Dissection of the pheromone-modulated flight of moths using single-pulse response as a template

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Abstract. The upwind flight of male moths to conspecific females is mediated by the chemical and structural characteristics of a pheromone plume. We describe the reaction of male *Cadra cautella*, the almond moth, to the interception of single pulses of sex pheromone, the smallest structural units of odour plumes. Following loss of a pheromone plume, males cast, that is fly a crosswind course without progressing upwind. The response of casting males to interception of a pulse of 0.25 s duration was, after a delay of 0.21 ± 0.07 s, to turn and briefly fly straighter upwind, resulting in average net upwind displacements of 18 cm in a 50 cm s^{-1} wind. Upwind progress in the single-pulse response was the result of steering more upwind and an increase in airspeed, although average ground speed remained unchanged. During the last third of the surge, males turned crosswind, returning to casting flight. These behavioural reactions to pheromone contact and loss support the phasic-tonic model of odour-modulated flight, in which an underlying tonic counterturning rhythm, expressed upon pheromone loss, is briefly overridden by phasic upwind surges, expressed upon interception of the pheromone filament. The surge portion of the cast-surge-cast response was diminished and more crosswind if individual pulses were shorter (0.02 s), probably due to 'sub-optimal' contact with pheromone. The cast-surge-cast response to interception of a single 0.25 s pulse was used as a template to interpret the form of flight tracks in plumes of known structure. The template matched portions of flight tracks of males flying in plumes of low pheromone pulse frequency, thus reflecting the male's pattern of pulse encounter. In plumes ensuring a high frequency of pulse interception, only the upwind surge portion of the template was expressed, resulting in nearly straight upwind flight tracks. Similar nearly straight upwind flight tracks occurred in flights along plumes of low pulse frequency with large volume. Thus flight tracks of male *C. cautella* to point sources of pheromone depend on both the frequency and the size of filaments encountered.

Key words. Almond moth; *Cadra cautella*; sex pheromone; anemotaxis; orientation; attraction; odour plumes.

To find a mate, males of most moth species follow a plume of sex pheromone upwind to a calling female. Pheromone is transported downwind in turbulent eddies, which range in scale from centimetres to several metres. Individual filaments of pheromone may be transported relatively undiluted for many metres before being torn apart and mixed with clean air by small-scale turbulence[1,2]. The pheromone plume mediating long-distance mate finding in moths is, therefore, of heterogeneous structure.

The most accepted explanation of upwind flight to a pheromone source invokes the integration of two mechanisms, optomotor anemotaxis and self-steered counterturning, both triggered by in-flight contact with the pheromone plume[3]. Upon contact with pheromone, the angle of steering with respect to the wind and the ground speed of flight are maintained at average 'preferred' values by optomotor anemotaxis, a feedback mechanism responsible for maintaining constant the angular velocity of image motion across the male's eye surface[4–6]. The frequency of turns back-and-forth across the wind is thought to be set by a self-steered counterturning generator[3,7]. The integration of these two programmes is modulated 'moment-to-moment' by the interception of individual odour pulses comprising the fine-scale structure of turbulent plumes[8–10], usually resulting in an upwind zigzag flight track[3]. Continued loss of contact with the pheromone plume causes the male to cast, i.e. halt upwind progress and widen the flight tracks across the wind[4,11]. Upon contact with a single pheromone filament, casting males stop counterturning and surge upwind briefly[8–10]. If no more filaments are intercepted, the male returns to casting flight. Changes in the shape of flight tracks of male moths reflect changes in the frequency of pulse interception[9], suggesting that upwind flight might be a summation of single-pulse responses[8–10,12]. In this study we characterised the response of casting *Cadra cautella* (Walker) (Lepidoptera: Phycitinae) males to the interception of single, brief pheromone pulses, and we used

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this response as a template to interpret flight tracks along point source plumes of differing structure.

Material and methods

Insects. *C. cautella* larvae reared on a stored-products diet[9] were separated by sex at their last larval stage, and males were reared in separate rooms. Pupae were transferred to 25 × 25 × 25 cm screen cages placed inside pheromone free-environmental chambers (25 °C, 75–80% R.H.). Daily transfer of all pupae to a new cage left only one-day-old adult males in the old cage, and these males were tested during the initial two hours of their first scotophase.

Wind tunnel. The low-turbulence of the pulling wind tunnel used to create the laminar airflows of 45 and 50 cm s^{-1} is described elsewhere[13]. The field of view of a video camera below the transparent wind tunnel floor was 80 × 90 cm at the level of the central axis of a pheromone plume. Wind tunnel room conditions were 5.5 lux from red and white incandescent lamps, 25 °C, and 80 ± 5% R.H. The floor pattern consisted of randomly arranged 9.5 cm diameter dots of red transparent plastic which provided non-directional visual cues for the flying moths[14].

Chemicals. The two acetates comprising *C. cautella* female sex-pheromone, (*Z*,*E*)-9,12-tetradecadienyl acetate (99.7% pure, IOB, The Netherlands) and (*Z*)-9-tetradecenyl acetate (97.3% pure, IOB, The Netherlands), were formulated gravimetrically into solutions of 1 μg μl^{-1} hexane, and then volumetrically in a ratio of 5.7:1.0. They were subsequently diluted to provide 4.5 ng in the 10 μl of solution added to the pheromone source filter paper, an optimal dose to elicit upwind flight of males exposed to ribbon plumes[9].

Plumes. The structure of plumes was evaluated frame-by-frame and the size of individual pulses was measured from horizontal and vertical high contrast video images of $TiCl_4$ 'smoke' plumes[9]. Smoke plumes were generated by pipetting $TiCl_4$ onto the filter paper serving as an odour source. A high intensity directional light from a fibre optic illuminator was aimed at the centre of the longitudinal axis of the smoke plume. This plume was then video-recorded against a black background. The resulting video image was analysed frame-by-frame, and the sizes of 100 pulses per treatment were measured.

Active plume generation. Pulsed pheromone plumes were created using an air pulser (Stimulus Flow Controller SFC-2, Syntech) to generate a stream of pulses of specified volume (flow rate from 0 to 50 ml s^{-1}), duration (0.2 to 600 s), interpulse interval (0.1 to 600 s), and repetition (1 to 1024 pulses)[9]. Air flow from the pulser was connected to an odour delivery device located underneath the wind tunnel floor and 20 cm downwind from the upwind screen. The air delivered by the pulser entered a chamber (8 mm diameter × 4 mm depth) containing a filter paper disk (Whatman No. 1) of 0.7 cm diameter, impregnated with 10 μl of the pheromone solution. The pheromone-laden air was forced out of the odour chamber through a disposable micropipette (2 mm external diameter, 1.2 mm internal diameter, 12.2 cm long), that crossed the wind tunnel floor and opened inside the wind tunnel working section, 11 cm above the floor. The micropipette introduced little turbulence into the laminar airflow downwind of the odour source device, and thus the structure of individual pulses was maintained throughout the working section of the wind tunnel. To ensure an essentially constant rate of emission from the pheromone source throughout the experimental sessions, the pheromone source was replaced every 10 min. To minimise contamination of the odour delivery system, the micropipette was replaced after testing 5 males, or after 10 min, whichever came first.

The pulser was set to deliver pulses of 0.1 s duration every 0.2 s for the rapidly pulsed plume, or every 1.5 s for the slowly pulsed plume, both generated at an airflow of 5 ml s^{-1}. The diameter of a pulse generated by injection of a volume of 5 ml s^{-1} for 0.1 s was 2.45 ± 2.68 cm (mean ± SD), with a length of 5.33 ± 1.16 cm for the rapidly pulsed plume and of 6.67 ± 1.2 cm for the slowly pulsed plume.

Passive plume generation. The passive odour source was a disk of filter paper (Whatman No. 1) 0.7 cm in diameter. It was held in a horizontal position, parallel to the floor, by an insect pin. The pin was attached to one end of a hollow copper tube (3 mm diam) that slid through a hole in the floor of the wind tunnel. The odour source was located 15 cm above the floor, in a point equidistant from the sides of the tunnel and 10 cm from the upwind screen.

The passive odour source generated narrow and continuous ribbon plumes of 0.8 ± 0.2 cm width × 0.1 ± 0.1 cm height. The addition of either a 1 × 1 cm or a 3 × 3 cm deflector made of clear plastic and positioned 4 cm upwind of the filter paper of the passive odour source resulted in two turbulent plumes, a narrow and a wide plume, respectively. Turbulence generated by the deflectors fragmented the ribbon plumes into pulses or filaments of smoke intercalated with 'clean' air. Video analysis of the structure of these turbulent smoke plumes showed that a stationary point, positioned in the centre of the plume 150 cm downwind from the source platform, was intermittently surrounded by pulses of smoke and clean air. Pulses occurred at a regular frequency which was characteristic of deflector size. The 1 × 1 cm deflector generated pheromone pulses of 0.07 ± 0.04 s duration, every 0.19 ± 0.06 s The interval of clean air between pulses, the mean interpulse duration, was 0.11 ± 0.01 s. The 3 × 3 cm deflector generated smoke pulses in average 0.17 ± 0.04 s of duration,

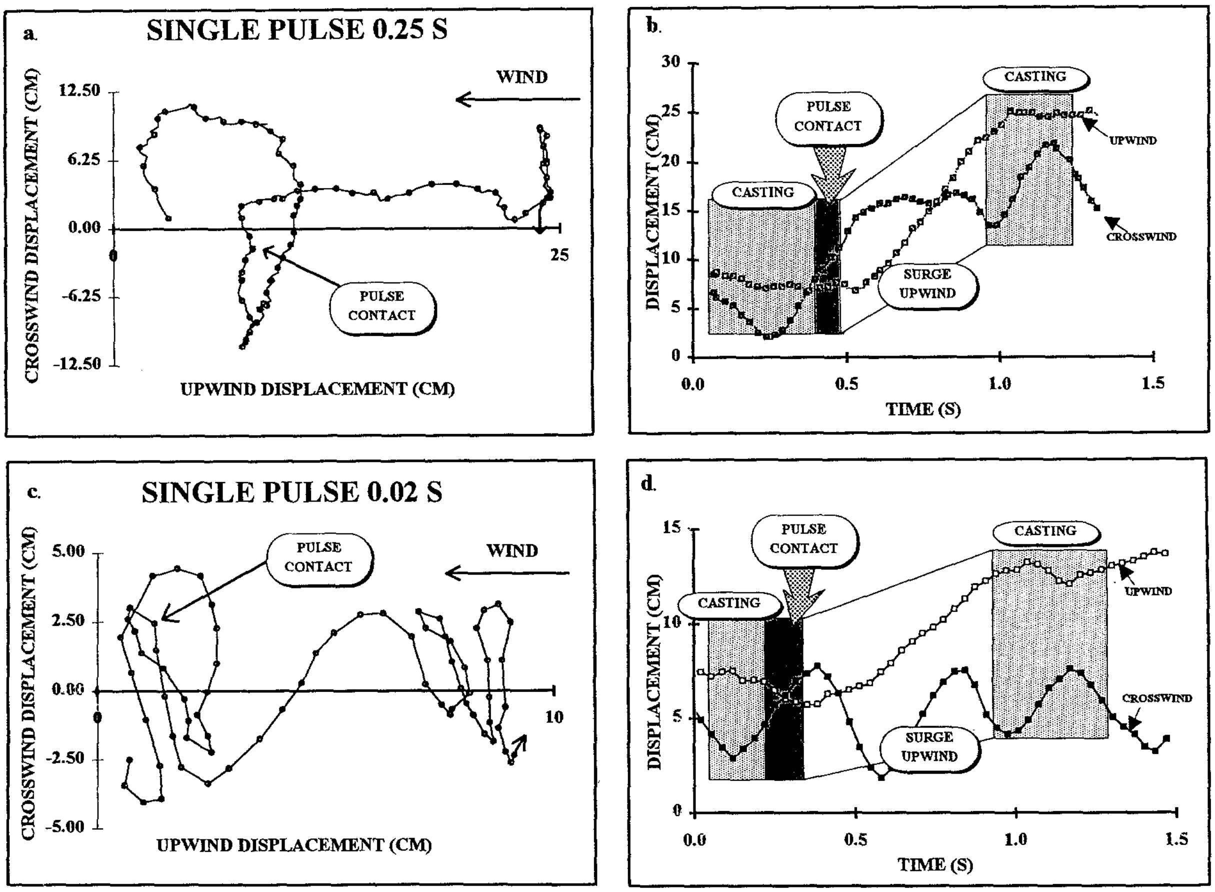

Figure 1. Response of casting *Cadra cautella* males to the interception of a single pulse of pheromone. Males following rapidly pulsed (5 Hz) pheromone plumes were induced to cast upon removal of the plume. Casting males were then challenged with a single pulse of pheromone. The response to interception of a single pulse was, after a short delay, a brief surge due upwind, followed by recurrence of casting. The straightness and duration of the surge upwind were correlated with the duration of the pheromone pulse intercepted. *a)* Flight track of a male that intercepted a 0.25 s pulse; *b)* dissection of the flight track (a) into its upwind and crosswind displacement; *c)* flight track of a male that intercepted a 0.02 s pulse; *d)* dissection of the flight track (c) into its upwind and crosswind displacement. The dissection of the flight track into its upwind and crosswind components shows a sudden interruption in the counterturning rhythm upon pheromone interception, followed by suppression of crosswind displacement and expression of a rapid upwind displacement (e.g. b). The suppression of crosswind displacement was incomplete if the pulse intercepted was short (e.g. c). The brief upwind surge fades and the male returns to casting, dominated by crosswind displacement. Only small fractions of the long casting flights are depicted. Dots represent the moth's position every 0.03 s.

every 0.25 ± 0.04 s. The mean interval between pulses for this deflector was 0.08 ± 0.01 s.

Single pulse. Males flying upwind along a rapidly-pulsed (5 Hz) pheromone plume were induced to cast upon removal of the plume in a position in the downwind half of the camera's field of view. A single pheromone pulse (0.25 s or 0.02 s duration) was then presented to the casting male. The generation of each pulse of pheromone was flagged by audio and visual signals recorded on a videotape. Frame-by-frame video analysis of single TiCl4 smoke pulses generated under same experimental conditions allowed accurate prediction of the position of a pheromone pulse in the wind tunnel at a given moment. Casting males that intercepted the single pheromone pulse had their track analysed[8,9].

Flight track analysis. Male upwind flight in a field of view 80 x 90 cm ending 15 cm from the odour release was video recorded through the tunnel floor, using a Sony RSC 1050 rotary-shutter video camera connected to a SLO 340 video recorder. Flight tracks of individual moths were transferred to a Sony SVM-1010 motion analyser, and played back frame-by-frame through a 41 cm Panasonic WV-5470 black-and-white video monitor. Two points of reference on the wind tunnel floor, and the moth's position in every second frame (every 1/30th s), were transcribed from the monitor onto transparent acetate. The X and Y coordinates of the moth's position in the two dimensional plane were obtained using a digitiser pad (Apple Graphics Tablet), and analysed for ground speed, airspeed, net speed, course angles, track angles, and drift angles using the triangle of velocities method[4], whereas inter-reversal distance, turn frequency and inter-reversal time were calculated directly from the track. The definitions of the parameters of flight are the

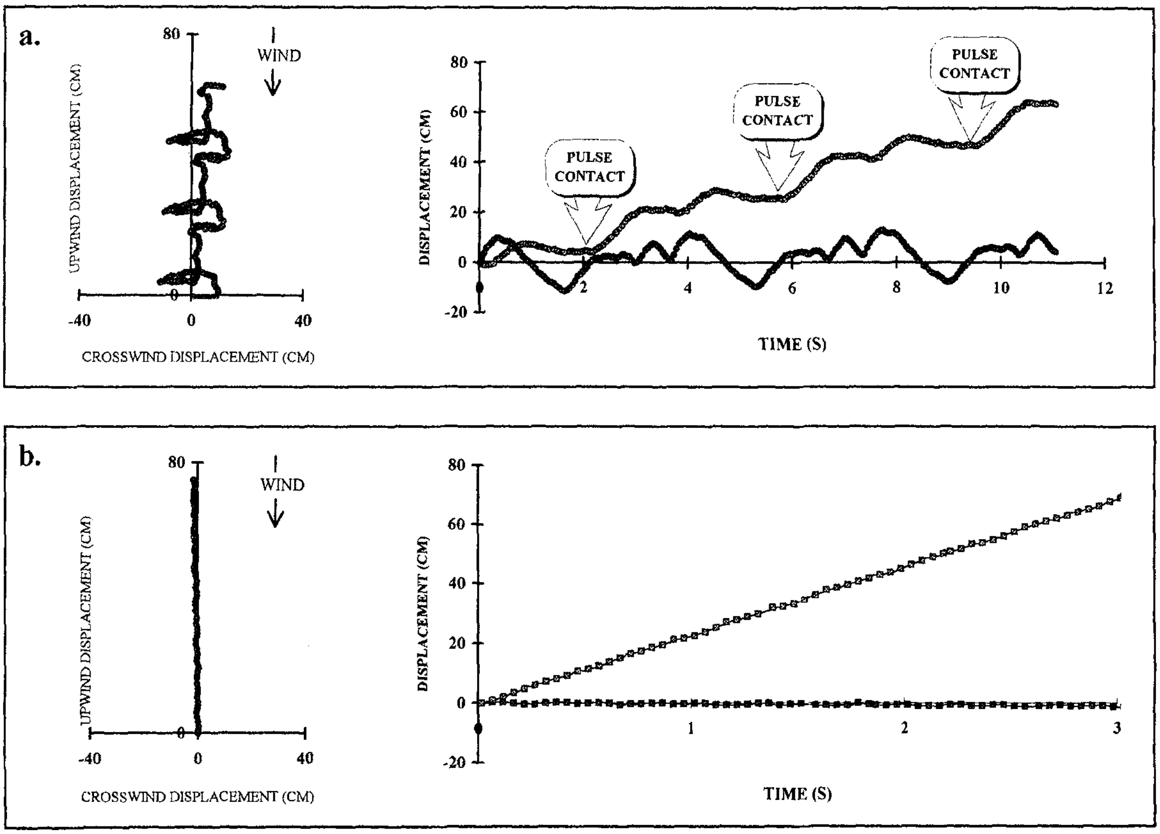

Figure 2. Theoretical flight tracks along plumes with 0.25 s duration pulses. *a)* In plumes of low pulse frequency, males cast until they contact pheromone. Following pulse interception males adopt a more upwind heading and fly nearly straight upwind. Alternating between surges upwind and casting results in tracks with zigzag portions interconnected by straight upwind legs. This form of flight results in slow upwind progress, with a nearly constant average ground speed. *b)* In high pulse frequency plumes a new surge upwind is elicited before the last surge wanes, resulting in nearly straight upwind flight tracks. Since the surge upwind in response to a single pulse is the result of a change in direction to upwind and not a change in ground speed, flight under high frequency of pulse interception should result in straighter upwind flights tracks than flight under low frequency of pulse interception, but the ground speed of flight should be similar under both interception regimes.

same as in Mafra-Neto and Cardé[15] and they are in accordance to the current nomenclature of flight parameters[16-18].

Results and discussion

Single pulse. All *C. cautella* males flying along the rapidly-pulsed plume initiated casting after the plume was removed. Once the plume was truncated, the nearly straight upwind flight tracks of males following rapidly-pulsed plumes became zigzaggy. The rhythmic turns and counterturns during the two seconds monitored following plume removal displaced the moths nearly the same crosswind distance, 14.5 ± 2.6 cm from the apex of the last turn. Males initiated casting flight 0.71 ± 0.15 s after the last possible interceptable pulse was transported downwind of the flying moth.

Interception of a single pulse of pheromone induced males to interrupt casting and to shift their flight thrust from crosswind to more due upwind. A surge straighter upwind was achieved by reduction of lateral displacement while the ground speed was maintained at the same level. The level of crosswind suppression and upwind surge depended on the duration, or size, of the pheromone pulse intercepted (fig. 1).

Pulse of 0.25 s duration. Interception of 0.25 s pulses induced males to abandon crosswind heading (after a latency of 0.21 ± 0.07 s), frequently in the middle of a turn, and adopt a straighter upwind flight, maintained for 0.72 ± 0.1 s at net upwind speeds of 22.12 ± 3.15 cm s^{-1}. This translates into 18.33 ± 4.4 cm of upwind net upwind displacement (figs. 1A, 1B). During the last third of the surge, upwind displacement waned and males flew more crosswind, which marked the commencement of casting. Although the net upwind speed increased substantially during the upwind surge, usually doubling its value, ground speed remained fairly constant throughout an entire response to single-pulse interception.

Pulse of 0.02 s duration. Interception of short pheromone pulses of 0.02 s duration resulted in briefer upwind surges (0.57 ± 0.13 s) and shorter upwind dis-

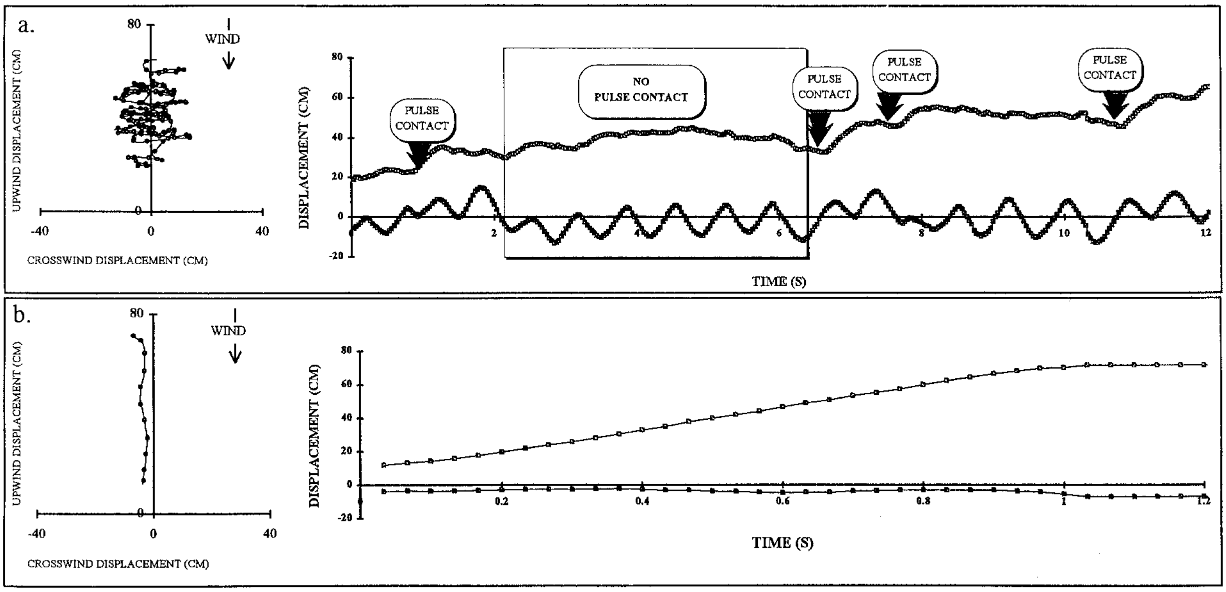

Figure 3. Actual flight tracks along pulsed pheromone plumes. *a)* Slowly-pulsed plume, 0.1 s pulses separated by 1.5 s interval. Five pulse interceptions are apparent in this flight track; each pheromone pulse interception is marked by the interruption of the counterturning rhythm in conjunction with a brief displacement upwind. During a period in which the male missed a pulse (from 3 to 6 s), counterturning was expressed in a rhythmic tempo with consistent interleg distances. *b)* Rapidly-pulsed plumes, with 0.1 s pulses separated by 0.1 s interval. Flight tracks under high frequency pulse interception conformed with the theoretical predictions in that the flight was straight upwind, but the actual ground speed was higher than predicted, indicating that these males employed more upwind thrust.

placements (11.43 ± 2.3 cm) than evoked by longer 0.25 s pulses ($p = 0.0025$) (fig. 1). Interception of shorter pulses also elicited lower levels of counterturning suppression, resulting in more sinusoidal upwind-surge flight tracks than observed for longer pulses. The net upwind speed for short pulses was 15.87 ± 3.22 cm s^{-1}, significantly lower than for longer pulses ($p = 0.048$).

A flight track model

If males fly upwind in turbulent plumes by responding to individual pulses and gaps of clean air, then upwind flight tracks to pheromone sources should be a summation of responses to odour interception dictated by the instantaneous fine-scale structure of the plume[8,10]. The effective rate of pulse encounter should be reflected, therefore, in the flight manoeuvres performed: if the rate of pulse encounter is low, males should cast between the surges upwind in response to interception of individual pheromone pulses (fig. 2A). If the rate of encounter is high, males should 'lock on' to the plume and perform a series of interconnected dashes upwind (fig. 2B).

Actual flight tracks

Slowly-pulsed plumes. Flight tracks of males intercepting new pulses at intervals of at least 1.5 s in slowly-pulsed plumes reflected the template of single-pulse interactions (fig. 3A). Two aspects of that template are evident in tracks to slowly-pulsed plumes: first, a brief suppression of crosswind displacement coupled with straighter displacement upwind, and second, the full expression of the counterturning programme between pulses with an unvarying turning tempo and crosswind displacement. The ground speed was 42.5 ± 4.25 cm s^{-1}, and the mean track angle was 73.9 ± 7.19 degrees.

Rapidly-pulsed plumes. Males encountering rapidly-pulsed plumes, with pulses separated by only 0.1 s, flew nearly straight upwind tracks (fig. 3B) presumably due to the expression of a new surge upwind before the last had faded. Although nearly straight flights were the predominant characteristic of rapidly-pulsed plumes, some males performed clear turns and counterturns. On average, males following rapidly-pulsed plumes flew faster ground speeds, airspeeds, and net upwind speeds than expected if upwind flight was to be the simple direct summation of individual surges upwind. Although the responses to pulse interception in slowly-pulsed plumes seem to be independent of each other, and therefore similar to that of individual single pulses, a decrease in the interval between pulse interceptions appeared to promote an interaction among behavioural responses, increasing the moth's flight speed. Interception of a single pulse caused males to change their course angle more due upwind, although average ground speed was unaltered. However, to maintain constant ground speed throughout the transition from a

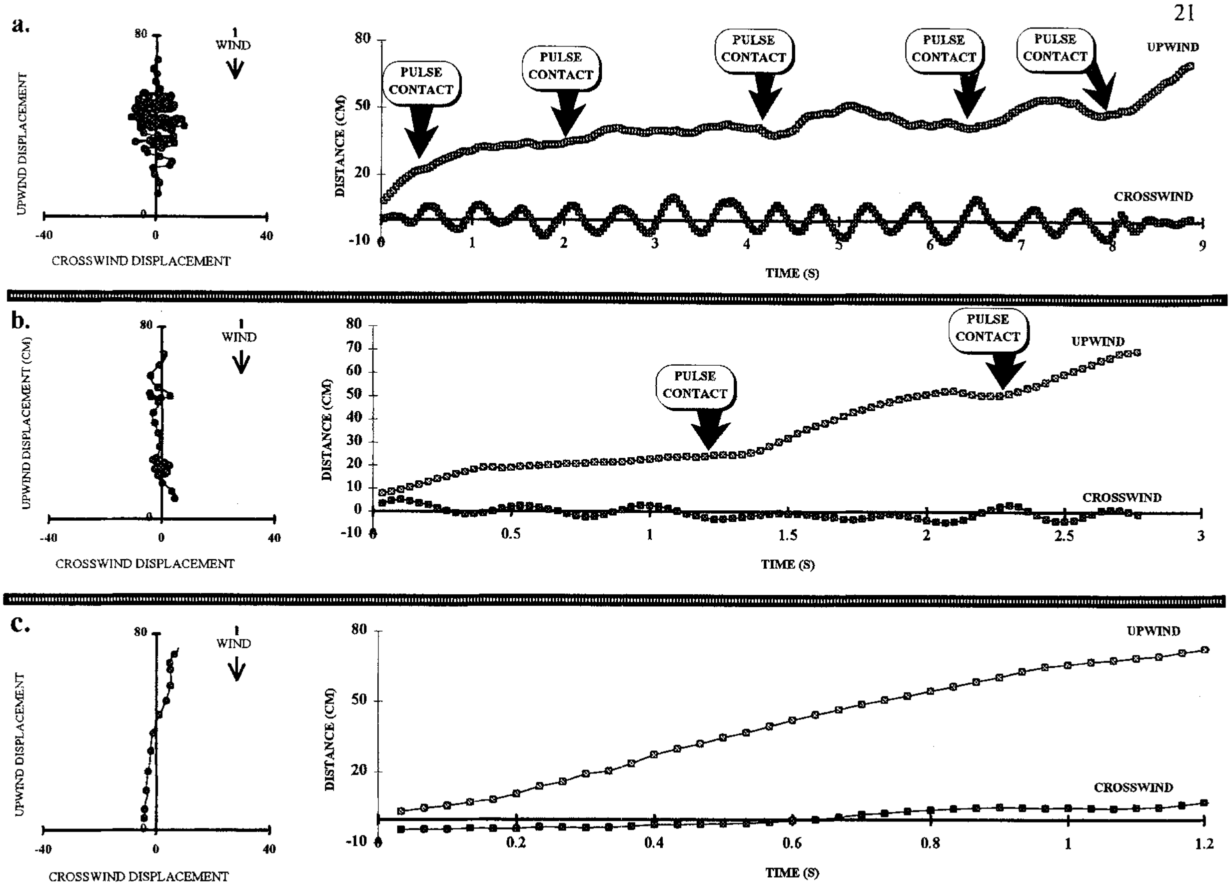

Figure 4. Flight tracks along point source plumes of differing dimensions. *a)* Track along a continuous ribbon plume of 0.8 ± 0.2 cm width, 0.1 ± 0.1 cm height, shows five interruptions of the counterturning rhythm, each combined with a brief upwind displacement. The narrow dimension of the plume probably provided only brief contacts with pheromone, resulting in incomplete suppression of the counterturning rhythm, resembling surges to short pulses, e.g. figure 1c. *b)* Flight track along a narrow turbulent pheromone plume generated by adding a 1 × 1 cm deflector 4 cm upwind of a pheromone source, which otherwise would generate a ribbon plume. This set-up produced 0.07 ± 0.04 s duration pulses separated by 0.19 ± 0.06 s gaps. Interception of the narrow turbulent plume resulted in surges upwind with moderate suppression of the counterturning rhythm. *c)* Males flew rapidly in nearly straight upwind flight tracks along a wide turbulent pheromone plume. Wide turbulent plumes were generated by adding a 3 × 3 cm deflector 4 cm upwind of the source, which produced 0.17 ± 0.04 s pulses separated by 0.25 ± 0.04 s gaps of clean air.

more crosswind flight of casting to the straighter upwind flight of surging, males increased their airspeed. For males already flying straight upwind, an increase in airspeed elicited by the interception of additional pulses translated into higher ground speeds; for males flying across the wind, an increase in airspeed was accompanied by a change in course angle towards upwind.

Ribbon plumes. Narrow, continuous ribbon plumes may to be difficult for males to follow, as they seem to lose contact with it frequently[9]. Because of the intermittent nature of pheromone contact, flight tracks to narrow ribbon plumes should reflect single-pulse responses, with typical brief surges upwind upon pulse interception, followed by periods of zigzagging across the wind line in the absence of pheromone. Males seemed to cast when they lost contact with the plume and once they regained contact with the plume, they surged upwind (fig. 4A). However, during the surge upwind, counterturning was not suppressed entirely, presumably because pheromone contact was very brief. Thus the responses to interception of pheromone of males flying along continuous ribbon plumes are similar to the response of casting males to the interception of a 0.02 s single-pulse.

Narrow and wide turbulent plumes. The narrow and wide, turbulent plumes were comprised of individual pulses of pheromone separated by gaps of clean air[8,9]. Males flying along narrow, turbulent plumes frequently turned crosswind and initiated casting, indicating that they often lost contact with pheromone (fig. 4B). Casting was seldom observed in males following wide turbulent plumes, suggesting that they rarely lost contact with the plume (fig. 4C). The complete cast-surge-cast template to single-pulse interception fits portions of the flight track of males following narrow turbulent plumes, indicating that the response to contact with this plume is similar to that of males following slowly-pulsed plumes or ribbon plumes. Due to their straightness, flight tracks of males flying to wide turbulent plumes typically lack regions in which the cast-surge-cast template to a single pulse is expressed. Even though wide turbulent plumes had pulses generated at lower frequency than narrow turbulent plumes, flight tracks along the former were similar to flight tracks along rapidly-pulsed plumes: upwind displacement dominated the flight while counterturning was suppressed. Thus, similar to an increase in pulse frequency, an increase in the size of turbulent plumes from narrow to wide resulted in higher ground speeds and straighter flight tracks. Similarities in the shape of flight tracks along wide turbulent plumes and rapidly-pulsed plumes, in spite of the former having significantly lower pulse frequencies, may be explained by longer upwind surges elicited by the large pulses (e.g. fig. 1) making up wide, turbulent plumes.

Conclusions

Males produced flight tracks that reflected either the full cast-surge-cast template of response to interception of a single pulse or only certain portions of this model, depending on the structure of the pheromone plume encountered. Flight along plumes in which contact with pheromone was frequent (due to size or frequency of the pulses) resulted in relatively straight flight tracks that we interpret to be a string of upwind surges. Males intercepting pulses at high frequency increased their average ground speed substantially, probably because a new surge was elicited before the last surge waned. Flight along plumes in which contact was less frequent generated tracks reflecting the complete cast-surge-cast response.

Differences in response to interception of single pulses during flight along pheromone plumes of different frequencies should reflect the differences in pheromone perception at the antennal receptor level. The sensory system of moths can resolve frequencies of pheromone pulse contact high enough to decode the structure of the plume[19,20]. In stationary electroantennograms of *Heliothis virescens* exposed to chains of pulses from 1 to 10 Hz[20], interception of individual pulses at low frequency elicited similar depolarization for each new interception, but pulse interception at frequencies above 5 Hz caused the antenna to become increasingly less able to recover fully to the baseline between pulses. At a frequency of 10 Hz, for example, the first pulse elicited a response similar to an individual single pulse, but subsequent arrival of pulses induced increasingly smaller, although unequivocally present, depolarizations.

Flying males modify their manoeuvres according to the current structural characteristics of the plume. The plasticity of moth upwind flight to pheromone sources appears to be the result of a constant modulation of single-pulse responses to the characteristics of the newly intercepted filaments. The behaviour of the male at the moment when the new pulse was intercepted became the baseline for the expression of the new single pulse response. If the male was counterturning, the interception of a new pulse resulted in a change in course, whereas if the male was already flying straight upwind, the male often accelerated airspeed. Thus, single pulse reactions seem to be modified by the male's recent history of pheromone interception instead of simply being the expression of a fixed, single pulse template. Interactions among the single pulse responses provide plasticity to pheromone-mediated flight; this strategy may enhance the efficiency of source location in variable winds.

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