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Chemo-anemotaxis: A behavioral response to sex pheromone in nonflying insects

(search behavior/locomotion/orientation/air currents/cockroach biocontrol)

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ABSTRACT **The cockroach, *Periplaneta americana*, running on a Y-ring globe, moves downwind if an air current is directed toward the head. However, if the air current carries sex pheromone, then upwind movement is elicited. This orientation behavior is apparently a mechanism to facilitate the orientation of males searching for pheromone-secreting females.**

Sex pheromones of some flying insects are well known to result in the male taking flight and flying upwind. Orientation in flight must require a complex integration of sensory information from various sources, including the eyes, setae, and antennae. For example, there is no way that the insect could distinguish upwind from downwind flight without input from the eyes unless the insect stops periodically and tests the wind direction. The discovery that the American cockroach, on the substratum, is stimulated by the female sex pheromone to walk and to move upwind in an air current that carries the sex pheromone makes available for study and analysis a much simpler case of upwind orientation than that described for flying insects.

Investigations of lepidopteran (1) and dipteran (2) orientation indicate that males repond to female sex pheromone by turning upwind (anemotaxis), thereby flying toward the pheromone source. Although upwind orientation is stimulated by sex pheromone, the pheromone itself does not provide spatial information. Shorey (3) observed that several species of moths orient upwind only when sex pheromone is present, and also suggested that chemotaxis may be used by male moths seeking a pheromone-secreting female (4). Little attention has been given to the potential repertoire of mechanisms involved in chemo-orientation of wingless or predominately nonflying insects that secrete volatile pheromones, aside from research on chemotaxis in trail-following in ants where the trail pheromone is deposited on the substratum (5) and research on bees tested in Y-tubes (6). Our studies with the American cockroach, *Periplaneta americana*, indicate that (i) males move upwind only when female sex pheromone is present in an air current, and (ii) increased locomotor activity of males in response to female sex pheromone is independent of the directional orientation mechanism.

Adult males respond to sex pheromone of the females with increased locomotor activity and courting displays (7). Our previous studies showed that, in still air, males orient towards a pheromone source at a distance of 20 cm, using true chemotaxis (8).

To test upwind orientation stimulated by sex pheromone, we constructed a Y-ring globe (5 cm diameter) similar to the design of Hassenstein (9) from a hollow styrofoam sphere. An adult male was secured dorsally to a wooden applicator stick which was clamped to a ring stand. This permitted the cockroach to freely carry a Y-ring globe. The Y-ring globe is an open loop system; the male cannot change its position relative to the directional source of air or sex pheromone but at each intersection he must turn 60° to the left or to the right as illustrated in Fig. 1. This design ensures positional consistency of the male to the air source and pheromone that is necessary to control informational input about the direction and strength of the stimuli. An air current (270 cm^3/min), dried over anhydrous calcium sulfate and filtered through glass wool, was directed 90° to the left or right 10 cm from the male's head from a tube 1 mm in diameter. Sex pheromone (5 μl or 0.63 mg) introduced into the air stream was obtained through preparative extraction techniques and column chromatography (8). Each male served as its own control, and for each experimental procedure the number of left and right turns and the time required for 20 males to complete 800 turns (400 control, 400 experimental) of the Y-ring globe was visually recorded. The data were analyzed by the Wilcoxon sign-rank test. All experiments were conducted in a dark chamber illuminated by Ruby photographic lamps, a light source not visible to cockroaches.

First, each male was exposed to still air and then to an air current; the response of each individual was recorded for 400 turns in still air and then 400 turns with air current. The males moved away from the air current ($P < 0.005$), and their locomotor activity in the air current increased 21% over 31.4 m ($P < 0.005$).

Second, males were exposed to an air current followed by an air current containing sex pheromone and the response of each individual was recorded as above. Males exhibited a significant turning tendency toward the air current containing sex pheromone as compared to turning tendency in clean air current ($P \leq 0.005$). Sex pheromone in an air current increased locomotor rate 37% as compared to movement in a clean air current ($P < 0.005$).

Third, males were exposed to a clean air current followed by a 1-min pulse of sex pheromone in still air. They were then reexposed to clean air current. Responses of individual males were recorded as above. When performances before and after pheromone exposure were compared, there was no significant change in turning tendency, i.e., turns continued to be away from the air current. Locomotor activity increased 35% ($P < 0.005$) after exposure to sex pheromone.

We conclude that sex pheromone releases chemo-anemotaxis, in that stimulatory air currents must contain pheromone; positive anemotaxis alone implies that pheromone perception leads to upwind orientation regardless of whether or not the air current continuously carries pheromone. Running activity is independent from the mechanism of directional orientation, since males exposed to sex pheromone in still air and then to an air current exhibited increased locomotion but did not move toward the air current. A similar phenomenon was reported by Schwinck (10, 11) in experiments with walking moths. In-

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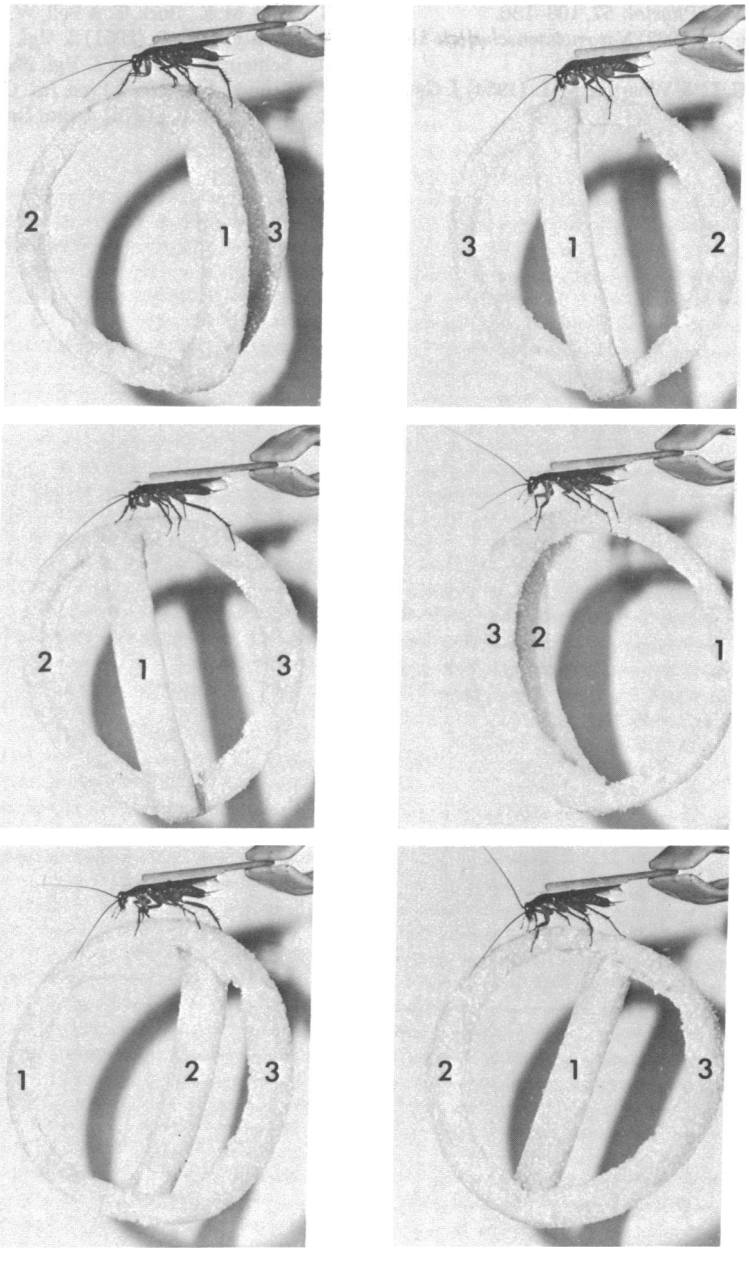

FIG. 1. Execution of left turn on a Y-ring globe (left photos, top to bottom) and right turn (right photos, top to bottom). Cockroach is cemented to a wooden applicator stick held by a clamp. Numbers on arms of the globe indicate turning motion.

creasing locomotor activity in cockroaches is probably related to "local searching," which may be an intrinsic response for locating a moving female target several meters from the searching male (12).

In moths, when sex pheromone was removed from air currents in a wind tunnel, zig-zag search patterns were observed perpendicular to the air current (10). Anemotaxis must operate for the moth to retain a fixed orientation relative to the air current; thus, the decrease in sex pheromone apparently stimulated "local search" expressed as zig-zag flight patterns (1). The cockroach, *P. americana*, which does not fly but only glides short distances, uses chemo-anemotaxis in response to air carrying sex pheromone. The term chemo-anemotaxis is appropriate because neither chemotaxis nor anemotaxis alone characterizes the behavior observed. We have preliminary evidence suggesting that cockroaches tack across wind, as do moths, when the air current no longer transmits pheromone, and this may be the mechanism by which males relocate an air current that carries sex pheromone. We submit that an air current carrying sex pheromone may be a practical method to lure cockroaches to traps or electrocution devices in large urban infestations.

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