4 Pheromone-modulated movements of flying moths

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In the earlier days of sex pheromone research, when it was thought that moth species each used one compound to communicate, it was known that different concentrations of pheromone must be affecting the movements of moths because too much or too little pheromone could result in reduced captures of males in traps. When in the early 1970s, it became clear that the majority of species used blends of compounds, the same trap capture-based inferences on movement were made, only now the issue was blend quality. Then we actually began to watch the moths; we advanced from previous inferences about 'synergism' and 'inhibition' (many authors), and 'primary' and 'secondary' pheromone components (Roelofs and Cardé 1977) to statements about 'close-range' and 'long-range' effects of chemical blends. From here we advanced to 'attraction' and 'arrestment', terms actually describing the gross movements of moths (Baker and Roelofs 1981). During this evolution of thought, J. S. Kennedy (1972) cautioned that we did not in fact know that pheromone chemicals directly affected the movements of moths, and that all the evidence had thus far indicated that the chemicals merely switched on a steering response to wind, not to the chemicals themselves.

Wright (1958) earlier had described a way that attractant compounds could be used directly for steering. The frequency of pheromone filaments in a plume could code for the towards-source direction. Later he abandoned this idea when evidence from his experiments showed the overwhelming influence of the optomotor anemotactic response in odour-mediated insect flight behaviour (Wright 1962, 1964). Optomotor anemotaxis was first demonstrated by Kennedy (1940) in the flight of yellow-fever mosquitoes. Farkas and Shorey (1972) brought chemical steering to the fore again when they claimed that their pink bollworm males steered only with respect to the chemicals, not to the wind at all, in successfully flying up a pheromone plume to the source in zero wind. In their view, the wind merely served to draw out the pheromone into a linear trail which was 'followed' chemotactically by flying moths in a manner similar to the way ants follow terrestrial trails. Kennedy and Marsh (1974) apparently neatly negated this idea when they demonstrated with another species how Farkas and Shorey had overlooked the powerful optomotor anemotactic response that had influenced displacement of the moths before the wind had been stopped. Kennedy and Marsh (1974) and Marsh *et al.* (1978) maintained that two purely anemotactic mechanisms, positive anemotaxis in the presence of odour and reversing anemomenotaxis upon odour loss, still best explained the ability of moths to locate a pheromone source in wind. Onset and offset of odour merely served to switch on these steering responses to wind.

If it were true that pheromone merely switched on anemotaxis, I would have very little to talk about from here on, because this talk is supposed to be about how pheromone chemicals modulate the movements of flying moths. Happily, I can continue on much longer because experiments by J. S. Kennedy and colleagues using clouds of pheromone (Kennedy 1982; Kennedy *et al.* 1980, 1981) and by our lab using zero wind (Baker and Kuenen 1982; Kuenen and Baker 1983) showed that, apart from triggering anemotaxis, sex pheromone does directly influence the movements of flying moths by altering the frequency and angular magnitude of zigzags. Unlike Farkas and Shorey (1972) who proposed that all turns were steered with respect to pheromone gradients (both lateral and longitudinal) Baker and Kuenen (1982; Kuenen and Baker 1983) invoked the concept of self-steering (Kennedy 1978, 1983). Pheromone stimulation would initiate and maintain a programme of movements, which for the oriental fruit moth, *Grapholita molesta*, consists of relatively narrow and regular 'zigzags' (Kennedy (Chapter 2), or counterturns (Bell and Tobin 1982; Kennedy 1983). As in *Plodia interpunctella* (Marsh *et al.* 1978), the turns are mainly performed in the horizontal plane with only about half as much movement occurring vertically (Willis *et al.* unpublished). Because the movements are part of a 'programme' originating from within the moth, they are therefore self-steered and rely on idiothetic cues for their execution (Kennedy 1978, 1983, Chapter 2). They would not, therefore, be the type of direct reactions to an odour gradient envisioned by Farkas and Shorey, but would fall into the class of indirect reactions to odour (Kennedy 1978), as more recently outlined by Bell and Tobin (1982).

From here on I will present further evidence, mainly using the oriental fruit moth, that supports the idea that zigzagging flight in orientation to pheromone is primarily self-steered, not gradient-steered. I will also present evidence that this self-steered zigzagging needs to be integrated with optomotor anemotaxis in order for the optimum efficiency of source location to occur. Finally I will argue that the self-steering programme in some moths can be maintained only through intermittent, not continuous, chemical stimulation.

We have observed the counterturning programme, uncomplicated by wind, by releasing male oriental fruit moths in zero wind into a stationary pheromone plume (Baker *et al.* 1984). Such moths initiated a series of left–right turns of about 180°–200° magnitude, each performed with about 60° accuracy, on average. Because the turns alternated left and right and had a high degree of angular regularity, they fall into the category of 'counterturns' (Kennedy (Chapter 2)). Another form of 'regularity', the *temporal* regularity of consecutive reversals, is not considered here, although they also had this type of regularity (Willis *et al.* unpublished). With no pheromone present (again beginning in zero wind) turning magnitudes were more varied, with many more shallow turns; the difference between consecutive turns, one measure of counterturning regularity, was also more varied than with pheromone present. Importantly, without any wind or in-flight experience in wind the counterturns meandered around in the plume and the tunnel. In pheromone, they were performed with high angular accuracy with or without wind, but without it there was no significantly preferred counterturning direction with respect to the source or the plume, as measured by interreversal track angles. Instead of being oriented with respect to the 'edges' of the stationary plume, the zigzags were as likely to run parallel to them, which is inconsistent with the idea that each counterturn is steered with respect to the plume's lateral gradients (Farkas and Shorey 1972) or otherwise 'related to' the plume's boundaries (Tobin and Bell 1982).

As visualized by smoke, the stationary plume diffused slowly outward from the central axis, resulting in the time-averaged boundaries expanding and reaching the walls of the tunnel after a minute or so. Therefore even many of the zigzags performed perpendicular to the edges were well within the plume's 'edges'. Thus the counterturns appear to have been self-steered according to a motor programme, the angular regularity of the consecutively performed turns being a result of an unknown internal mechanism or perhaps also due to external, visual feedback (Ludlow 1984; David (Chapter 5)).

The counterturning tracks had a consistent alignment to anything other than to the immediately preceding turns only when wind was present, or in zero wind when males had already taken flight before the wind stopped (Baker and Kuenen 1982; Baker *et al.* 1984). The latter males already had a chance to experience wind optically and to compensate for wind-induced drift through optomotor anemotaxis. Their success at locating the source was significantly greater than that of males that had experienced wind only mechanically while on the ground (Baker *et al.* 1984). Thus the counterturns were polarized in a direction generally across the wind-line by the optomotor response to wind-induced drift (Ludlow 1984; David (Chapter 5)). It is apparently only a coincidence that they are *also* oriented consistently with respect to the edges of the plume and that the moths thus appear to be steering by them.

Other previous experiments in wind with this species (Kuenen and Baker 1982b) and with others (Cardé and Hagaman 1979; Farkas *et al.* 1974) indicate that the concentration of pheromone inversely affects linear velocity of flight and directly affects the frequency (and therefore amplitude) of the counterturns. At the highest concentrations, the moths' upwind zigzags are the narrowest and are executed very often entirely within the boundaries of the time-averaged plume, not what one would expect for chemotaxis in such plumes that have theoretically wider behaviourally 'active' boundaries than weaker plumes.

Oriental fruit moth males flying to the most concentrated sources eventually bring themselves to a point where in-flight arrestment of progress toward the source occurs. This cessation of progress is not brought about by a further concentration-mediated change in linear velocity or counterturning frequency, but rather by an apparent sudden increase in the course angle between each reversal, resulting in 90° cross-wind tracks where such tracks used to be about 70° (Kuenen and Baker 1982b). Thus it appears that the concentrations causing arrestment do not significantly affect the self-steered programme, but somehow they modify the optomotor response.

Blend quality alterations also can result in in-flight arrestment of oriental fruit moths, among others (Baker and Cardé 1979b; Baker *et al.* 1981; Linn and Roelofs 1981, 1983; Linn *et al.* 1984), and it may be that similar anemotactic changes also account for arrestment to off-ratios. The movements resulting in upwind flight and arrestment to blend ratios need to be examined in the same detail as those for blend emission rates. One thing is clear from existing data for several species of moths: upwind flight effects can usually and most sensibly be ascribed to the *blend* of components, not to individual components in the blend. For the oriental fruit moth, Baker and Cardé (1979b) and Baker *et al.* (1981) argued, with clear experimental evidence, that the blend of three components acted as a unit to influence all behaviours associated with upwind flight, despite erroneous citations of this same work declaring that individual components each evoked different behaviours (Boeckh and Ernst 1983; Boeckh *et al.* 1984). As soon as the blend is dissected, and only partial combinations or individual components are emitted, attraction to the source is reduced, especially at close range (Baker and Cardé 1979b; Baker *et al.* 1976, 1981; Linn and Gaston 1981; Linn and Roelofs 1983). Authors who try to calculate 'nested' upwind flight active spaces for successive individual compounds in a blend (e.g. Buda 1980) inevitably ignore the data which show significantly lower thresholds for the blend compared with any component alone or with incomplete blends, which would translate in the field into larger active spaces for upwind flight to the complete blend than to any partial mixture. A final mistake is that the behaviour involved in nested upwind flight active spaces is often imprecisely defined. What is forgotten is that *upwind flight* must be evoked by the chemical(s). I would agree with the possibility sometimes raised by neurophysiologists (E. E. Davis, personal communication) that at some point far downwind an emitted blend may be perceived as only one component, for example, the one predominating in the emissions or the one for which there are the most receptor sites. All the others may be below receptor thresholds at that distance. But the critical question here would then be whether the major component alone could elicit upwind flight. If it only elicits activation or take-off, as *cis*-8-12:Ac does for

G. molesta (Linn and Roelofs 1983), then it too is below threshold for upwind flight, and it is still the blend that defines the *upwind flight* active space (Baker *et al.* 1981; Linn and Roelofs 1983). It does not matter whether the moth perceives or is excited by this compound, unless one wishes to redefine the active space of interest as that for *perception* or *wing fanning* or *taking flight*. Partial blends or individual components at close range may be able to evoke responses other than upwind flight, such as copulatory attempts (Bradshaw *et al.* 1983). More experiments with more species certainly are needed to further our understanding of how blends affect behaviour.

The time-period immediately following arrestment is characterized by widening counterturns at right angles to the wind with a cessation of progress towards the source ('casting', see Kennedy 1983), concurrent with an increase in altitude that takes the moth up and out of the plume, and then with increased displacement in the downwind direction (Kuenen and Baker 1983). Casting flight also occurs when the pheromone source is lost, as when the source is removed, but there is a slight but significant delay following loss of the plume before this begins (Kuenen and Baker 1983; Marsh *et al.* 1978, 1981). During this interval, narrow upwind zigzagging continues in clean air, often for two or more turns. Because there are no lateral gradients present in clean air, this behaviour is consistent with a self-steered programme of counterturns, not a single gradient-steered counterturn.

The switchover to casting demonstrates the concentration-dependent continuity of the counterturning programme (Kennedy 1983; Kennedy *et al.* 1980, 1981). In addition, the self-steered nature of the casting counterturns was revealed in experiments in zero wind where males flew out the end of a truncated, stationary plume (Baker and Kuenen 1982; Kuenen and Baker 1983). The longer intervals between reversals upon flight into clean still air, plus the change in magnitude and direction of the turns, were similar to what occurs during casting in clean wind. If wind is present to polarize the casts and it then shifts direction, as it often does in the field, the cast shift with it and the moth continued to maintain 90° reversing tracks across the wind-line (David *et al.* 1983). Then the result is often that the plume is re-intersected at a point closer to the source than where it was lost by the moth (David *et al.* 1983). The wide casts thus may not only aid in relocating pheromone, but may also contribute to progress toward the source in a shifting wind-field.

The narrow counterturning programme during more intense pheromone stimulation and wide counterturning during weak stimulation appears, therefore, to function in keeping the moth in contact with pheromone (Kennedy 1983). But an additional function may be to allow the moth to detect the wind direction quickly, either following a lull, or as it shifts (Baker 1984; Cardé 1984; Kuenen and Baker 1983). Kennedy (Chapter 2) has called this 'tracking the wind direction', and the moth may be constantly 'feeling for the error sign' of image flow across its eyes by zigzagging quickly. This function of counterturning remains to be demonstrated experimentally, however, especially since not all flying insects exhibit zigzagging movements in response to odour (such as *Drosophila*, although upon odour loss they do counterturn across the wind; C. T. David, personal communication).

Perhaps the most interesting evidence for the self-steered counterturning programme in wind comes from experiments in which flying *Adoxophyes orana* males were engulfed in a cloud of pheromone of near-uniform concentration (Kennedy 1982; Kennedy *et al.* 1980, 1981). Upon entering such clouds, males previously casting in clean air briefly narrowed their reversals and made a 'surge' of upwind progress. No excursion across a lateral gradient could have triggered each narrow counterturn because no lateral gradient existed. The males made only brief upwind progress, although the narrow cross-wind counterturning continued for quite a while. A mean of 27 such counterturns was recorded from individual males after they were engulfed by the cloud, each occurring without any change in concentration or the presence of lateral gradients (Kennedy *et al.* 1981).

The lack of sustained upwind progress was not due to the somewhat low concentration of pheromone in the cloud relative to a plume (Tobin and Bell 1982) because a cloud generated by a different technique and having a side corridor of uniform mean concentration twice as high as that of a plume that had evoked upwind zigzagging (and over 100 times higher than the first tunnel-filling cloud) also failed to elicit sustained upwind flight. Likewise, the lack of upwind progress was not due to an excessively high concentration of pheromone, because a point-source plume placed within both low- and high-concentration clouds caused significant levels of upwind narrow zigzagging in the plume (Kennedy *et al.* 1980, 1981).

This brought up the very important point that perhaps males require intermittent, not continuous, stimulation with pheromone, such as occurs in a structured plume, in order to maintain the narrow zigzagging programme and upwind progress. Willis and Baker (1984) confirmed and extended these findings using the oriental fruit moth. Males would not take off and fly upwind in a uniform cloud of pheromone, regardless of its concentration, but would if a point-source plume was within the cloud. Higher cloud concentrations reduced the likelihood of zigzagging up the plume. As in the study of Kennedy *et al.* (1980, 1981), males entering a side corridor uniformly permeated with pheromone would usually narrow their zigzagging at the pheromone–clean air boundary, but here oriental fruit moth males would also progress upwind along the edge and not just zigzag in its vicinity. Higher frequency of zigzags and lower linear velocity of flight occurred along the most concentrated side corridor compared with a weaker one. Males would also zigzag upwind if a corridor and its edge were positioned horizontally along the floor, not vertically. Willis and Baker (1984) concluded that the self-administered, intermittent stimulation resulting from flight in and out of pheromone aided in maintaining the narrow counterturning programme along the edge, and each turn was not steered by the gradient. In addition, because the edge was likely to be somewhat heterogeneous in a zone several centimetres wide owing to turbulent mixing, males could have been receiving slightly fluctuating stimulation from it and this too could have aided in promoting counterturning.

We recently tested the effects of continuous versus intermittent pheromone stimulation in a more direct way in the wind-tunnel, by giving males both a uniform continuous cloud, and one that was pulsed either 1 or 0.5 times per second (Baker *et al.* unpublished). We checked our ability to produce the pulsed clouds by means of smoke plus an infra-red photometer, and also by using an electroantennogram (EAG) sensor placed in the cloud of pheromone at the concentration used for evoking upwind flight. It became clear rather quickly that we could not make our cloud's amplitude and speed of oscillation come anywhere close to what a moth experiences in a plume. A male's receptors register deep, quick stimulation to a plume, with sharp onsets and offsets, whereas we were able to give them only slow, shallow fluctuations. Nevertheless, significantly more males took off and zigzagged farther upwind when the cloud was pulsed at either rate than when it was presented continuously. The males zigzagged upwind without the aid of lateral gradients to steer the counterturns. Kramer (Chapter 6) found that fewer *Bombyx mori* males would walk directly upwind when presented with continuous pheromone compared with pulses at a narrow range of frequencies.

It is not surprising that the zigzags of males flying upwind to the pulsed clouds averaged about twice the width of those flying upwind to the plume, considering the relatively slow and shallow amplitude of stimulation we were able to give them. In previous experiments, weak point-source plumes elicited zigzags approximately double the width of those performed in plumes from sources loaded with 10 to 30 times the amount of pheromone (Kuenen and Baker 1982b). Murlis and Jones (1981) showed that at 15 m downwind from a source of ionized air, the mean concentration of ions was about 50 times lower than at 2 m. The mean of burst peaks (peak-to-trough amplitude) was about 75 times lower at 15 m than at 2 m, although the peak-to-mean ratios stayed relatively constant at a value of about 20, regardless of distance. Therefore, it is conceivable that our pulsed cloud not only mimicked the shallower amplitude of stimulation a male would receive tens of metres downwind of a moderately emitting source, but it may also have mimicked the longer durations and decay times of the pheromone bursts that would occur at such distances (Murlis and Jones 1981).

Considering what has been observed about pheromone-mediated attraction and arrestment in flying moths, it is apparent, as pointed out by Kennedy (1983), that peak-to-trough amplitude fluctuations in pheromone concentration appear to be a key, for some species, to initiating and maintaining narrow counterturning and males' progress toward the source. I suggest additionally that an optimal blend ratio and emission rate may be one that on the one hand maximizes fluctuations in neuronal firing (flickering) at locations far from the source where the plume's filaments are less concentrated, but also minimizes *fusion* of the neuronal fluctuations when the peak amplitudes of the plume's filaments become high very close to the source. The moth's own zigzagging movements may help prevent fusion near the source. However, to an off-ratio or excessive emission rate, the male may eventually reach a zone where even these excursions into clean air can no longer enhance flickering, and arrestment will occur. Kaissling (Chapter 22) has found that receptor cells can respond to rapid, experimentally administered pulses of pheromone such as would occur in a plume, and we were able to record plume fluctuations with the EAG.

For moths requiring fluctuating pheromone stimulation, the traditional way of defining the active space in terms of a time-averaged concentration (Bossert and Wilson 1963) would need to be revised, but in a way that takes into account more than peak pheromone flux (Elkinton and Cardé 1984). Peak-to-trough amplitude (Kennedy 1983) would be sufficient for describing a threshold stimulation for many moths, but would not be adequate for those species with an upper threshold such as the oriental fruit moth (Baker and Roelofs 1981). Here, fusion of the fluctuating signal may also need to be invoked, and the thresholds of flickering and fusion would thus play a part in defining the upwind flight active space for a particular blend and emission rate. The plume's structure would now play a much larger role in the active space and would depend on the wind speed and the amount of large- and small-scale turbulence, among other factors. The small-scale turbulence would be generated from foliage or from other surfaces such as pheromone traps (Lewis and Macaulay 1976).

Recently, interneurones that respond phasically to pheromone bursts have been discovered in *B. mori*, and interestingly some also seem to respond to transverse visual pattern movement (Olberg 1983a). The interneurones exhibit two distinct firing frequencies, 'high' and 'low', and alternate between there states upon repeated presentations of pheromone. Usually, increases (but sometimes also decreases) trigger changes in state. If such interneurones were present in *G. molesta* they would require fluctuating pheromone stimulation to change stages, and the frequency of state changes may be what modulates the counterturning program.

EAG responses of males of many species have often revealed that one pheromone component presented as a brief 30 ms puff will evoke a high-amplitude, fast-decaying response, whereas a second component (e.g. *trans*-11-14:Ac in the red-banded leafroller moth) will elicit a lower-amplitude and more slowly-decaying EAG response (Baker and Roelofs 1976; Roelofs and Comeau 1971). The *trans* isomer of the oriental fruit moth pheromone blend has been implicated as a key cause of arrestment of upwind flight, not only when present in a high ratio at natural concentrations (Baker and Cardé 1979b; Baker *et al.* 1981; Linn and Roelofs 1981), but also at excessive concentrations of the optimal ratio (Linn and Roelofs 1981).

The neuronal events that would result in arrestment due to fusion of the neuronal fluctuations may be the following. First, close to the source the highly concentrated filaments may saturate the receptors. They not only may be unable to continue to reflect the actual peak concentration as it increases past the receptors' capacities (Baker 1985), but the surplus molecules also may then take longer to locate unoccupied receptor sites and be cleared by enzymatic degradation (Kaissling 1971). The receptors, therefore, would be more likely to fire continuously at significant rates even during intervals when the moth is actually in a pocket of clean air or 'outside' the plume during a reversal. For an off-ratio of normal concentration (e.g. too much *trans* in the red-banded leafroller moth blend), the slower time-course apparently required for clearing the *trans* component would be more likely to 'fill in', with neuronal firing, the troughs between actual contact with pheromone filaments.

Conclusions

For some species of moths, pheromone elicits two major responses, one being a self-steered programme of narrow zigzags, the other the optomotor reaction to wind-induced drift which polarizes the zigzags in the upwind direction. The two responses, when integrated, result in optimal pheromone source location. For two species, fluctuating pheromone stimulation is required for upwind zigzagging, whereas continuous uniform stimulation causes the wide casting and eventual downwind displacement characteristic of casting flight in clean air. Pheromone blend ratios and emission rates may modulate movements by producing neuronal fluctuations (flickering) necessary for upwind flight far downwind. Production of flickering may need to be balanced against the blend's tendency to produce a fusion of the fluctuation closer to the source, which may result in arrestment of progress before the source is located. 'Active space' will need to be redefined for those species requiring fluctuating pheromone stimulation for upwind flight.

Future research should be conducted in the field to examine the flight orientation behaviour of males under natural wind and plume-structure conditions. It will be essential to measure, simultaneously with flight track recordings, the wind direction and the plume's physical structure (e.g. with smoke or ions). But in addition the plume's *perceived* structure at the neuronal level will need to be recorded, because the properties of a neuronal system (receptor capacity, latency, etc.) will be what determines the behaviourally relevant type of plume fluctuation.

Such research will bring together for the first time a knowledge of the orientation movements of pheromonally stimulated flying moths *and* neurophysiological recordings obtained under natural conditions at the same time and location as the flight behaviour. Our understanding of how insects perceive and respond to odour should increase with this approach.

Dedication

This chapter is dedicated to Professor J. S. Kennedy for his more than 40 years of contributions to the study of insect behaviour, and for the inspiration he has given to me and to my students.

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