1990

Proceedings of the Tenth International Symposium on Olfaction and Taste.
Doving, K. B. (ed.) Graphic Communication System A/S, OSLO pp. 18 - 25.

UPWIND FLIGHT AND CASTING FLIGHT: COMPLIMENTARY PHASIC AND TONIC SYSTEMS USED FOR LOCATION OF SEX PHEROMONE SOURCES BY MALE MOTHS

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A. Maneuvers Used in Pheromone-Mediated Flight

It is important to fully understand the means by which flying male moths locate sources of sex pheromone. In doing so we will likely gain insight into insect olfactory mediated flight behavior of all types, including female flight in response to volatiles from host plants (Haynes and Baker 1989) or parasitoid female responses to host insect volatiles. There are significant similarities between female responses to host odors and male responses to sex pheromone (Schneiderman et al. 1983, Haynes and Baker 1989). The challenges facing flying insects trying to progress toward all sorts of different odor sources are very similar, as will be the insects' solutions to them. Importantly, without knowledge of the behavior involved in such orientation, the neurophysiological mechanisms of olfaction will remain unknown due to our inability to relate the patterns of neuronal activity to any relevant behavior.

In order to locate a source of sex pheromone a male moth must control its direction and speed of displacement in a moving medium, the wind, and because wind is the movement of air in the horizontal plane the male has only two reactions available at any instant to effect such control: change his course angle (the direction towards which it is thrusting, relative to the wind line) and change his airspeed (the speed through the air mass next to his body) (Marsh et al. 1978). The two main mechanisms known to be used for pheromone source location by flying moths, *optomotor anemotaxis* (steering with respect to the wind) and *self-steered counterturning* (Baker and Kuenen 1982, Kuenen and Baker 1983, Kennedy 1983, Baker 1986, Kennedy 1986), both rely on these two behavioral reactions. The direction of thrust (steering) can be changed by either yawing or rolling the body, the importance of the latter having only recently been emphasized (Willis and Baker 1987, David and Kennedy 1987, Baker 1989a,b). The amount of thrust can be changed either by a change in total wing force (e.g., wing-beat frequency) or by a change in the angle of the body relative to the ground (pitch angle) (David 1986). The changes in the strength and direction of the wing force in the horizontal plane are inextricably linked to changes in lift (hence altitude) that are also under visual feedback control (David 1986). Altitude is also controlled by pheromone-stimulated moths (Preiss and Kramer 1983), and thus places restrictions on the movements that are be made in the horizontal plane because of the interplay between lift and thrust (David 1986).

There is no evidence at this point that moths use chemotaxis, or steering with respect to a gradient, either alone or integrated with other mechanisms, in order to locate a pheromone source, although longitudinal and lateral gradients in a plume of pheromone do exist, averaged over a long time or a very short time (Baker 1989a). The resultant tracks always will bear some orderly relationship to the long-time-averaged gradients, but it is important to realize that in order to reach the source of pheromone, a male moth <u>always</u> has to progress up such a gradient into increasingly higher zones of concentration. Whether or not he steers according to the information provided by this longitudinal gradient is another matter entirely. Stating that a moth flies up a gradient to reach the source is no more helpful concerning understanding the orientation mechanisms involved than in stating that he flies upwind to reach the source. A moth <u>must</u> do both in order to get there, but investigations have shown that he steers only with respect to the wind (Kennedy and Marsh 1974, Marsh et al. 1978).

In optomotor anemotaxis, feedback for the control of these reactions is derived visually from the apparent transverse and longitudinal movement of images, especially the ground pattern, over the eyes (Kennedy 1940, Kennedy and Marsh 1974, Marsh et al. 1978, David 1986). The control of course angle is a steering reaction and control of airspeed is a reaction related to the force of thrust created by the moth's wing movements.

In self-steered counterturning it is not known what external feedback, if any, is employed (Kennedy 1983, 1986, David 1986). The regularity in the tempo of counterturns both in and out of contact with pheromone (Baker and Haynes 1987, Willis and Baker 1987) indicates that there is a motor program underlying these reversals. Thus in the performance of counterturning, the direction and force of the thrust (course angle and airspeed) may need no external feedback whatsoever. The tempo at which the program runs appears to be set by the concentration at any instant (Kennedy 1983, 1986, Baker 1986, Baker and Haynes 1987), with high concentrations causing higher-frequency reversals and low concentrations causing lower-frequency reversals (Kuenen and Baker 1982).

Not all moths necessarily integrate counterturning with optomotor anemotaxis while flying upwind in the plume (Haynes and Baker 1989). Rather, the courses they steer and even the resultant track angles are all centered strongly around 0°, or straight upwind while in the plume (Haynes and Baker 1989). However, thus far it appears that *all* moths do counterturn during widely oscillating casting flight across the wind moments after losing the plume (Marsh et al. 1978, Baker and Kuenen 1982, Kuenen and Baker 1983, Kennedy 1983, Baker and Haynes 1987, Baker and Vogt 1988, Haynes and Baker 1989, Baker 1989a,b). Casting flight is known to occur <u>only</u> after a moth has had contact with pheromone, and thus must be considered to be pheromone-mediated flight. Hence pheromone-mediated flight is flight that occurs <u>both</u> while a male is in contact with pheromone-bearing air, or for the up to tens of seconds that may follow such contact (Baker 1989a,b). Repeated contact and loss may occur perhaps hundreds of times even during flight within a plume's time-average boundaries, because most natural plumes have a fine, filamentous structure (Wright 1958, Kennedy and Marsh 1974, Marsh et al. 1978, Murlis and Jones 1981, Kennedy 1983, Murlis 1986 Baker and Haynes 1989).

The tracks of males not using counterturning while in contact with pheromone may still exhibit some (perhaps less temporally regular) zigzagging due to the moth rapidly losing and contacting the filaments. Thus the male might reiteratively over split-second intervals, begin to go into casting behavior (involving both counterturning and changes in course angle (Baker and Haynes 1987, Haynes and Baker 1989) and revert back into positive anemotaxis, in which he attempts to fly straight upwind (Haynes and Baker 1989). For such males this behavior would be similar to that originally proposed for all moths by Kennedy and Marsh (1974). For males that counterturn even while in contact with pheromone, such contact following low-frequency counterturning during casting would merely reset the frequency to its highest level, with a nearly straight upwind resultant (Baker and Haynes 1987, Willis and Baker 1988). This oscillating surge upwind is performed by males engulfed by the leading edge of a cloud of pheromone (Kennedy et al. 1980, 1981, Willis and Baker 1984). The response quickly wanes, apparently due to adaptation or habituation caused by the lack of fluctuating pheromone stimulation (Kennedy et al. 1980, 1981, Willis and Baker 1984, Baker et al. 1985).

In a recent model explaining zigzag flight in males, counterturning was proposed as not being a factor (Preiss and Kramer 1986). Rather the deviations from directly upwind were said to be due to a threshold-related error in the detection of significant transverse image movement in males that use only optomotor anemotaxis to try to steer straight-upwind. Because of the visual error, it was thought that the males repeatedly stray off the windline (Preiss and Kramer 1986). However, evidence that runs counter to this model has recently emerged (David and Kennedy 1987, Willis and Baker 1987). Among the problems with the model were the fact that tethered, rather than free-flying males, were used, preventing unrestricted movement in all three planes of rotation, thus failing to measure lateral flight forces that would have normally occurred due to rolling during free flight (David and Kennedy 1987, Willis and Baker 1987, Baker 1989a).

A system that uses counterturning during both upwind flight and during casting may have several functions and advantages over straight-line upwind flight. It involves a continuum from narrow to wide zigzagging (Kennedy 1982, 1983) that depends on pheromone concentration, and may help facilitate contact with pheromone filaments in the plume, especially during rapid shifts in wind direction (Baker and Haynes 1987). Secondly, the counterturning may aid the optomotor anemotactic system in more rapidly detecting changes in off-axis image flow due to shifts in wind direction, which might otherwise be below the visual threshold for a longer period during straight-upwind flight (Cardé 1984, Baker et al. 1985, Kennedy 1986). *Grapholita molesta* males that wing fan while walking toward the source do not counterturn at all, but rather walk in a straight line directly upwind (Willis and Baker 1987). Because they have contact with the ground, they get their information about wind direction from pressure differences across their bodies, and they do not need to counterturn to optimize sensing the wind visually.

B. The Importance of Fluctuating Pheromone Concentration in Sustaining Upwind Progress

Some male moths need intermittent or fluctuating stimulation from pheromone in order to sustain their upwind progress toward the source. Kennedy et al. (1980, 1981) and Kennedy (1982) showed that male *Adoxophyes orana* would not progress upwind in a uniform cloud of pheromone, but would readily fly upwind in a point-source plume placed in that same cloud. Something about the plume, conjectured to be fluctuating stimulation created by its fine structure, evoked the sustained upwind flight. These results were confirmed with another species, *Grapholita molesta* (Willis and Baker 1984). The requirement for intermittent stimulation in *G. molesta* males was then experimentally demonstrated (Baker et al. 1985) when males failed to zigzag upwind in continuous clouds of pheromone but readily did so when these same clouds were pulsed and interspersed with swaths of clean air. Although they did not progress upwind, both *A. orana* and *G. molesta* males continued to counterturn for some time across the windline while in the cloud, with *G. molesta* males appearing to cast across wind as if they had just lost pheromone (Willis and Baker 1984, Baker et al. 1985).

Wright (1958) had earlier pointed out the existence and possible importance of the fine structure of odor plumes to behavior. Murlis and Jones (1981) used ionized air and an ion detector to investigate further the nature of structured plumes (Murlis 1986). However, without the accompanying behavioral evidence (Kennedy et al. 1980, Kennedy et al. 1981, Kennedy 1982, Willis and Baker 1984, Baker et al. 1985) that the structure might actually affect the efficacy of the pheromone in evoking upwind flight, Murlis and Jones' important work might well have suffered the same fate as Wright's, which was to be generally ignored.

The speed of males' reactions to fluctuating pheromone concentration can be quite great. Whether they are tiny pyralids or huge *Polyphemus* silk moths, male moths usually respond to the loss of pheromone within 0.4-0.5 sec by means of a detectable shift from upwind flight to casting flight (Marsh et al. 1978, Marsh et al. 1981, Baker and Haynes 1987, Baker and Vogt 1988, Haynes and Baker 1989). Even female moths flying upwind in response to host odor change into casting flight within 0.5 seconds following flight into clean air (Haynes and Baker 1989). Male *G. molesta* have the fastest response to pheromone loss measured in moths thus far, *ca.* 0.15 sec (Baker and Haynes 1987). The reaction time (the change to more directly upwind movement) in this species in response to an *increase* in concentration is equally fast (Baker and Haynes 1987); response latencies of males of other species to an increase in pheromone concentration have not been measured.

Electroantennogram recordings in the field and in the laboratory indicate that while within a pheromone plume, moths will encounter pheromone filaments at a rate of between one every two sec to 3 per sec or so, taking into account the behaviorally relevant windspeeds observed and the airspeeds that males use in such winds (Baker and Haynes 1989). Estimates of such contacts based on monitoring ionized air filaments are virtually identical, *ca.* five contacts every 2 sec (Murlis and Jones 1981, Murlis 1986).

The short latencies of response to the onset and loss of pheromone in *G. molesta*, coupled with the knowledge that males flying upwind may contact pheromone filaments only once or twice every second or so (Baker and Haynes 1989), led to the realization that perhaps the zigzagging flight tracks of this species are shaped by the split-second modulations of the two programs to the loss and gain of pheromone (Baker and Haynes 1987). The reiterative change from more directly upwind flight to casting and back again might occur several times each second, and thereby change the width and angles of the track legs, sometimes even resulting in sawtoothed-shaped tracks when the contact and loss occurs regularly according to left and right positions of the moth along its track (Baker and Haynes 1987). Both the anemotactic and counterturning systems in this species have this rapid reaction to fluctuating concentration, whereas adjustments in airspeed occur much more slowly.

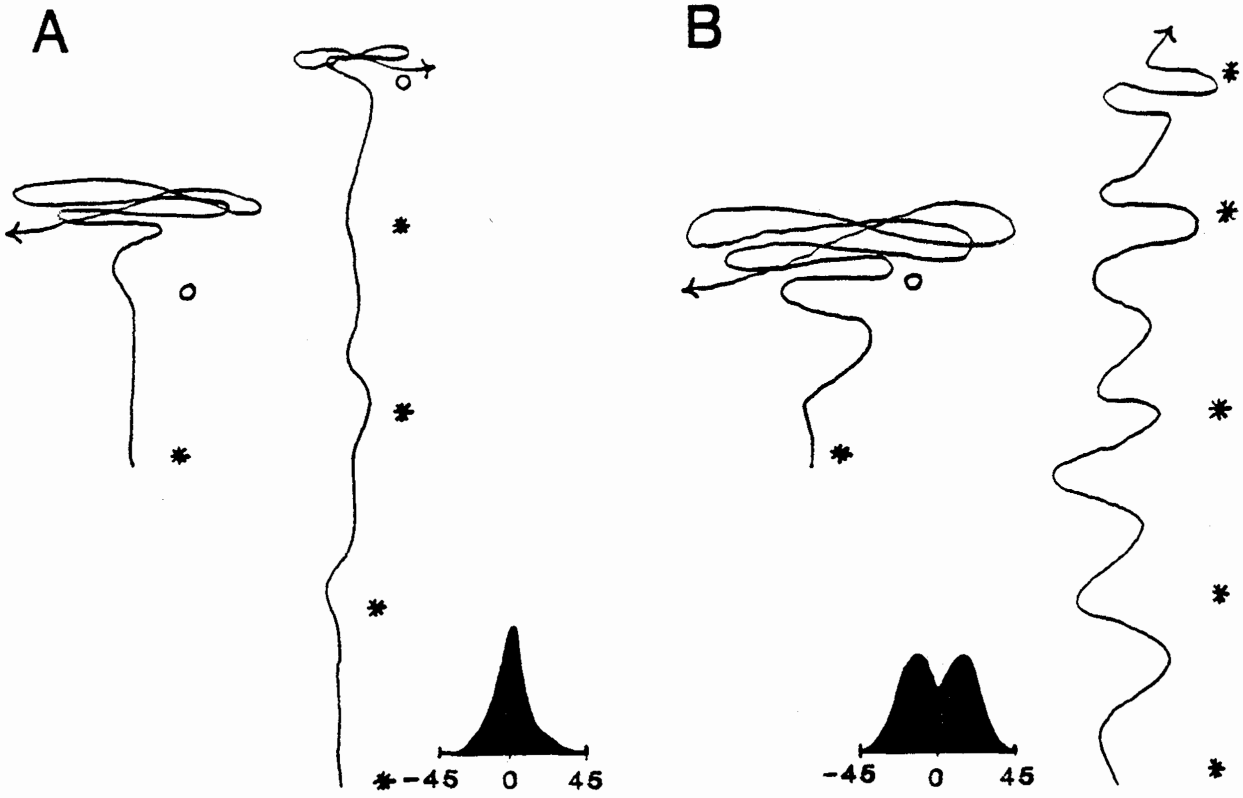

Figure 1. Hypothetical flight tracks during flight in a plume of pheromone (viewed from above, wind and pheromone from the top of the page) of the males of two species that have either a slower (A), or faster (B), reaction to pheromone loss. While flying upwind in plume, the males are hypothesized to encounter filaments of pheromone at a rate of 2 per sec (marked with asterisks). Next to each sustained upwind track in A and B is the distribution of course angles that males would use during such flight. A) At left, the programmed reaction to pheromone loss of a slower-reacting male that is allowed to play out in clean air (open circle). At right, the relatively straight upwind flight track in a plume that results from reiterative contact with the filaments every 0.5 sec. B) Same as in A, except that these tracks result from faster-reacting males such as *G. molesta*. The flight tracks of such males while flying upwind in a plume will have many more apparent and regular zigzags, plus they will have a bimodal distribution of course angles.

The reaction times, therefore, of different species of moths to pheromone ON and OFF may be what create differences in flight tracks while within a plume of pheromone. More slowly reacting moths, such as the navel orangeworm (Haynes and Baker 1989), may under typical conditions steer courses that are centered about due upwind due to the fact that the encounters with arriving filaments are frequent enough, relative to the reaction latency of casting, such that casting is rarely initiated (Figure 1 A). Faster-reacting species such as the oriental fruit moth (Baker and Haynes 1987), on the other hand, may under these same filament frequencies always steer off the wind-line and exhibit counterturning while in the plume, because the filaments arrive too slowly to reiteratively trigger straight upwind flight. Counterturning related to casting flight will therefore almost always be expressed due to the longer intervals between filaments relative to the (shorter) reaction latency of casting, even though the frequency of filament arrival is identical for the two species (Fig. 1B). The reiterative upwind surges caused by the filaments nevertheless usually keep the casting from being fully expressed and keep the male's progress going in the upwind direction (Figure 1B). It appears that the reaction times to pheromone OFF of different species are related to their counterturning frequency during casting, with slower-reacting species having a slower counterturning frequency during casting than *G. molesta* (Marsh et al. 1978, 1981, Baker and Haynes 1987, Haynes and Baker 1989, Baker and Vogt 1988).

The knowledge that behavioral programs can be rapidly modulated by encounters with single filaments of pheromone or with pockets of clean air has suddenly placed a heavy emphasis on understanding the reaction and recovery speeds of neurons and synapses along sensory pathways (see Section D below) (Kaissling 1974, Kaissling 1986a,b, 1987). The new awareness of the rapidity of both the speeds of the behavioral reactions and the behavioral requirement for intermittent stimulation has also resulted in neuroethologists focusing more on challenging neuronal preparations with experimentally controlled repetitive pulses of pheromone rather than single, long-duration pulses (Rumbo 1983, Kaissling 1986a,b, Christensen and Hildebrand 1987a,b, 1988, Christensen et al. 1989, Baker et al. 1989a,b). In addition, single antennal neurons have now been challenged by the fluctuating filaments in actual plumes from pheromone sources that earlier had been shown to either evoke sustained upwind flight or arrestment (Baker et al. 1989a,b).

C. How the Maneuvers Help in Locating Natural Pheromone Sources in the Field

The simplest model explaining how male moths use these reactions in order to locate a sex pheromone source in a natural field situation is the following, based on the above-listed experimentally determined responses of moths over the years, in addition to field observations (David et al. 1982, 1983, David and Birch 1989). ***Flying male moths locate a sex pheromone source by progressing rapidly upwind upon gaining contact with pheromone and quickly switching to casting flight upon flying into clean air*** (David et al. 1982, 1983, David and Birch 1989). This way of behaving will serve the moths well because of the way wind moves in some environments.

The wind at or above a crop canopy often carries pheromone away from the source in straight lines for tens of meters, even though the plume itself may be greatly sinuous and meandering along its long axis (Fig. 2A, B). Thus only pheromone-laden wind bears a consistent direction relative to the source - directly away from it - and by flying upwind only in such parcels of air (*i.e.*, only when it smells pheromone) the moth will progress directly toward the source (David et al. 1982, 1983, David and Birch 1989) (Fig. 2B). It thus behooves the male to respond as rapidly as possible during the time he smells the odor so as to make as much progress as possible when this floating signpost pointing toward the source is present (David et al. 1982, 1983, David and Birch 1989).

In a shifting wind-field, however, a male progressing rapidly upwind in pheromone-laden air will eventually fly into a large parcel of clean air (Fig. 2B). He must now cease upwind progress as quickly as possible. If he were not to do so and continue to fly upwind in the clean air even for a short time, he would no longer be flying on a line toward the source (Fig. 2A, right). His failure to stop and change direction would also result in his needlessly distancing himself still more from the important pheromone-bearing air that is rapidly swinging away from him (Baker and Haynes 1987). However, by oscillating to and fro (casting) with increasingly high airspeed (and groundspeed) and an ever-decreasing reversal tempo to increase the air that is scanned, the male may be lucky and relocate the "lost" plume on one of his casting reversals (Fig. 2B). A quick upwind surge upon recontacting pheromone will again result in direct progress toward the source before the next encounter with a large parcel of clean air occurs. The rapidity of upwind progress will depend on how steady the wind direction had been when the air had moved over the source to create a either a long or short parcel of pheromone-laden air traveling directly away from the source (David et al. 1982, 1983, Baker and Haynes 1987, David and Birch 1989).

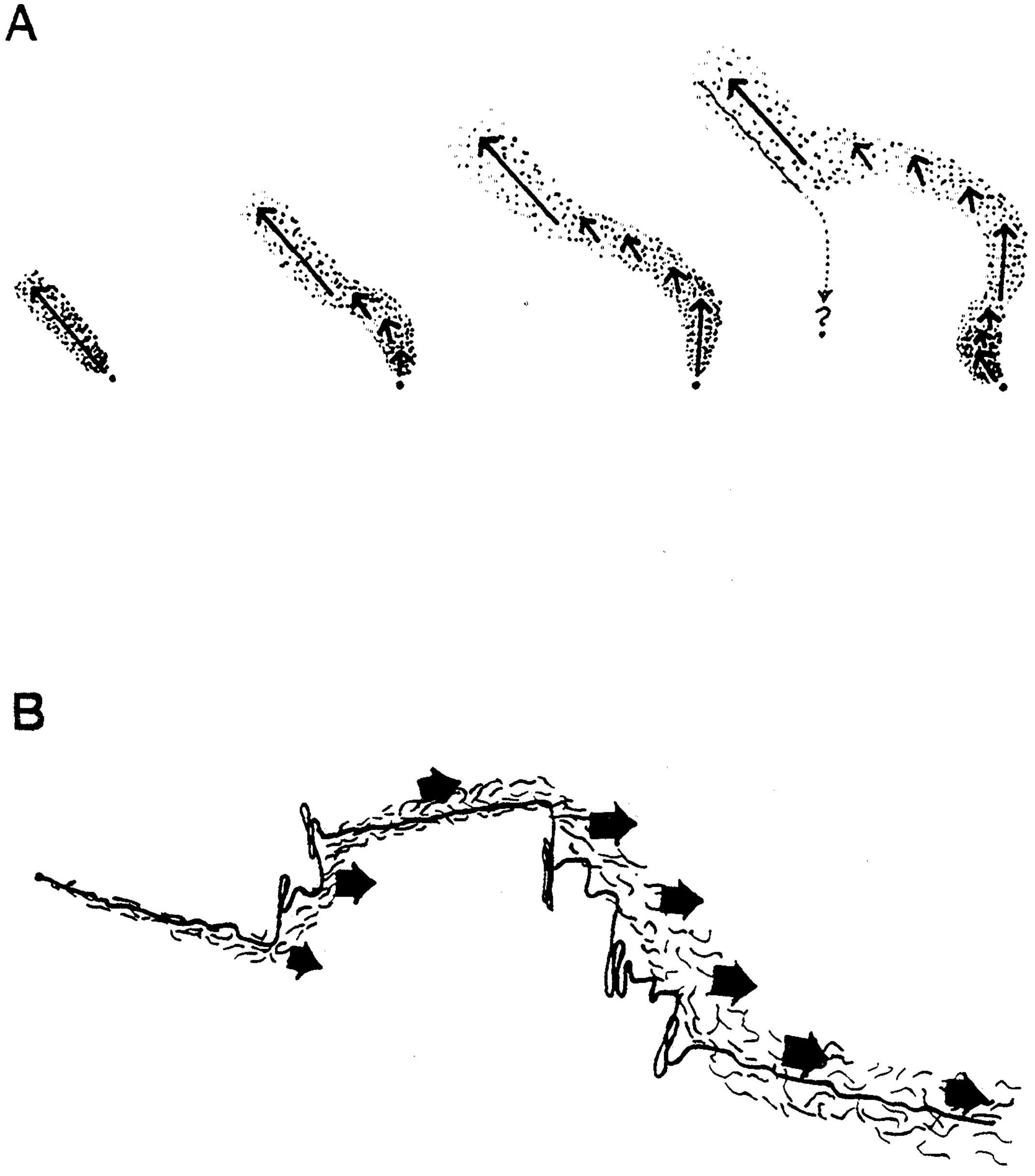

Figure 2. A) Depiction of how a sinuous plume of pheromone, here illustrated without small-scale fine structure, can develop in wind over short grass in the field, according to the experiments of David et al. (1982, 1983) and David and Birch (1989). Plumes and wind in a forest may move differently (Elkinton et al. 1987). Over short grass, the parcels of pheromone-bearing wind move away from the source in straight lines, beginning here with a fairly long, straight parcel (far left) before the wind begins swinging (center left and right). In the final "snapshot" (far right) it is clear how a male flying upwind in the fairly long, straight parcel will progress directly toward the source, but eventually enter a large parcel of clean air. If he were to continue flying upwind in the clean air, his track (dotted line) would become increasingly directed away from the source due to the shift in wind direction. However, if he reacts quickly and begins casting, as in B), he will have a chance of relocating the pheromone-bearing wind and flying upwind in it, again each time directly toward the source. B) An illustration of a pheromone plume in a shifting wind-field, with the fine structure depicted as well as the flight track of a male flying toward the source (based on experiments of David et al. 1983 and David and Birch 1989). Wind direction is indicated by large arrows.

Working in a forest, Elkinton et al. (1987), found that wind often does not move in the same way as it does over grass in a field. The parcels of pheromone-bearing air often curve in various trajectories and do not follow straight lines away from the source. As such, much of the time they are poor "signposts" of the toward-source direction. In fact, sometimes they curve around so much that they head back in toward the source, and a gypsy moth male flying upwind in such parcels would be flying directly away from the source (Elkinton et al. 1987). Therefore alternative, less direct means of locating females are thought to be used during such times, such as the repetitive flying up and down tree trunks that gypsy moth males are often known to perform. There are short periods of time, however, during which the wind velocity increases and distributes pheromone such that the long axis of the plume and the wind direction are coincident. Elkinton et al. (1987) hypothesized that perhaps much of the successful pheromone-source location done by gypsy moth males may be accomplished during these periods by using the standard means of upwind flight interrupted by casting.

The process of pheromone source location, especially when taking into account the discontinuous fine structure of the plume. thus quite clearly involves reiterative exposures to large and small parcels of clean air and to pheromone filaments, both types of exposures requiring quick reactions, casting and upwind surges. In the above canopy situation in shifting wind, the males' (such as *G. molesta*) quick program modulations in response to individual filaments and small pockets of clean air make sense. The moths must respond to every small pocket of clean air as if it is the big one that is looming ahead, by going into casting flight. If it is only a small pocket, contact with a new pheromone filament quickly resets the counterturning and anemotactic programs to create an upwind surge. If it is a big pocket, then the programs play out in a long-lasting response to create the ever-widening tracks that may result in fairly rapid rediscovery of pheromone-bearing air (Fig. 2B).

D. A Proposed New Dual System of Phasic and Tonic Neuronal and Behavioral Responses

The above discussion of the enormous task of locating a pheromone source under shifting wind conditions in the field should clearly reveal that the sensory nervous system pathways should be constructed to extinguish as quickly as possible the pheromone stimulus once it has arrived. In so doing, the surest detection of, and quickest behavioral reaction to (upwind surge), the next rise in pheromone can take place. Or, just as importantly, the relaxation of the counterturning and anemotactic programs can with assurance be played out fully in the large pocket of clean air. The existence of highly phasic pathways from the antenna through the deutocerebrum is now well-documented, and explains very nicely the observed behavioral responses to changes in pheromone concentration (Rumbo 1983, Kaissling 1986a,b, Christensen and Hildebrand 1987, 1988, Baker et al. 1989a,b, Christensen et al. 1989).

However, no explanations have been put forth up to this point as to the possible underlying neuronal mechanisms resulting in casting flight, the persistent, long-term pheromone-mediated behavioral response that is carried over into clean air. The persistence could first of all be due to the lingering of, and low-level receptor response to, undegraded pheromone molecules on and in the antennae long after contact with actual pheromone filaments has ceased. However, not necessarily unrelated to this is the recent discovery of interneurons in the protocerebrum of *Manduca sexta* that fire with "long-lasting excitation" for at least eight seconds after the stimulus is removed, and only when that stimulus is the correct blend of pheromone components (Kansaki 1989). Whether due to the presence of undegraded pheromone or not, this type of persistent firing by an interneuron could conceivably be what drives a counterturning oscillator during the long periods of casting flight in clean air.

I propose that such interneuronal firing represents the second half of a dual system underlying the observed behaviors, with bursts of upwind flight using phasic, and casting flight using tonic stimulation. The tonic system might be switched on all the time that pheromone is or has recently been present, and the phasic bursts related to the arrival of individual filaments might repeatedly cut in and supercede the tonic system to create upwind surges. There is evidence that tonic and phasic information is carried in separate channels in the deutocerebrum of at least two species of moths (Christensen and Hildebrand 1987, 1988, Christensen et al. 1989).

The reiterative upwind surges, then, in response to each pheromone filament, might be viewed as being overlaid on an ever-present tendency to counterturn due to an oscillator whose frequency is driven by the frequency of action potentials from the tonic system. If the spacing between two filaments of pheromone becomes too great, the anemotactic system relaxes its requirement for more upwind-coupled visual feedback and permits more crosswind movement through time. Similarly, with a large spacing between filaments, the rate of tonic firing would subside, slowing the rate of counterturning, and resulting in increasingly wider casts as the time following pheromone loss increases. The persistent counterturning in uniformly concentrated pheromone clouds as well as in clean air (Kennedy et al. 1980, 1981, Willis and Baker 1984, Baker et al. 1985) is also consistent with the idea that a tonic sensory pathway drives counterturning. More work will surely reveal whether such a dual system does in fact exist and how the tonic and phasic activities might interact with each other.

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