

Behavioral Antagonism in the Moth *Helicoverpa zea* in Response to Pheromone Blends of Three Sympatric Heliothine Moth Species Is Explained by One Type of Antennal Neuron^a

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ABSTRACT: We have discovered a type of sensillum on the antennae of male corn earworm moths, *Helicoverpa zea*, that houses two types of receptor neuron (RN) that explains both the upwind flight attraction of males to their own species' pheromone blend and arrestment to the quite similar blends emitted by females of three other sympatric North American heliothine species. The first RN type is a large-spiking neuron that is most sensitive to (*Z*)-9-hexadecenal (Z9-16:Ald), the secondary *H. zea* pheromone component that along with the major component, (*Z*)-11-hexadecenal, causes attraction to the female. This RN is also responsive to (*Z*)-9-tetradecenal (Z9-14:Ald; not a *H. zea* pheromone component) at higher dosages. The sensitivity of this RN thus explains the attraction that has been observed in other studies when small proportions of Z9-14:Ald are added to Z11-16:Ald to mimic the conspecific blend. The second type of RN in this sensillum is a small-spiking neuron that is again responsive to Z9-14:Ald (which in larger proportions acts as a strong antagonist to upwind flight), but this RN is actually more sensitive to two other strong behavioral antagonists, (*Z*)-11-hexadecenyl acetate and (*Z*)-11-hexadecenol. Thus, activation of this single broadly tuned 'antagonist' RN could explain why *H. zea* males will orient only to their conspecific females. These three compounds are emitted by females of three other North American species, *H. subflexa*, *H. phloxiphaga*, and *H. virescens*, as agonists in their blends, which also contain the *H. zea* components Z11-16:Ald and Z9-16:Ald. This antagonist RN may also explain why a blend of Z11-16:Ald and a small amount of Z9-14:Ald is never as attractive to *H. zea* males as the conspecific blend. Enhanced specificity for the conspecific blend arises because the antagonist RN is never stimulated to fire, even when large proportions of the pheromone component, Z9-16:Ald, are added to Z11-16:Ald. When Z9-14:Ald is used instead of Z9-16:Ald, however, and the proportion of Z9-14:Ald becomes too great, the threshold of the antagonist neuron as well as that of the agonist neuron is exceeded, and the upwind flight response begins to be suppressed.

There are different types of receptor neurons on male moth antennae that are involved in the attraction of males to their two-to-four-component female-emitted pheromone blend. Each (agonistic) pheromone component receptor type is usually tuned optimally only to one component of the conspecific blend and is housed in a long hair-like sensillum. Thousands of these sensilla festoon the antennae of male moths. Other neurons exist that are involved in antagonistic behavioral responses of males. These are tuned to respond only to components in non-conspecific female blends and are involved in reducing the attraction of males to such blends.

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We have discovered a type of sensillum on the antennae of male corn earworm moths, *Helicoverpa zea* (Boddie), that houses both the agonistic and antagonistic types of receptor neurons (RN) that explain both the upwind flight attraction of males to their own species' pheromone blend and arrestment to the quite similar blends emitted by females of three other sympatric North American heliothine species.¹ The first RN type in this sensillum is a large-spiking neuron that is sensitive to (*Z*)-9-hexadecenal (Z9-16:Ald), the secondary *H. zea* pheromone component that along with the major component, (*Z*)-11-hexadecenal (Z11-16:Ald), causes attraction to the female.² This RN is also responsive to (*Z*)-9-tetradecenal (Z9-14:Ald; not a *H. zea* pheromone component) at higher dosages. The sensitivity of this RN thus explains the attraction of *H. zea* males that has been observed in other studies when small proportions of Z9-14:Ald are added to Z11-16:Ald to mimic the conspecific blend.³ Approximately 20% of the 325 sensilla that we sampled on *H. zea* antennae were of this type. Another 70% of the sampled sensilla contained a RN tuned only to the major component, Z11-16:Ald.¹

The second type of RN in this sensillum is a small-spiking neuron that is again responsive to Z9-14:Ald, which in larger proportions acts as a strong antagonist to upwind flight,³ but this RN is actually more sensitive to two other strong behavioral antagonists, (*Z*)-11-hexadecenyl acetate (Z11-16:Ac)⁴ and (*Z*)-11-hexadecen-1-ol (Z11-16:OH). Thus, activation of this single broadly-tuned 'antagonist' RN could explain why *H. zea* males will orient only to their conspecific females. These three compounds are emitted by females of three other North American species, *H. subflexa*, *H. phloxiphaga*, and *H. virescens*, as pheromone components (agonists) in their blends, and these females also emit the *H. zea* pheromone components, Z11-16:Ald and Z9-16:Ald. This antagonist RN may also explain why a blend of Z11-16:Ald and a small amount of Z9-14:Ald is never as attractive to *H. zea* males as the conspecific blend. Enhanced specificity for the conspecific blend arises because the antagonist RN is never stimulated to fire by Z9-16:Ald, only the agonist neuron is, even when large proportions of this pheromone component are added to Z11-16:Ald. However, when Z9-14:Ald is used instead of Z9-16:Ald and the proportion of Z9-14:Ald becomes too great, the threshold of the antagonist RN is exceeded, and the upwind flight response begins to be suppressed by the firing of this neuron.³

It is interesting that both the agonist and antagonist types of RNs in *H. zea* are more broadly tuned, *i.e.*, are more accepting of, a wider range of compounds than is usually the case in moth sex pheromone communication systems. Indeed, following quantitative measurements we made of the amounts of these compounds actually emitted from the odor cartridges used for stimulation in this study, we found that the agonist-sensitive RN is *equally* responsive to Z9-14:Ald (a non-pheromone component) and Z9-16:Ald, a rare occurrence for a pheromone-component-tuned RN. The agonist-sensitive RN was found to be tuned with a slightly lower threshold to Z11-16:Ac, with nearly equal sensitivity to Z11-16:OH. This RN's threshold for Z9-14:Ald was significantly higher, but the amounts of this compound emitted by *H. virescens* in its blend are also higher, so that even the lower sensitivity should be sufficient for this *H. zea* RN to respond to this compound found in *H. virescens* emissions.

Such flexibility in response by both the agonist- and antagonist-sensitive RNs could create the potential for interesting shifts in blend discrimination by males. These neurons may therefore have been one of the ways in which reproductive character displacement in pheromone blends could have occurred, for instance, in *H. zea* as an adaptive response to the presence of *H. virescens*. Other examples of broadly tuned, more flexible, receptor systems can be seen, for instance, in moths such as *Yponomeuta rorellus* as an apparent adaptive reproductive character displacement in the presence of other sympatric and synchronic *Yponomeuta* species.⁵ In *Y. rorellus*, both a broadly tuned agonist-sensitive type of RN as well as antagonist-sensitive RNs are present. The

presence of such accommodating pheromone component receptors on male antennae may fortuitously create the opportunity for mutations in the female-emitted blend to be accepted by males and the mutation to be carried along in the population without the need for a simultaneous, complementary, component-specific mutation to occur in the receptor system in the male population.

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