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CHEMILUMINESCENT TAGS FOR TRACKING
INSECT MOVEMENT IN DARKNESS:
APPLICATION TO MOTH PHOTO-ORIENTATION

Joseph L. Spencer¹, Lawrence J. Gewax², James E. Keller³ and James R. Miller³

ABSTRACT

The flight tracks of *Manduca sexta* (Lepidoptera: Sphingidae) flying toward a 5 watt incandescent light bulb were recorded under low light conditions with the aid of a camera-mounted photomultiplier and a glowing marker technique. Small felt pads bearing a chemiluminescent (glowing) material, Cyalume®, were affixed to the abdomens of free-flying moths. Tagged insects orienting to a dim incandescent bulb were easily visible to the naked eye and were clearly captured on videotape. On their initial approach to the light source, *M. sexta* were found to orient at a mean angle of $-0.22^\circ \pm 2.7^\circ$ (mean \pm SEM). The speed of the initial approach flight (0.4 ± 0.03 m/s) was significantly faster than the speed immediately after passing the light (0.29 ± 0.02 m/s; $t = 6.4$, $P < 0.0001$, $n = 61$). Flight tracks obtained from transcribed video records show *M. sexta* initially fly approximately at a light source and only after passing it, do they engage in circular flight around the source. *M. sexta* flight to lights does not entirely match any paths predicted by several light orientation mechanisms, including the commonly invoked light compass theory.

The nocturnal flight of many insects is known to be influenced by the presence of celestial light sources. Nocturnally active insects are thought use celestial lights as navigational points of reference; rising and falling catch totals at light traps between new and full-moon nights support the notion that nocturnal insects are attracted to, or at least affected by moonlight in significant numbers (Nemec, 1971). A flying insect able to maintain a constant angle between its direction of motion and a distant light source, like the moon or a bright star, would travel efficiently in a straight line. However, with the advent of campfires, candles and porch lights it became possible for insects to erroneously orient to artificial lighting, which, unlike celestial lights, can be nearby. Insect attraction to these lights has been a source of human wonder and topic of poetry and song for ages.

The most often invoked modern explanation for the seemingly suicidal flight of moths, described to circle and plunge into flickering candle flames, is

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known as the light compass theory (Buddenbrock, 1937). According to Buddenbrock's theory, a flying moth, orienting with respect to a local light source, makes ever more frequent course adjustments as it approaches the source in order to hold the light's image at a constant position in its visual field. The path of such an insect would initially be straight, but would transform into a logarithmic spiral as the light was approached. Such a spiraling flight would end with the insect plunging into the candle flame or battering itself against the surface of an incandescent bulb.

Though the light compass explanation is widely professed, the casual observer will note that few insects ever spiral classically to their doom; most insects either ceaselessly circle a flame or fly straight into it. Clearly, there must be other orientation mechanisms in use by insects attracted to candles and porch lights, as well as other reasons (like predation) to explain the light-seeking behavior of some insects and arthropods (e.g., who has not seen gangs of spiders in webs clustered around outdoor lighting, or feeding mantids perched beneath corner street lamps on a summer evening?). [A detailed review of the literature on spatial orientation and insect/arthropod vision in general may be found in Wehner (1981)]. In addition to the light compass theory (Buddenbrock, 1937), there are two other popular explanations: the open space hypothesis of Mazokhin-Porshnyakov (1960), and the Mach band theory championed by Hsiao (1970; 1973), and supported by evidence from numerous authors (see Hsiao, 1970 for references).

The open space hypothesis (Mazokhin-Porshnyakov, 1960) has as its central tenet that field-dwelling nocturnal insects use light as an indicator of open space, and when exposed to it at night, exhibit a positive phototaxis which would normally facilitate escape from enclosed areas like leaf litter and thick plant canopies. This hypothesis predicts that insects should move in paths directed toward lights. Encountering bright artificial lighting during scotophase may stimulate daytime-like patterns of activity, including attraction to light, in diurnal insects. Behavior in the close vicinity of lights is not expressly predicted by this hypothesis.

The Mach band theory has at its core the phenomenon of lateral inhibition, a contrast-enhancing mechanism common to the visual systems of numerous taxa. First demonstrated by Hartline (1956) using the compound eye of *Limulus polyphemus*, the horseshoe crab, lateral inhibition involves enhancement of edge contrast around objects in the visual field by inhibition in unstimulated receptors next to stimulated ones, which in the case of a moth approaching a flame, would be around the periphery of the light's image. Lateral inhibition results in the enhancement of light-dark boundaries; the dark boundary is perceived to be darker than it really is and the light boundary much brighter. The areas of enhanced light and dark are called Mach bands after Ernst Mach who first observed enhancement of light-dark boundaries in humans.

Light orientation by a Mach band mechanism also may involve changing insect responsiveness to light. It was proposed (Robinson and Robinson, 1950) that flight orientation toward lights is composed of two phases: initially an insect is attracted and exhibits a positive phototaxis, but once it nears a light the phototaxis becomes negative and the insect attempts to escape. Interpreted in light of Mach band theory, it is supposed that the dazzling brightness near the light causes insects to become negatively phototactic and to attempt an escape by flying toward the darkest region of their visual field. But, as a consequence of lateral inhibition, the darkest area in their visual field is found next to the brightest light at the dark Mach band. The insect becomes "trapped", according to this theory, flying toward the perceived darkest areas (Mach bands) at the periphery of the light's looming

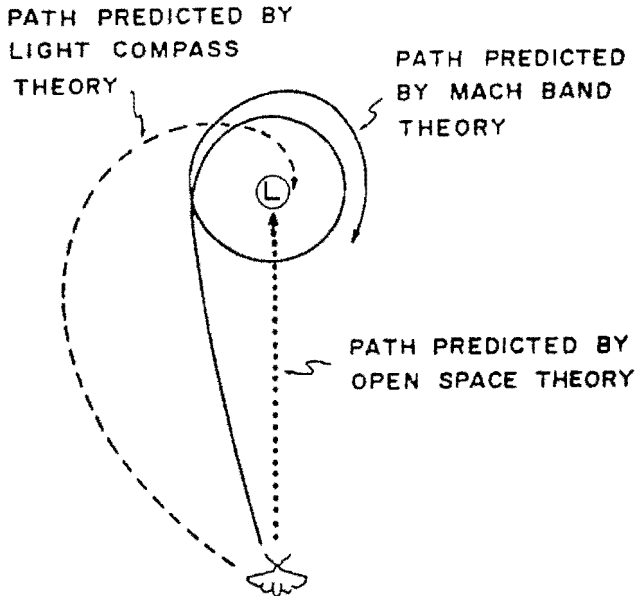


Figure 1. Flight paths of moths flying towards a light as predicted by three orientation theories (adapted from Hsiao, 1973 and used with permission).

image, and in doing so it maintains a near circular path around the light. The above described theories lead to different predicted flight tracks and light orientation angle distributions (Figs. 1 & 2).

In this study, we sought to quantify the light-oriented flight tracks of *Manduca sexta* (L.) (Lepidoptera: Sphingidae), the tobacco hawkmoth, a strong-flying, night-active moth shown to orient toward lights at night (Stewart *et al.*, 1969). An unbiased evaluation of predictions derived from the light orientation theories demanded recording of flight tracks from free-flying moths be done in near darkness. However, studying the orientation of flying insects to a single dim light under dark conditions is at best a challenge.

With the exception of insects that “carry” their own light, like lightning beetles (Coleoptera: Lampyridae), finding and accurately tracking nocturnal insect movement is difficult, especially when the subjects are rapid fliers like hawkmoths. We found that standard video/cinematic recording methods required more light than was available under conditions when crepuscular or nocturnal insects are active. Moreover, supplementing ambient lighting sufficiently enough to meet the minimum equipment light requirements may interfere or inhibit expression of the behaviors of interest. Military surplus night-vision devices or low lux video equipment offer a partial solution to the illumination problem, but often at significant expense and loss of resolution.

While planning our investigation, we found inspiration in the lightning beetle’s “self-contained” light and devised a simple method for tagging insects with chemiluminescent (glowing) material obtained from within Cyalume®

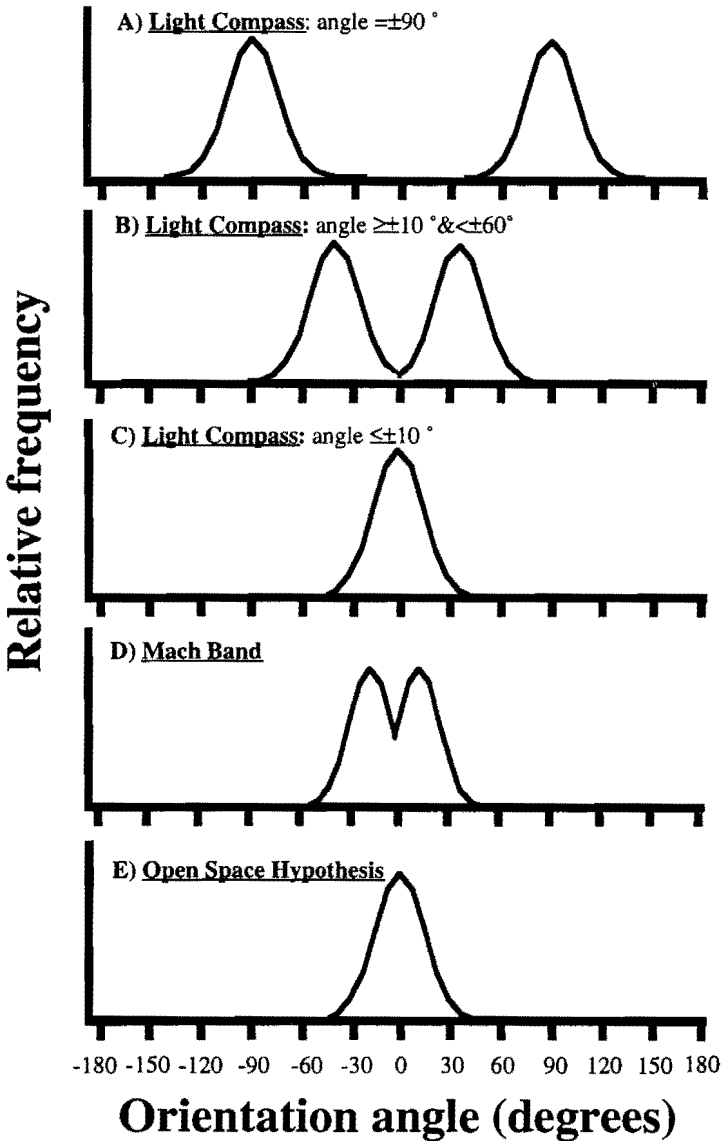


Figure 2. Flight orientation angle distributions predicted by: Light Compass theory with mean approach angle equal to: A. $\pm 90^\circ$, B. $\geq \pm 10^\circ$ & $< \pm 60^\circ$, C. $\leq \pm 10^\circ$; D. Mach Band theory, and E. Open Space hypothesis. A normal distribution of orientation angles about the mean was assumed for each.

light sticks. Once tagged, moving insects and their paths were observable in near-total darkness. With the aid of a photomultiplier device attached to a black and white camera, we recorded and quantified the rapid free-flight paths of individual glow-tagged *M. sexta*, visible as a bright moving spot in video records, as they oriented to a tiny light.

MATERIALS AND METHODS

Insects: Adult diet-reared *Manduca sexta* (ca. 1 week old) were provided by Dr. M. Rubin from the Department of Physiology at Michigan State University. Insects were obtained 1 or 2 days before orientation trials and held in 1m² aluminum screen cages and provided *ad libitum* with a 10% sucrose solution.

Light source: A single 5 watt incandescent white Christmas tree bulb controlled by a rheostat was used as a light source. Attached at the top of a 1 m tall rod in a portable stand, the bulb's brightness was adjusted so illumination at 10 cm above and 10 cm to the side of the light was 19 and 12 lux respectively, corresponding to the lowest possible rheostat setting.

Test site: Experiments were conducted after dusk in an enclosed pole barn located ca. 2 miles south of Michigan State University at the Department of Entomology's Collins Rd. Field Research Site. Stray illumination from a few nearby bright lights was excluded by blocking windows and covering 8 translucent skylights with thick black plastic for the duration of experiments (July–Sept., 1991).

Video system: A Sony AVC-3450 B/W video camera equipped with a "Javelin" photomultiplier (Apollo Lasar Division, Los Angeles, CA 90035) and a Sony 12.5–50 mm TV Zoom lens set at 12.5 mm were mounted on a tripod suspended from barn rafters 4.5m above the floor. From this height, the camera field of view was 7.6 m² at floor level and 4.7 m² at the height of the bulb. Because the photomultiplier's phosphor was extremely sensitive to light, the camera system was shielded from direct light. The system was protected by positioning a small opaque disk between the light source and the camera lens, at a point 1 m above the light. The disk shaded the camera from the bulb's direct light, but did not block the recording of moth flight through the area around the bulb. A white felt disk (ca. 1 cm dia) bearing a small amount of glowing Cyalume® was attached at the center of the disk to indicate the position of bulb below and serve as a reference point for flight track analysis. To reduce reflections from the floor into the camera and to provide a uniformly dark background, the floor around the light was covered by 12- 1.0 × 1.5 m sheets of flat-black posterboard and the base of the light stand was wrapped with a dark cloth.

The camera was connected to a NEC HQ DX-1000U VHS videocassette recorder positioned on a platform in the barn rafters above the camera. A video monitor (21" Sony Tritrion), also positioned in the barn rafters, was periodically used to check the quality of the video image. The TV screen was kept darkened and was positioned so not to be visible from the arena or release sites on the floor below.

Moth Tagging: To track fast-flying moths in near-dark conditions a small glowing tag was attached to the abdominal tip of each insect. The tag consisted of a small disk of white felt (ca. 0.75 cm dia) glued with cyanoacrylate adhesive to one end of a 3 cm length of nylon thread (Stream and Tackle supersoft 0.5 lb test monofilament line). Tags were attached by first anesthetizing the moths lightly on an open CO₂ diffusion table, and removing scales from the dorsal aspect of the last 2–3 abdominal segments with a piece

of masking tape (scales stick to the tape and are easily pulled off). A small drop of rubber cement was applied to the scale-free area, and the free end of the nylon thread (attached to the felt pad) was inserted. Once the rubber cement had dried, and the tag was secured, moths were placed into individual styrofoam containers inside a closed box for transport to the test site. All lights (except the 5 watt experimental light source) in the facility were turned off prior to application of the chemiluminescent material and flight testing (timed to coincide with full darkness outside).

Moth tags became luminescent once treated with the non-toxic chemiluminescent (glowing) liquid obtained from Cyalume® light-sticks (manufactured by American Cyanamid Company, Chemical Light Department, Milton, FL 32570). Light is produced when the two components of the liquid are mixed (under normal use conditions, bending of the light-stick breaks an ampule containing catalyst which mixes with a colored substrate to produce cool-chemical light). The two components were collected by cutting light-sticks open and separating the substrate (colored liquid free inside the glow stick) and catalyst (contained in a glass ampule) into separate vials. When combined in an approximate 1:1 ratio, and applied to the felt disk (two drops/disk) portion of the tag, the mixture glowed brightly for ca. 30–40 minutes. If Cyalume® is applied directly to the wings, thorax or abdomen of *M. sexta*, it rapidly stops glowing; direct treatment with Cyalume® also wets the insects and they do not fly.

Insects were flight tested immediately after their tags were treated with Cyalume®. Total mass of the tag, chemiluminescent material and rubber cement was ca. 0.08 g. In preliminary tests, *M. sexta* (mean individual moth mass ca. 3.0 g) flight did not appear to be affected by carrying this additional weight (in earlier tests, much smaller male gypsy moths, *Lymantria dispar*, and armyworm, *Pseudaletia unipuncta*, flew to lights wearing a smaller version of this device weighing 0.02 g).

Orientation trials: Insects carrying glowing tags were released from a 1 m tall platform whose position was varied around the perimeter of the flight area. Video was recorded continually during a series of orientation trials which lasted ca. 1 hr. To aid in the later identification of flight trials on the long video records, a swatch of reflective white cloth was moved into and out of the camera's field-of-view just prior to placing each moth on the release platform. Preflight wing fanning behaviors were usually observed before insects took flight. Moths failing to initiate flight within a few minutes were warmed in the experimenter's hands and replaced on the platform. It was occasionally necessary to gently toss an insect vertically into the air to stimulate flight. Only rarely did insects not fly toward the light source when released.

We recorded 83 individual flights during 6 nights of recording. Each flight track was transcribed by plotting the successive frame-by-frame (30 frames/second) position of the glowing tag (seen as a bright moving dot on video) onto an acetate sheet placed against the screen of a television monitor. From each tracing, an orientation angle was determined by first drawing a best fit line through the points comprising the insect's initial flight towards the light (beginning where the insect first entered the field of view and ending at the point where it passed the light source). The orientation angle was measured between (a) the position of the light and (b) the point on the best fit line where the flight track passed the light (Fig. 3a). The measurement was made from a position on the best fit line 0.75 m backwards from point b. Calculated approach angles for flights passing to the right or left of the light were assigned a positive or negative sign, respectively. Approach angles were analyzed using an unpaired analysis, and tested against the null hypothesis that

the angles did not differ from 0° (i.e., flight directly into the light). It was not possible to accurately measure changes in elevation using our video system. We believe variation due to within flight changes in elevation to be small; we observed most insects to approach and circle within a horizontal plane at the level of the light with little vertical movement during orientation.

Individual flight track lengths were calculated by summing the distances between successive points on the frame-by-frame plot and multiplying that value by a scaling factor determined from an internal measurement standard (a meter stick held horizontally at the height of the light and video-taped at the beginning of each session). Rate of flight was calculated by multiplying track length by the number of video frames comprising the track times the interval between successive frames (0.033 s/frame). Using this method, rates of flight were determined for the frames comprising the initial inward approach flight toward the light, and compared to that for an equal number of frames on the outward flight after passing the light. Individual inward and outward flight speed data were analyzed by paired t-test with $\alpha = 0.05$.

RESULTS

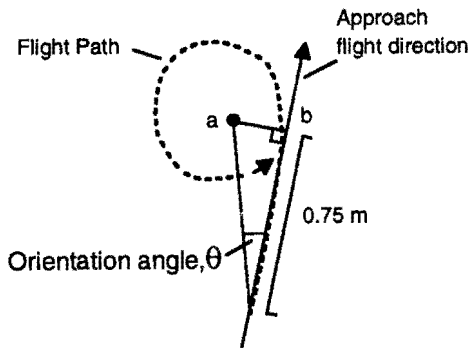
Eighty-three flight tracks were recorded, 63 met an orientation criterion: they exhibited a change in direction or rate of displacement upon approaching the light. Of the remaining tracks, twelve were non-orienting flights and were not analyzed further, eight were unusable because the insect landed on the arena floor, lost its tag during flight, or etc. A path deviation near the light was observed in 83% (52/63) of flights (in three of these, moths turned acutely just before reaching the light). A change in rate of displacement $\geq 10\%$ of the approach rate was observed in 86% (54/63) of the flights; 78% (49/63) of flights had both directional and rate changes upon nearing the light. There was a linear component to the approach in 93% of all flights. The mean light orientation angle was $-0.22^\circ \pm 2.7^\circ$ (mean \pm SE) (range -90° to $+50^\circ$) (Fig. 3b) and was not significantly different from 0° ($t = -0.08$, $P = 0.94$, $n = 63$). Only 4/64 flights had measured orientation angles of 0° . Eighty percent (49/61) of insects slowed down after passing the light. The mean rate of displacement while approaching the light (0.4 ± 0.03 m/s) was significantly faster than the rate (0.29 ± 0.02 m/s; $t = 6.4$, $P < 0.0001$; $n = 61$) after insects passed the light (two insects that landed on the light were omitted from this analysis).

DISCUSSION

M. sexta trailing glowing-chemiluminescent tags were easily visible to the naked eye in flight and during subsequent viewing of video records. In frame-by-frame analysis, the moving tag permitted accurate plotting of flight paths.

There was considerable variation in *M. sexta* orientation angles to the light source, however, most approaches were directed towards the light. A mean angle of approach near zero ($-0.22^\circ \pm 2.7^\circ$) (Fig. 3b) suggests *M. sexta* fly more or less directly to the light, an observation consistent with the open space hypothesis and light compass orientation with very small light orientation angles (Fig. 2). However, after a predominantly linear initial approach, some insects flew approximately circular loops centered around the light source; looping circular flights are consistent with the Mach band hypothesis, but would be expected to occur much closer to the light. We did not observe

A)



B)

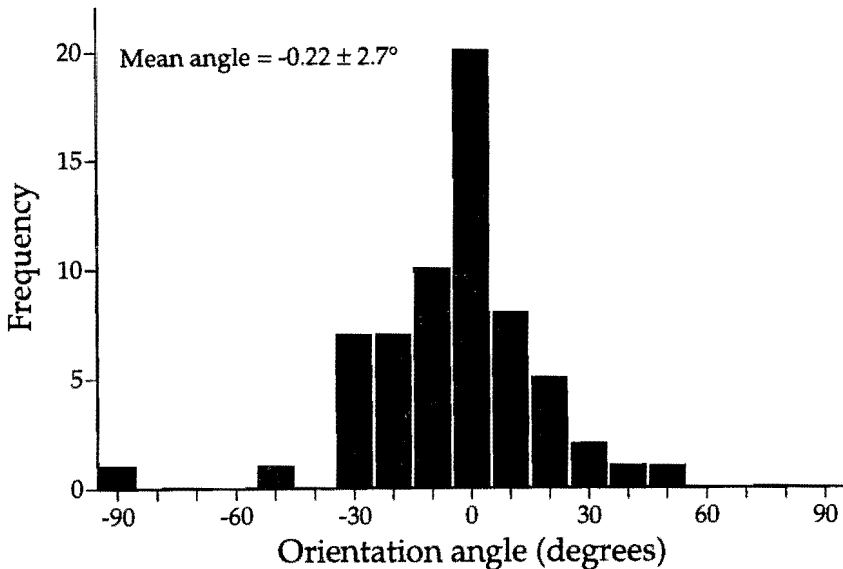


Figure 3. A. Light orientation angle measurement method. Approach angles (in degrees) were measured between (a) the position of the light source and (b) the point where a best fit line to the moth's initial inward flight path crossed a perpendicular to the light source. The measurements were made at a position on the best fit line 0.75 m from point (b). B. Frequency histogram of *Manduca sexta* orientation angles measured while flying toward a 5 watt incandescent light bulb. The mean orientation angle (\pm SEM) was not significantly different from 0° (unpaired t-test; $t = 0.08$, $P = 0.94$, $n = 63$).

logarithmic spirals consistent with light compass orientation in *M. sexta* flight paths.

The combination of linear flight toward light and subsequent circling or turning flights suggests that *M. sexta* may employ multiple light orientation mechanisms. The linear inward flight may be a consequence of a positive phototaxis manifest as an attraction to light or use of the light as a reference point (as suggested by the light compass theory). Very near the light, *M. sexta* may become deterred and express a negative phototaxis manifest in brief circling flight before flying off or landing some distance from the light. Away from the bright light, they regain their positive phototaxis and fly toward it once more (an observation consistent with those of Robinson and Robinson (1950) regarding changing responsiveness to light). Hsiao (1973) suggested a similar pattern of attraction followed by repulsion was occurring in *Helicoverpa zea*.

In his experiments with *Helicoverpa zea*, Hsiao (1970, 1973), used a system in which moths were tethered to styrofoam "boats" floating on a flight "pond". Once flying, the insect powered the boat around the two-dimensional liquid surface, a conductive metal keel on the boat interacted with an electric field in the pond and permitted precise recording of the insect's path over time. Under these conditions, *H. zea* exhibited a strong tendency to orient toward the dark side of an interface between juxtaposed bright and dark stimuli, and to engage in circular "flight" around a point light source, observations supportive of the Mach band hypothesis. However, Hsiao's tethered moth experiments may have altered moth behavior.

We suspect that the ingenious use of boats and tethered moths, while an excellent method to track the insects, imposed a "speed limit" upon test subjects and robbed them of flight momentum. Thus, in Hsiao's arena, *H. zea*, turning and orientation occurred at speeds far slower than those during free-flight to lights. Slower speeds would afford insects more time to respond to changing spatial relationships and thus greater than normal fine control over turning and course adjustments resulting in "flight" tracks of unusual precision.

Flight momentum may be a significant factor limiting behavior as insects approach and pass a luminous source. *M. sexta* are heavy-bodied, fast-flying moths; the combination of their forward momentum with the rapidly changing spatial relationship between the mover (the moth) and the stationary light source may make a timely response to changing stimulation impossible. The situation is analogous to an automobile driver encountering a sudden sharp turn. A slow-moving driver can negotiate a tight curve, but the inertia of a fast moving car makes following the same prescribed path physically impossible. It is possible that the speed and momentum of a flying *M. sexta* physically limit its capacity to change course even when faced with information indicating course adjustments are needed to maintain an established spatial relationship with a light source.

In these records, insect flight slowed significantly beyond the point of their closest approach to the light, a position where the image of the light would be brightest and moving at a maximal rate across the visual field. Perhaps, the slowing is a consequence of attempting to turn back toward the light as it is passed. Of insects changing course near the light, 80% (39/49) exhibited a turn toward the light, suggesting many insects were still positively phototactic at what, in many cases, was the point of closest approach to the light. Most turns were initiated close to the light; 28%, 26% and 28% of turns occurred within successive 12 cm zones extending outward from the light whose luminosity dropped rapidly from 12 to 3 to 1 lux over those same intervals (luminosity at 5 cm was 46 lux).

One might argue that by the time *M. sexta* fly past the light they have become negatively phototactic and are caught in Mach band chasing flight. However, the diameter of our light source was <0.5 cm; flight toward its Mach bands would put the insect far closer to the light than we observed. Nevertheless, we cannot rule out the possibility that the large differential between *M. sexta*'s size and that of the bulb may make it impossible to sustain Mach band oriented flight or any close flight around such a small bulb.

When the orientation angle and the complete orientation paths of each track obtained during this experiment are considered, there is little evidence to suggest that *M. sexta* ever follow a logarithmic spiral path when approaching a light. The observation that most tracks contained an initial linear approach phase followed by a curvilinear circling phase lends support to a mixed mechanism model for *M. sexta* light orientation. Flight paths of insects navigating according to light compass or Mach band theories could look very similar depending on the angle of orientation to light. Insects employing the light compass mechanism with a small orientation angle (e.g., $\pm 10^\circ$) would have an angle distribution very similar to that which would be expected for Mach band navigating species, except that the Mach band distribution would have a gap around 0° (Fig. 2).

Confusion among the orientation theories could also exist at the level of flight track interpretation. For instance, moths orienting according to a light compass mechanism with orientation angles of ca. $\pm 90^\circ$ would not spiral into a light, but instead fly in circles around the light source, an expectation consistent with the Mach band theory. The effects of various orientation angles on the flight paths of light compass-orienting insects are discussed in detail in Fraenkel & Gunn (p.111; 1961). Interindividual variation in orientation angle could further complicate interpretations. Sothibandhu and Baker (1979) found that on a given night, the angle of orientation to a light trap by individual underwing moths, *Noctua pronuba*, was the same as the orientation angle to the moon, and that the angle was individual-specific. Without knowing *M. sexta*'s preferred flight heading with respect to luminous stimuli, or if *M. sexta* even maintains one, distinguishing between likely light orientation mechanisms will be difficult. We can say *M. sexta* likely incorporates open space hypothesis-like initial orientation (attraction towards light), followed by sustained circular flight, which could be generated by Mach band-like orientation, a light compass mechanism with orientation angles of ca. $\pm 90^\circ$, or execution of a simple motor program that turns the insect in the direction of the eye most stimulated.

Observing insect movement can provide insight into general mechanisms behind insect behavior. Despite the importance of understanding how stimuli affect patterns of movement, we know relatively little about the behaviors and natural movements of most insects. In this paper, we have described a simple technique for marking and recording activities of an insect under otherwise difficult conditions. Chemiluminescent tagging is a technique which has applications where inadequate lighting makes observation difficult. Though used here as a trailing marker, glowing tags could be affixed directly onto insects whose behaviors might dislodge a dangling tag. In addition to use in light sensitive video recording, the tags are bright enough to be useful for following large scale nocturnal movements of individuals in the field.

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