with GA cockroaches (Fig. 4A). Two of these strains were used in behavioral and GRN dose-response studies. Although both were less GA than the lab-selected strains (Fig. 4B and table S2), in both strains glucose stimulated the bitter-GRN (Fig. 4C) and depressed the sugar-GRN (table S1). In four GA strains, the behavioral feeding responses negatively correlated with bitter-GRN responses (Fig. 4D and table S3). The wild-type and field-collected strains did not differ in GRN sensitivities for both fructose and caffeine (fig. S5 and table S1), confirming that a similar mechanism gave rise to glucose aversion in multiple cockroach populations.

Most natural genetic polymorphisms in taste receptors modify behavioral responses over a finite range, from exquisite sensitivity to complete insensitivity to a particular tastant [e.g., (24)]. In bait-selected cockroach populations, however, the modal specificity of glucose has been dramatically
transformed from “sweet” and highly phagostimulatory to “bitter” and highly deterrent. Generally, bitter-GRNs of insects coexpress a large number of GRs (18, 25) and are therefore broadly tuned to respond to various deterrents (18, 21, 22). The coexpression patterns of GRs ultimately account for the unique sensitivity of bitter-GRNs and their capacity to selectively respond to specific deterrents (18). Our electrophysiological studies with GA cockroaches suggest two major hypotheses: One or more mutations have either (i) modified the structure of GRs on the bitter-GRN to accept glucose and/or (ii) caused the misexpression of native glucose GRs on the bitter-GRN. The structure-function adaptation has emerged, expressing chemosensory gain-of-function adaptation that confers behavioral resistance to anthropogenic sugars, protecting the German cockroach from insecticides.

References and Notes
19. Materials and methods are available as supplementary materials on Science Online.

Acknowledgments: We thank R. Santangelo, V. Knowlton, A. Ernst, J. Mahaffey, R. Ahnolt, N. Bao, D. Bieman, and D. Mukha for equipment and cockroach collections and T. Tanimura, F. Marion-Poll, A. A. Dahanukar, and three anonymous reviewers for constructive comments. This research was supported in part by NSF (IOS-1052238) and U.S. Department of Housing and Urban Development (NCHHU0001-11) awards to C.S. and by the Blanton Whitmire Endowment at North Carolina State University. Data associated with this manuscript have been archived in DRYAD Digital Repository (http://datadryad.org/).

Supplementary Materials
www.sciencemag.org/cgi/content/full/340/6135/972/DC1 Materials and Methods
Fig. S1 to S5
Tables S1 to S3
References (26–28)
Movies S1 to S4
7 January 2013; accepted 26 March 2013
10.1126/science.1234854
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Acknowledgments: We thank R. Santangelo, V. Knowlton, A. Ernst, J. Mahaffey, R. Ahnolt, N. Bao, D. Bieman, and D. Mukha for equipment and cockroach collections and T. Tanimura, F. Marion-Poll, A. A. Dahanukar, and three anonymous reviewers for constructive comments. This research was supported in part by NSF (IOS-1052238) and U.S. Department of Housing and Urban Development (NCHHU0001-11) awards to C.S. and by the Blanton Whitmire Endowment at North Carolina State University. Data associated with this manuscript have been archived in DRYAD Digital Repository (http://datadryad.org/).
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Science 340 (6135), 972-975,
DOI: 10.1126/science.1234854

Sugar Aversion

Several populations of the German cockroach have become averse to the glucose used as bait in toxic traps, which has severely reduced the traps' effectiveness. Wada-Katsumata et al. (p. 972) show that this aversion is a result of changes in the peripheral gustatory system, whereby glucose, as well as "sweet" receptors, stimulated an aversive bitter compound receptor.