Proc. Natl. Acad. Sci. USA
Vol. 85, pp. 9826–9830, December 1988
Neurobiology

Adaptation of antennal neurons in moths is associated with cessation of pheromone-mediated upwind flight

(olfaction/pheromone plume/sensory adaptation/intermittent stimulation/odor quality)

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Communicated by Wendell Roelofs, September 8, 1988 (received for review April 18, 1988)

ABSTRACT **A wind-borne plume of sex pheromone from a female moth or a synthetic source has a fine, filamentous structure that creates steep and rapid fluctuations in concentration for a male moth flying up the plume's axis. The firing rates from single antennal neurons on *Agrotis segetum* antennae decreased to nearly zero within seconds after the antennae were placed in a pheromone plume 70 cm downwind of a high-concentration source known from previous studies to cause in-flight arrestment of upwind progress. In a separate experiment, the fluctuating output from chilled neurons on *Grapholita molesta* antennae became attenuated in response to repetitive, experimentally delivered pheromone pulses. The attenuation was correlated with a previously reported higher percentage of in-flight arrestment exhibited by moths flying at cooler compared to warmer temperatures. These results indicate that two peripheral processes related to excessive concentration, complete adaptation of antennal neurons, or merely the attenuation of fluctuations in burst frequency, are important determinants of when upwind progress by a moth flying in a pheromone plume stops and changes to station keeping. Also, adaptation and attenuation may affect the sensation of blend quality by preferentially affecting cells sensitive to the most abundant components in airborne pheromone blends.**

The requirement for intermittent odor stimulation in sustaining behavior has emerged as an important principle in animal olfaction, from spiny lobsters to moths (1–3). Even though researchers have long been aware of the broken, filamentous fine structure of airborne pheromone plumes (4, 5), it is only recently that the importance of a plume's fine structure in evoking sustained upwind flight in moths has been demonstrated (1, 2). It has been speculated that as male moths fly upwind in a pheromone plume, sensory adaptation of their receptors or habituation of sensory pathways may be significant factors in their success in locating a female (6, 7). There has, however, been no direct neurophysiological evidence that either mechanism can occur and interfere with flight in plumes or clouds of pheromone, because few cellular recordings have been performed that utilize the kinds of rapidly fluctuating exposure to pheromone that occurs when the moth is in a wind-borne plume (8–10). More importantly, no studies have correlated neuronal output from such stimulation with upwind flight. Recently, we found that electroantennogram peak-to-trough amplitudes became attenuated only when the antennae were placed in the same excessively concentrated plumes that caused upwind flight progress to cease and change to in-flight station keeping (arrestment) (11). The relationship between electroantennogram depolarizations and action potentials from individual neurons is often unclear, however, and whether such a diminution in summed receptor potentials reflects a concomitant attenuation of fluctuating action potential frequencies is arguable.

Some neurophysiological studies that have used rapidly pulsed pheromone stimulation have focused on whether or not the sensory cells can track the tempo of each arriving pulse by responding with any action potentials whatsoever and have not emphasized the reduction in frequency of action potentials in each burst (8). Others have noted such attenuation of bursts from rapidly arriving pulses but have failed to explain its behavioral significance (8, 9). An important recent study has revealed how some higher-order neurons are designed to preserve and even accentuate fluctuating input from the antennal neurons (10). Although a link to behavior was not directly established, this work underscores the importance that insects' pheromone-processing systems place on fluctuating stimulation.

Adaptation or habituation have been suspected as causes of in-flight arrestment of upwind progress in moths entering clouds of uniform pheromone (1). Arrestment of upwind progress also is known to occur in plumes from point sources that emit excessive amounts of the correct blend of components or incorrect ratios of components at proper emission rates (12, 13). Suboptimal blends and excessive emission rates may be emitted by nonconspecific females and encountered in natural settings by male moths, and arrestment of upwind progress would prevent males from making interspecific mating mistakes. Cessation of upwind progress also occurs naturally during flight to a conspecific female when sudden shifts in wind direction cause the male to lose the plume and fly into clean air (14, 15). The station keeping and wide tracks during casting allow the male to eventually relocate the plume and continue upwind.

To gain further insight into the relationship between receptor output and the change from upwind flight to arrestment, we recently recorded from the single antennal neurons of two species of moths and challenged the neurons with rapid pulses of pheromone under temperature and concentration conditions that either do, or do not, cause in-flight arrestment. For one species we placed the single-cell neuronal preparation directly into the pheromone plume itself and recorded the responses of individual neurons as they might fire during flight in a plume.

MATERIALS AND METHODS

All neuronal recordings were made extracellularly by the cut-sensillum technique of Kaissling (17, 18). An antenna was excised from the head, and the antennal base was placed in a saline-filled pipet ground electrode. The usable lifetime of such preparations routinely is 1 hr or more for larger sensilla, although 10–20 min is average for smaller sensilla, such as from *Grapholita molesta* (Busck), which was used in this study. The tip of a sensillum trichodeum was cut with a glass knife and then contacted with a saline-filled pipet recording electrode. Neuro-

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Abbreviation: CNS, central nervous system.

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nal responses were recorded in both ac and dc. Male antennae from two species were used, *Agrotis segetum* (Schiff) and *G. molesta*. For all neuronal responses, a complete blend of the pheromone components active in evoking complete upwind flight to the source by males of each species was always used. For *A. segetum* the blend was a 0.6:1:5:2.5 ratio of decenyl acetate/(*Z*)-5-decenyl acetate/(*Z*)-7-dodecenyl acetate/(*Z*)-9-tetradecenyl acetate, respectively (19). Serial dilutions were made in hexane such that 0.3, 3, 30, and 300 μg of (*Z*)-5-decenyl acetate were applied to rubber septum dispensers. The first three dosages were all known to promote sustained upwind flight to the source, whereas the 300-μg loading had been shown to be excessive, causing cessation of upwind flight in nearly 100% of the males that had begun upwind flight farther downwind in a flight tunnel. The blend for *G. molesta* was the natural pheromone blend ratio, 6% (*E*)-8-dodecenyl acetate and 3% (*Z*)-8-dodecenyl alcohol (20) in 1 μg of (*Z*)-8-dodecenyl acetate (21) on filter paper.

For *A. segetum*, recordings of single antennal neurons while in a pheromone plume were performed by placing the antennal preparation 70 cm downwind of the pheromone source at the end of a small wind tunnel (80 cm long × 20 cm i.d.). Wind was generated at 0.5 m/s in the tunnel at 22°C. When the sensillar preparation was ready, the specificity of the neurons in that sensillum for a particular component was determined by applying puffs from cartridges containing 1 μg of a single component. The preparation was then positioned 10 cm from the end of the tunnel. A rubber septum containing the lowest dosage of pheromone was then placed on a wire and inserted into a small hole 70 cm upwind of the antenna. A point source of smoke had indicated that the plume structure and time-averaged diameter appeared similar to those commonly observed in larger wind tunnels. Through preliminary experimentation, the best alignment of the septum with the antenna for optimal receptor activity was found. The response of the neuron while in the plume was recorded for ≈20 s, and the source was then removed and replaced with the next-higher dosage following a 30-s period of clean air. This process was repeated until the antenna had been exposed to the highest concentration. The tip of a new sensillum on the same antenna was then cut, and the neuron was recorded in the same fashion. No more than two sensilla were recorded from on the same antenna. Recordings were made from cells responsive to either (*Z*)-5-decenyl acetate or to (*Z*)-7-dodecenyl acetate.

For *G. molesta*, experimentally generated 20-ms pulses of pheromone were delivered to either slightly chilled or room temperature antennal preparations with a specially designed apparatus. The 1 μg of pheromone was on a strip of filter paper (2 cm long × 0.5 mm wide) placed at the very end of the constricted tip of a disposable 10-ml syringe, 2 mm from its 1-mm (i.d.) opening, similar to the technique of Kaissling (8). Puffs of air were generated through the pipet by activating a loudspeaker having a 13-cm-diameter diaphragm. The loudspeaker's electromagnet was set for a single on–off of 20 ms every time the operator pressed a button. The desired tempo was determined by an electronic timer generating a tone. The airspace downstream of the large diaphragm was connected via Teflon tubing to a second much smaller diaphragm configured as a flaccid cap of ultrathin latex and covering the wide end of the syringe lumen. Activation of the loudspeaker magnet caused a pressure pulse to deform the latex membrane on the syringe, resulting in a small puff of air passing over the pheromone wick situated at the very tip. The pheromone-laden puffs issued at a right angle from the tip of the pipet into the 2-mm opening of a 1-cm (i.d.) glass tube through which air was flowing at 0.5 m/s over the antennal preparation set up 20 cm downstream of the pipet tip. Cooling of an airstream continuously flowing over the antenna, from 23°C to 17°C, was accomplished in ≈1 min by placing a small piece of dry ice on top of the glass tube 10 cm from its tip. A small thermocouple monitored the temperature decline. The airstream was thus chilled without changing the temperature of the pheromone source or the air in the pulser. The airstream was warmed in 1 min by removing the dry ice and warming the chilled portion of the glass tube by covering it with the hand. Data were obtained and analyzed for eight (*Z*)-8-dodecenyl acetate-sensitive cells, four of which were chilled first, then warmed, and four of which were warmed first, then chilled.

RESULTS

In a previous study, *A. segetum* males were shown to exhibit upwind flight all the way to rubber dispenser sources containing moderate pheromone dosages (3–30 μg) but terminated upwind flight in the plume if the dosage was 300 μg (19). When we exposed single (*Z*)-5-decenyl acetate-sensitive neurons to such plumes 70 cm downwind of the source, they maintained their levels of bursting with the arrival of each pheromone filament for over 20 s to the 0.3-, 3-, and 30-μg dosages but adapted within 3–5 s to the 300-μg plume (Figs. 1 and 2). Our working definition of adaptation in these plumes is a >95% reduction in action potential frequency from the first 1-s period of action potential bursting to subsequent 1-s intervals. Not all of the cells became adapted to filaments from the 300-μg source, but the majority (30 of 32 cells) did adapt. The adaptation was marked by a rapid decline in spike amplitude as well as frequency. The cells recovered after a few minutes of clean air but rapidly adapted again when the

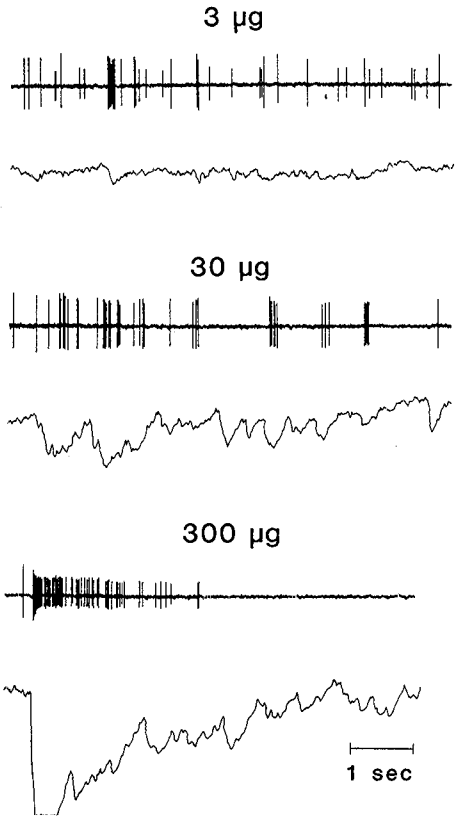

FIG. 1. Action potentials (top traces) and simultaneously recorded dc potentials (bottom traces) of a (*Z*)-5-decenyl acetate-sensitive neuron (large spikes) on a male *A. segetum* antenna during the first few seconds of exposure after being placed 70 cm downwind of a rubber septum containing 3, 30, or 300 μg of the sex pheromone blend [dosage refers to (*Z*)-5-decenyl acetate portion of blend]. Small spikes in the 3-μg recording are the background firing level of a second neuron, which eventually subsided. Note adaptation of the cell in the 300-μg plume.

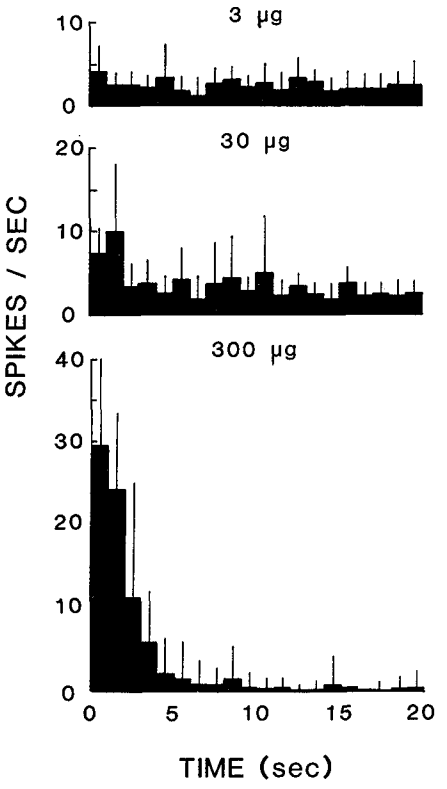

FIG. 2. Mean action potential frequencies of antennal neurons of *A. segetum* sensitive to (*Z*)-5-decenyl acetate ($n = 32$) during the first 20 s after being placed directly into a pheromone plume, 70 cm downwind from sources of various dosages. The first bursts of action potentials in the first few seconds of exposure to the plume were of the highest frequency in response to 300 μg of pheromone, but the neurons adapted quickly. This is a dosage that results in nearly 100% arrestment of upwind flight (19). Vertical lines denote SD.

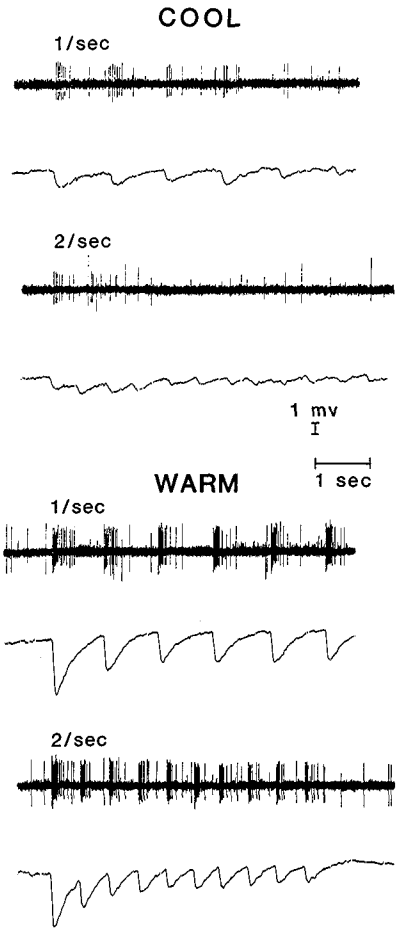

FIG. 3. Action potentials and simultaneously recorded dc potentials (downward-going sawtoothed lines) from a (*Z*)-8-dodecenyl acetate-sensitive cell on the antenna of *G. molesta* in response to pulses of the pheromone blend loaded at 1 μg of (*Z*)-8-dodecenyl acetate on filter paper. The pulses were experimentally delivered at rates varying from 1 per 2 s to 4 per s, but only the 1 and 2 per s rates are shown. The cell was challenged with pulses beginning when it was cool (17°C), and then after the last pulse rate of 4 per s was tested, the cell was warmed and challenged at 23°C (warm).

300-μg source was reintroduced. Also of interest is that only 5 of 12 cells sensitive to a second component, (*Z*)-7-dodecenyl acetate, became adapted in this same plume. This leads to the possibility that arrestment in this species is due not only to antennal neurons adapting and sending a false signal of reduced ambient concentration to the central nervous system (CNS), but in addition, the signal sent to the CNS might now be erroneous in terms of the blend ratio that is actually present.

Neurons on *G. molesta* male antennae sensitive to (*Z*)-8-dodecenyl acetate responded at 23°C with bursts of action potentials that corresponded to the pulse rate of pheromone delivered at up to three pulses per s (Figs. 3 and 4). Also, at 23°C, following the first pulse for any single tempo of stimulation, the peak frequency of action potentials in each burst remained relatively constant over time. In contrast, bursts of action potentials from cells cooled for 1 min by a 17°C airstream became attenuated in response to rates of 2 pulses per s or faster (Figs. 3 and 4). During upwind flight, *G. molesta* antennae will encounter pheromone filaments at a frequency of 0.5–2/s, on average, but multiple bursts of 3 or 4/s commonly occur (15). The attenuation of peak-to-trough frequency of spikes to each pulse occurred within 1–2 s after the first pulse.

A previous study had demonstrated that a 6°C decrease in temperature from 26°C to 20°C causes a significant narrowing of the spectrum of blends and dosages that will evoke sustained upwind flight to the source by free-flying *G. molesta* males (22). When males do become arrested, the time course from the beginning of upwind flight in the plume until arrestment is often <5 s, or about the same as that of the observed adaptation of receptors. The narrowing of upwind flight responses at the lower temperature is characterized by a lower tolerance of males for even moderately high emission rates, to which they now become arrested when they would not have at the higher temperature. Interestingly, under the cool conditions and higher emission rates there is also a shift in the specificity of male responses to blends, in which males will now not tolerate blends with the natural proportion, or higher, of (*E*)-8-dodecenyl acetate. They become arrested before reaching the source. Blends with an unusually low proportion of this component, however, continue to evoke sustained flight to the source at higher concentrations, until at the highest emission rates even they evoke arrestment (22). Such a shift is consistent with a possible differential attenuation of fluctuating output from chilled (*Z*)-8-dodecenyl acetate-sensitive neurons compared to (*E*)-8-dodecenyl acetate-sensitive neurons.

The attenuation of frequency modulation due to cooling appears to be linked to a rate-sensitive mechanism in the sensilla. The average slopes of the dc-coupled potentials' onsets and recoveries were shallower at the cooler compared to the warmer temperatures, and this was even more pronounced at the higher frequencies of pulsed pheromone, in response to which the dc potential could not recover to baseline with each pulse (Figs. 3 and 4). Thus, the neurons from cooler antennae exhibited more severely diminished

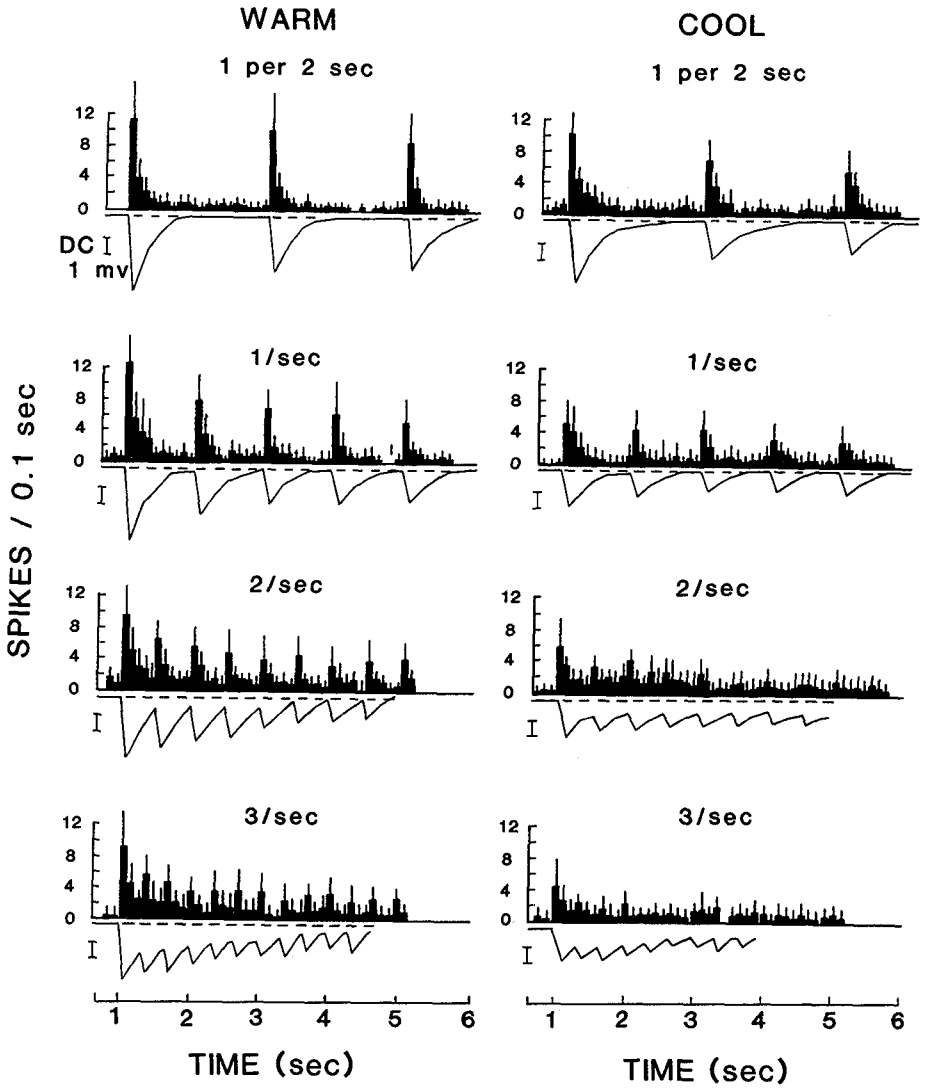

FIG. 4. Mean action potential frequencies (bars) and means of simultaneously recorded dc-coupled responses (downward-going sawtoothed lines) of antennal neurons from *G. molesta* challenged with pheromone pulses at rates varying from 1 per 2 s to 3 per s at 23°C (warm) and 17°C (cool). Responses, including the slopes of every onset and 0.2-s recovery interval of every dc-coupled depolarization, are the mean of eight neurons. In the cool condition, note how the shallower slopes of dc onsets and recoveries are correlated with lower peak-to-trough dc amplitudes and reduced action potential frequencies in response to each pulse, especially at the higher pulse frequencies. At the higher pulse rates, after several seconds, the peak/noise ratio in the dc tracings became too low to allow reliable measurement. Vertical lines denote SD.

peak-to-trough amplitudes of dc depolarizations at slower tempos of exposures to pheromone pulses than did neurons from warmer antennae (Figs. 3 and 4). The rate-sensitive nature of the response might be due not only to temperature-related retardation of spike generation and disadaptation, among other phenomena (23, 24), but also to a retardation of various nonreceptor cell events including cuticular adsorption and migration through pore tubules, transport to the receptors through the proteinaceous sensillum liquor, and clearing of the pheromone, including degradative metabolism of pheromone molecules (17, 25).

DISCUSSION

We have reported at least two types of changes in receptor output that may be responsible for cessation of upwind flight in moths. One we are calling attenuation, a kind of partial adaptation (8, 9) in which the overall fluctuations in action potential frequencies from the antennal neurons would become insufficient to sustain upwind flight. The frequency of firing would not go to zero but would merely become too continuous to stimulate certain CNS interneurons, which respond to changes in stimulation (26, 27). This may be what happens in uniform clouds of pheromone. A second change in receptor output is adaptation, in which the firing frequency would go to zero.

These findings directly implicate the peripheral olfactory system's ability to handle fluctuating input as a key initial promoter of sustained upwind flight. They also offer a specific explanation as to how the processing of odor quality and quantity could be intimately intertwined; two different component-specific receptors may adapt, or their output become attenuated, at different rates when in the same excessively concentrated pheromone plume. Both the partial and complete adaptation that we observed appear to be related to high concentrations, and there is often great disparity in the abundance of major and minor pheromone components in airborne pheromone blends. This disparity would promote the differential adaptation of receptors specific for the major component in a blend when the total blend concentration is high. The ratio of action potentials from cells specific for major and minor components now would be different from their ratio to a lower, optimal concentration of the same blend. Two different concentrations, one excessive, thus might evoke significantly different sensations of odor quality.

A previous report (9) had proposed that differences in the disadaptation rates of cells specific for different pheromone components might account for successful orientation to the source by males. One feature of this model had focused on the disadaptation rates of cells over intervals of exposure much longer than the ones described in our present study, on the order of minutes. Another feature took into account slight differences in the fine structure of plumes at different distances and invoked a hierarchical succession of firing of different cell types at different distances, based on their different concentration thresholds and disadaptation rates.

One problem with this model is that it fails to take into account that such distance-encoding information is unnecessary in the normal orientation behavior of male moths. Moths steer with respect to the wind, not chemicals (28, 29). Their pheromone-activated optomotor anemotactic system, however, does need to be reiteratively triggered by rapid fluctuations in concentration such that upwind progress is sustained long enough so that the source is reached (15). It is thus imperative that sensory cells retain their competence to respond repeatedly and faithfully to such fluctuations to sustain such progress. Another problem with this model is that in invoking a hierarchical succession of cells acting at different distances (9), it fails to take into account the fact that the behavioral evidence thus far supports the hypothesis that the complete blend of pheromone components is the optimal stimulus at all distances (30, 31). Different components do not seem to have different roles in upwind flight at different distances. Third, our data showing relatively low firing rates of antennal neurons in plumes of optimal concentration for upwind flight suggest that traditional concentrations delivered to antennal neurons for single-cell recordings have often exceeded behaviorally optimal levels. Thus, the adaptation in response to successive pulses that was previously conjectured to aid in source location (9) may thus turn out to be correlated more with the cessation of upwind progress in excessively concentrated plumes.

Therefore, in contrast to the above model (9), our results suggest a direct link between sensory adaptation and the failure to reach the source, one aspect of that being that adaptation may incorrectly change the across-fiber ratio of input to the CNS and erroneously signal a wrong blend, when in fact the real ratio of components in the plume has never changed. It is possible that the CNS could adjust its sensitivity to the reduced input along a component-specific pathway and thus create an adequate signal despite severe receptor adaptation. But the fact that the adaptation and attenuation seen at the periphery are associated with a failure to sustain upwind flight in two species suggests that such CNS compensation, if occurring, is not sufficient to improve the signal's intermittency or across-fiber ratio at these concentrations and temperatures. In fact, some deutocerebral pathways in moths depend on a blend of the correct quality for accentuating signal intermittency. The onset and offset of each pheromone pulse are highlighted by the integration of nearly simultaneously arriving inhibitory and excitatory input from antennal neurons (10). Thus, adaptation that interferes with blend quality may also interfere with the intermittency needed by some CNS circuits.

We do not think that all antennal sensilla necessarily have identical reactions to temporal stimuli. Our sampling of cells was not extensive enough to allow us to make statements about the proportions of cells that do, or do not, optimally send frequency-modulated signals to the CNS. Recent studies have indicated that there is a variety of signal-processing pathways in the CNS of *Manduca* (10) and *Heliothis* (T. A. Christensen, H. Mustaparta, and J. G. Hildebrand, personal communication). Some deutocerebral cells fire intermittently in response to blends presented intermittently, and others fire continuously in response to single components whether they are pulsed or not. Nevertheless, in our study there was a high correspondence between antennal neuronal output and the behavior, which suggests that the output of neurons from which we were recording is important to behavior, regardless of what their final proportion in the antennal population turns out to be. It is logical, however, to expect that similar blend-sensitive enhancers of pheromone fluctuations (10) will be present in the CNS of the species we worked with. In this case, the ability of sensory pathways, beginning with the antennal neurons, to continue to send fluctuating output to higher centers, will depend among other things on the plume's physical structure, the concentration of filaments in the plume, the moth's airspeed, and the temperature of the antennal sensilla, as well as on the emitted blend ratio of components.

We thank J. Jönsson for constructing the puffing apparatus and the small wind tunnel; R. Vetter for drawing the figures and rearing *G. molesta*; and Eva Annerfeldt, Carolina Berglund, and Ann Sophie Naumman for rearing *A. segetum*. This work was supported by National Science Foundation Grant BNS 8310980 (to T.C.B.) and grants from the Swedish Natural Resources Council to J.L., C.L., and T.C.B.

1. Kennedy, J. S., Ludlow, A. R. & Sanders, C. J. (1981) *Physiol. Entomol.* **6,** 395–412.
2. Baker, T. C., Willis, M. A., Haynes, K. F. & Phelan, P. L. (1985) *Physiol. Entomol.* **10,** 257–265.
3. Schmitt, B. C. & Ache, B. W. (1979) *Science* **205,** 204–206.
4. Wright, R. H. (1958) *Can. Entomol.* **90,** 81–89.
5. Murlis, J. & Jones, C. D. (1981) *Physiol. Entomol.* **6,** 71–86.
6. Shorey, H. H. (1970) in *Control of Insect Behavior by Natural Products*, eds. Wood, D. L., Silverstein, R. M. & Nakajima, M. (Academic, London), pp. 249–284.
7. Bartell, R. J. (1977) in *Chemical Control of Insect Behavior, Theory and Application*, eds. Shorey, H. H. & McKelvey, J. J. (Wiley-Interscience, New York), pp. 201–213.
8. Kaissling, K.-E. (1986) in *Mechanisms in Insect Olfaction*, eds. Payne, T. L., Birch, M. C. & Kennedy, C. E. J. (Clarendon, Oxford), pp. 193–199.
9. Rumbo, E. R. (1983) *Physiol. Entomol.* **8,** 195–201.
10. Christensen, T. A. & Hildebrand, J. G. (1988) *Chem. Senses* **13,** 123–130.
11. Baker, T. C. & Haynes, K. F. *Physiol. Entomol.*, in press.
12. Willis, M. A. & Baker, T. C. (1988) *J. Ins. Behav.*, in press.
13. Linn, C. E., Jr., & Roelofs, W. L. (1983) *Physiol. Entomol.* **8,** 291–306.
14. David, C. T., Kennedy, J. S. & Ludlow, A. R. (1983) *Nature (London)* **303,** 804–806.
15. Baker, T. C. & Haynes, K. F. (1988) *Physiol. Entomol.* **12,** 263–279.
16. Baker, T. C. & Cardé, R. T. (1979) *Environ. Entomol.* **8,** 956–968.
17. Kaissling, K. E. (1974) in *Biochemistry of Sensory Functions*, ed. Jaenicke, L. (Springer, Berlin), pp. 243–273.
18. Van der Pers, J. N. C. & Den Otter, C. J. (1978) *J. Ins. Physiol.* **24,** 337–343.
19. Löfstedt, C., Linn, C. E., Jr., & Löfqvist, J. (1985) *J. Chem. Ecol.* **11,** 1209–1221.
20. Cardé, A. M., Baker, T. C. & Cardé, R. T. (1979) *J. Chem. Ecol.* **5,** 423–427.
21. Roelofs, W. L., Comeau, A. & Selle, R. (1969) *Nature (London)* **224,** 723.
22. Linn, C. E., Jr., Campbell, M. G. & Roelofs, W. L. (1988) *Physiol. Entomol.* **13,** 59–67.
23. Hatt, H. (1983) *J. Comp. Physiol. A* **152,** 395–403.
24. Hatt, H. (1983) *J. Comp. Physiol. A* **152,** 405–409.
25. Vogt, R. G. & Riddiford, L. M. (1986) in *Mechanisms in Insect Olfaction*, eds. Payne, T. L., Birch, M. C. & Kennedy, C. E. J. (Clarendon, Oxford), pp. 201–208.
26. Baker, T. C. (1985) in *Comprehensive Insect Physiology, Biochemistry, and Pharmacology*, eds. Kerkut, G. A. & Gilbert, L. S. (Pergamon, Oxford), Vol. 9, pp. 621–672.
27. Olberg, R. M. (1983) *J. Comp. Physiol.* **152,** 297–307.
28. Kennedy, J. S. (1983) *Physiol. Entomol.* **8,** 109–120.
29. Baker, T. C. (1988) in *Insect Flight*, eds. Goldsworthy, G. G. & Blaney, W. (CRC, Boca Raton, FL), in press.
30. Baker, T. C. & Cardé, R. T. (1979) *Environ. Entomol.* **8,** 956–968.
31. Linn, C. E., Jr., Campbell, M. G. & Roelofs, W. L. (1988) *Science* **237,** 650–652.