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INTERACTION BETWEEN VISUAL AND PHONOTACTIC ORIENTATION DURING FLIGHT IN *MAGICICADA CASSINI* (HOMOPTERA: CICADIDAE)Thomas E. Moore¹, Franz Huber², Theo Weber², Ulla Klein², and Cornelia Bock²

ABSTRACT

Visual and phonotactic orientation often occur simultaneously in diurnal cicadas, and these animals generally have their largest sensory elaboration in eyes and hearing organs. Phonotactic orientation occurs principally during flight. Males and females of *Magicicada cassini* commonly perform low-altitude (< 5 m) and short-distance (< 15 m) flights in their natural habitat at flight speeds of 3 to 6 m/s. During flight, the long body axis is tilted 10° to 45°, head upward. Wing beat frequencies of tethered animals at 24° to 26°C averaged 28.8 Hz. Body temperature in the field for flying individuals averaged 4.6°C above ambient.

Compound eyes of females possess about 7% more facets than males, and the binocular field of view for both is especially expanded dorso-frontally, frontally, and fronto-ventrally.

The role of vision for phonoresponses, and in flight and landing behavior, was studied in nature by comparing controls with cicadas with eyes partly to completely covered with aluminum paint. Cicadas with their three ocelli covered behaved like controls and exhibited low-altitude and short-distance flights with landings on neighboring shrubs, as did cicadas with only both caudal halves or both dorsal halves of the compound eyes covered. Those with both compound eyes covered completely (with or without additionally covering the three ocelli) flew to higher altitudes and for longer distances. Higher and longer flight courses were also seen in cicadas (A) with only one compound eye covered, which in addition circled during walking and flight toward the side of unrestricted vision, (B) with both frontal or both ventral halves of their compound eyes covered, and (C) with either the binocular or monocular fields of the eyes covered. Thus, the paired fronto-antero-ventral regions of the compound eyes provide visual information for habitat-dependent low-altitude flights and landings.

Females with intact compound eyes and ocelli responded to playbacks of just the frequency/intensity sweep at the end of the buzz in calling songs of a male by flying within 1.2 m above the ground and landing on a nylon screen-covered small bush directly above the loudspeaker from distances of 2 to 8 m, mostly from lower vegetation. Males that were blinded, or blinded and deafened, sang less and flew less than normal males. However, they performed all of those behaviors, and all also walked and fed.

Periodical cicadas (*Magicicada*, Tibicininae) are known for synchronized adult emergence and noisy aggregations of millions of individuals of three

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intermingled species in each brood population (Alexander and Moore 1962). Broods are isolated geographically and chronologically, such that in some years no periodical cicada adults emerge, and most areas of the eastern United States have only one brood population appearing as adults at intervals of either 13 or 17 years.

In all *Magicicada* species, daily flights affect spacing and aggregation of both sexes during feeding, chorusing, mating, and ovipositing. Flights are mediated by both acoustical and visual cues. Each species in these aggregations establishes mating leks. These aggregations continue to mix, every day and unpredictably, during the emergence period. Toward the end of the reproductive season, males die sooner than females, leading to little or no chorusing, and then females disperse progressively further from the lek sites. The cohesive effect of the acoustical cues of chorusing males on these cicada populations is obvious.

Both sexes of all six species of periodical cicadas live and feed on shrubs and trees of different species, sizes, and shapes, and females lay eggs in their living twigs. Their niches overlap almost completely, the three species of 13-year or 17-year cicadas being separated principally by diurnal acoustic behavior leading to aggregation sites that change every day and are seldom exclusive to a single *Magicicada* species. Adults frequently change location in these complex visual environments by short-distance and low-altitude flights, which we call bush-hopping. These flights are associated with sound communication and reproductive activities and are most commonly observed during bright sunlight and at ambient temperatures above 25°C with little wind (Alexander and Moore 1958, 1962; Dunning et al. 1979). Otte (1990) and Toms (1992) discuss the common correlation between hearing and flying in orthopteroid insects, interactions basically similar to those found in cicadas.

The present paper describes the interaction of vision (compound eyes and ocelli) and phonoresponses of males and females of *Magicicada cassini* (Fisher) in walking, but especially in flight and landing behavior, within a natural habitat.

MATERIALS AND METHODS

Field work was done in a second growth wooded and recently grazed area in Jackson County, Missouri, southeast of Kansas City, from 7–23 June, 1981. Predominant woody vegetation at this site included smooth sumac (*Rhus glabra*), dogwood (*Cornus* sp.), elderberry (*Sambucus canadensis*), honey locust (*Gleditsia triacanthos*), osage orange (*Maclura pomifera*), slippery elm (*Ulmus rubra*), and black walnut (*Juglans nigra*), surrounded by mixtures of grasses and forbs. The shrubs ranged to several meters in height and the taller trees ranged to about 10 m in height.

The study period was in the middle of the adult emergence of Brood IV 17-year cicadas. That site had *Magicicada cassini* in large numbers (at least 40,000/hectare), a very few *M. septendecim* (Linnaeus) (perhaps 200/ha), and no *M. septendecula* Alexander and Moore – but extensive choruses of *septendecula* were heard high in trees several km away. At the beginning of the study period a strong chorus of *cassini* was present with ovipositing females and mating pairs abundant; only a few adults still emerged each night for the next several days. Despite sampling several hundred living and dead individuals during the entire period, we found no individuals infected with the parasitic fungus *Massospora cicadina* Peck, and therefore, the behaviors reported are not likely distorted by disease.

Temperature Measurements

Daytime ambient temperatures ranged from 18.9°-33.5°C (\bar{x} = 26.5°C) during the 10 days between 8 and 23 June on which we made our observations, and percent relative humidity ranged from 44%-79% (\bar{x} = 63.8%) during the eight days in that period on which we recorded it (measured by a sling psychrometer with mercury thermometers). Insect body temperatures were measured using a Bailey BAT-12, battery-operated, thermometer with an IT-1E sensor thermocouple (copper/constantan) inserted into the mesothoracic musculature and read after a standard delay of 1-2 s. Flying cicadas were hand-caught and immediately punctured with the temperature sensor to record body temperatures. Wing beat frequencies of cicadas in free flight in the field could not be detected from background noises, so wing beat frequencies of hand-held (by the legs) cicadas in the field were recorded at 19 cm/s with a Roberts Stereo tape-recorder and analyzed later with a storage oscilloscope.

Flight Posture and Speed

Body posture during flight was estimated in the field and measured from still photographs of flying cicadas (in 1981, and from Brood V in 1982 in Ohio). Photographs were projected and body angles determined with a protractor (lense axis parallel to soil surface). Body postures during flight were similarly estimated from stopped frames of 16 mm and 8 mm movies. Flight speeds were recorded with a stop watch during continuous straight and slightly upward-directed flights from a takeoff site in a shrub to a landing site in a taller tree (horizontal distance 11 meters) at times of the day with little or no wind.

Eye Measurements and Visual Field

The red-pigmented compound eyes of all periodical cicadas exhibit principal pseudopupils (Fig. 1 D) which can be used to determine the binocular field of view (Stavenga 1979). Cicadas, with legs and wings cut off, were positioned on a goniometer (homemade, courtesy of K. Kirschfeld, Tübingen). Bright white light from a light guide was directed from the side, and both compound eyes were illuminated from above in the axis of view of the observer, using a semitransparent mirror positioned at 45°. The animal, either dorsal or ventral side up, was adjusted such that its head could be rotated around the pitch and roll axes. In each zero – or centered – position, the principal pseudopupils (Fig. 1) appeared at the same distance from the inner border of their corresponding eyes. Then the head was tilted in steps of 10° throughout 360° in the pitch axis. At each step of pitch, the binocular overlap was measured by tilting the head in the roll axis (left and right) until the principal pseudopupil disappeared in each eye at the inner border of that eye. Morphometric measurements of heads of males and females were taken with width of the vertex as the main parameter; size of compound eyes was determined by measuring the total head minus the width of vertex and dividing by 2, with vertical and horizontal axes of compound eyes and ocelli determined with a measuring, dissecting stereomicroscope.

Visual Orientation and Light Intensity

For visual orientation tests, the eyes and/or ocelli of freshly caught cicadas from nearby shrubs were covered with Testor Enamel #1146, "Silver" (powdered aluminum in lacquer, Testor Corp., Rockford, Ill., USA). The enamel dried within 30 s, whereupon they were returned to the cage until tested. Cicadas that displaced small patches of enamel during vigorous

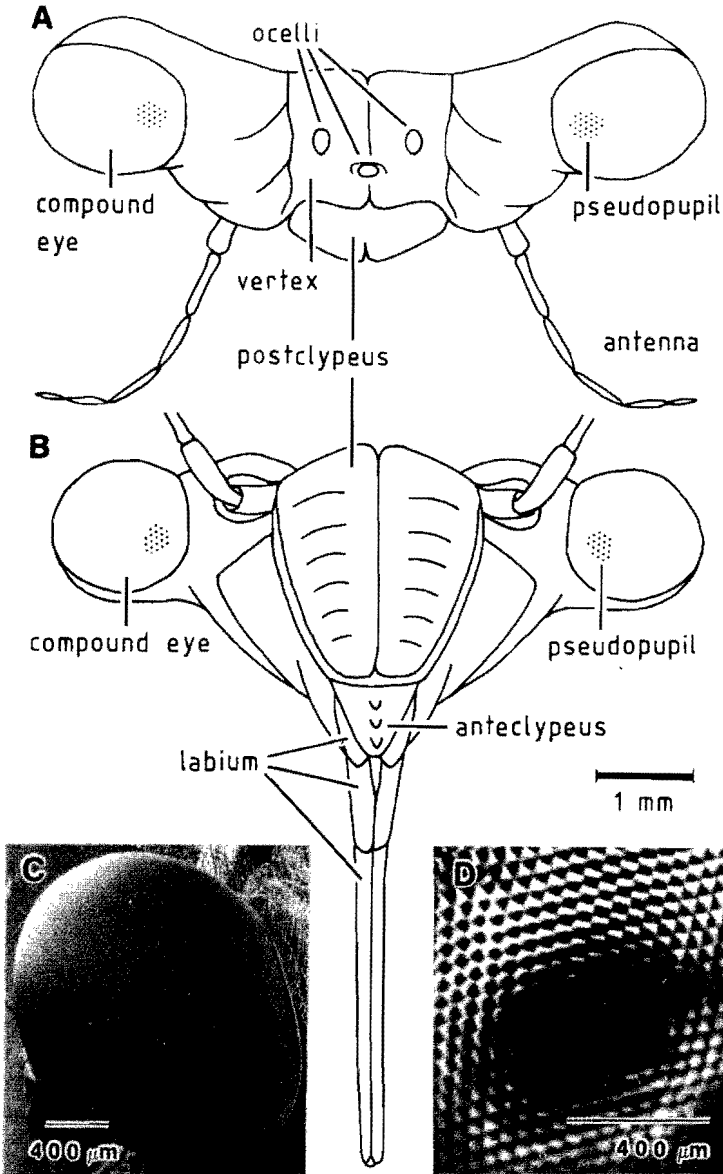


Figure 1. A-B, outline orientation of structures of the head of *Magicicada cassini*, viewed from dorsal (A) and frontal (B) aspects; principal pseudopupils (stippled areas in A and B) are diagrammed to scale according to zero head position. C, scanning electron micrograph of the whole left compound eye, viewed frontally. D, light microscope photograph of a sector of a compound eye exhibiting a principal pseudopupil (frontal area, orientation as in left compound eye in B).

grooming of the head with the front legs were not used. To gain some idea of the effectiveness of blinding with enamel, we measured the drop in sunlight intensity through a piece of clear plastic with an enamel-covered section with a Weston Electric Sunlight Illumination Meter, Model 756, under five sunlight intensities, each read twice (10 measurements). At 38,736 lux, the enamel-covered plastic sheet caused a drop to 10.76 lx, at 81,776 lx a drop to 32.28 lx. As the plastic alone caused a drop from 34,432 to 32,280 lx, and from 81,776 to 76,396 lx, the enamel reduced light intensity at a covered eye by at least three orders of magnitude; form vision was completely abolished.

For observation of walking, takeoff, and flight course, single animals were placed on a platform (surface area 30 x 30 cm) covered with either a black curtain or a grey screen placed 30 cm above ground in the center of the experimental area, as shown in Figs. 2 and 7-12. Before takeoff, verbal descriptions of walking behavior and orientation of the cicada with respect to sun position and wind direction were recorded on tape, and, in some cases, filmed at 24 frames/s with a Super 8 mm movie camera (Nizo 4080 with 1:12 zoom lens and macro lens) and evaluated as shown in Fig. 3. Tests were carried out during times of bright sunlight with little or no wind (speeds below 1.33 m/s), between 1000 and 1600 hr. At these times the general area was filled with competing conspecific choruses of unpredictably varying intensities in every direction, but the three taller trees (T) behind the vehicle and not far from the platform (Figs. 2 and 7-12) often had a little smaller chorus than much of the surrounding vegetation.

After takeoff, verbal descriptions of the flight courses, altitudes, and directions (including changes by circling, drifting, etc.) were tape-recorded and later drawn onto a map of the habitat. Sun position, wind direction and speed, ambient temperature, time of day, and landing site (if seen) were listed for each flight.

Locomotor and Singing Behavior

Experiments on locomotor and singing behavior of blinded and of combined blinded and deafened males were carried out under sunny conditions on three different days using cicadas held in caged trees. Four small trees (Fig. 2), 1.5 m tall, were covered with white nylon netting. Vegetation in the surrounding area higher than 60cm was removed. The caged trees formed an irregular "T," three were about 12 m apart, the fourth was 26 m from the end two and 30 m from the middle tree. Temperatures recorded inside versus outside the cages were within 1°C of each other. Sunlight intensity measured inside versus outside the cages varied depending on the relative proportions of leafiness of the trees and whether or not they were shaded by vegetation 5-10 m in height. The northernmost cage, with a 21,520 lx reduction in light intensity, contained the animals with only compound eyes covered in both kinds of experiments, and that caged tree was also closest to the largest nearby trees which contained the strongest consistent chorus. We used the southernmost cage for control (normal) males in both kinds of experiments, and for subsequent phonotactic experiments as well; it had a reduction in sunlight intensity of 8,608 lx inside the cage. The other two cages had only 2,152 lx reductions.

For blinding cicadas, we used the same enamel described above; for deafening, we removed the lateral portions of both tympanal membranes with fine forceps, aided by a binocular dissecting microscope; in both cases we used freshly caught males from surrounding vegetation. All animals were given a minimum of a half hour in the cages before beginning 5-minute observation periods. Blinded males were studied on 9 June, 1123 to 1646 hr, with wind speeds of only 0.28-1.9 m/s and ambient temperatures of 30-35.6°C, in four observation periods for a total of 20 min of observations, 25 males per cage, in

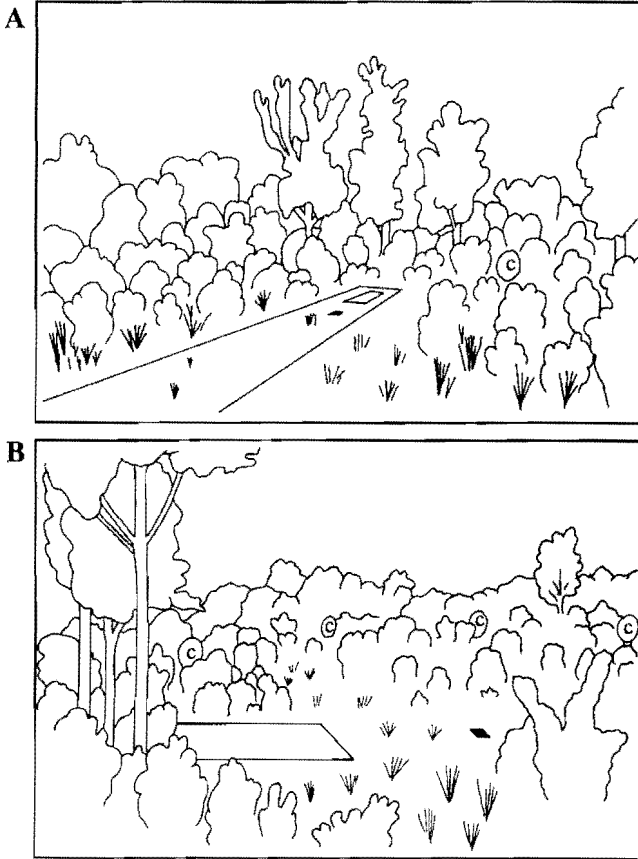


Figure 2. Diagrams of major landmarks and proportional contours of principal vegetational horizons of the experimental area from two views: A, viewed from the south-southeast; and B, viewed from the west. Grassy areas and smaller shrubs (up to 1 meter) in the foreground; shrubs and trees with a height above 4 m comprise the horizon; three taller trees indicated adjacent to parked car and near cicada releasing platform; c—shrubs covered with nets which contained captured cicadas used for experiments on effects of blinding and deafening; open rectangle—site of parked car; closed square—location of platform for releasing cicadas; larger and longer three sides of an open rectangle in A—region of lowest vegetation without shrubs used as access route for car.

the following factorial combinations: control (normal) males, only ocelli covered, only compound eyes covered, both compound eyes and ocelli covered. Males both blinded and deafened were studied on 16 June, 1440–1650 hr, at ambient temperatures of 24.9–28.5°C, and again on 17 June, 1346 to 1700 hr, at 28.8–30.5°C, at wind speeds comparable to those on 9 June, with three observations per day for a total of 30 min of observations, 20 males per cage, in the following factorial combinations: control (normal) males, only deafened

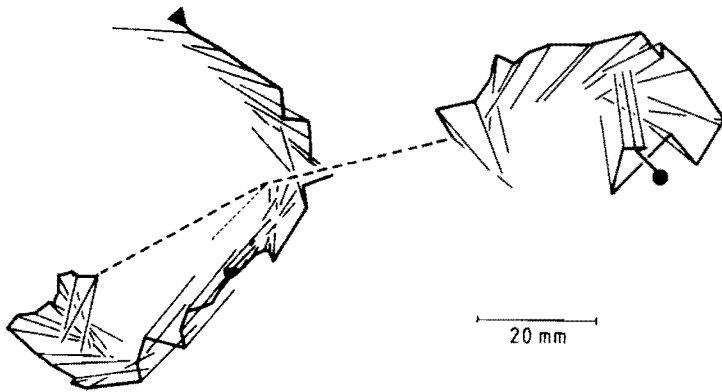


Figure 3. Computerized diagram of walking (solid line) and flight (dashed line) courses from a 17.5 second cinematographic record (24 frames/s) of one *Magicicada cassini* male. Triangle indicates the start (on the platform), circle indicates the end of the record. Longitudinal axis of body in relation to mean trajectory, measured every 250 ms (6 frames), shown by thinner solid lines.

males, males with only compound eyes covered, males both deafened and with compound eyes covered.

Phonoresponses Involving Flight

Flight during phonotaxis was stimulated by playing a tape-recorded loop of shortened buzzes without ticks, cut from tape-recorded calling songs of *M. cassini*, on a Nagra 4.2L tape-recorder at 38 cm/s through a Nagra DA Amplifier with added Jensen Supertweeter. The supertweeter speaker pointed directly upward, placed next to the trunk of a 1.5-m-tall tree covered with nylon screening in which 20 males were enclosed. The 6 s tape loop contained five buzzes lasting 0.8–1.0 s each, separated by silent intervals lasting 0.25–0.42 s. This part of the song was broadcast at a volume slightly exceeding the background sound-pressure levels, between 1630 and 1700 hr on 19 June for durations of 30 s each time, followed by a silent period of at least 30 s during which responses of freely flying animals from surrounding vegetation were noted at the nylon-covered tree.

RESULTS

Wing Beat Frequency, Flight Speed, and Body Temperature

Analyses of recordings of wingbeats of females ($N = 7$ from two females, range = 20–39/s, $SD = 6.9$, at $26^{\circ}C$) showed a mean of 28.1 wingbeats/second; while for males ($N = 8$ from three males, range = 25–39/s, $SD = 5.1$, at 24° – $26^{\circ}C$), the mean was 29.3/s. Thus, both sexes showed similar wingbeat frequencies. We also measured thoracic body temperatures for 19 males and 12

females that were flying or had just landed from a flight. For males (range = 26°-35.8°C), the mean was 31.9°C, and the mean elevation above ambient temperature was 4.3°C (range = 2.2° - 8°C). For females (range = 25.3° - 34.3°C), the mean was 27.1°C, with a mean elevation above ambient temperature of 4.8°C (range = 0° - 9.3°C).

Flight speeds, estimated from straight flights with winds of less than 0.44 m/s, covered a range between 3-6 m/s, about twice as fast as reported for *Magicicada septendecim* (White et al. 1983). We found no statistically significant difference between flight speeds in males and females, but did not correct for differences in body weight.

Natural Flight Behavior

Both sexes of *M. cassini* flew most frequently during bright sunlight between 1000 and 1700 hr. These flights almost always occurred between neighboring shrubs and trees close to the tree- or shrub-top levels, based on flights of 153 undisturbed individuals observed during a period of 10 days. Only 12 animals flew higher than the surrounding vegetation.

If a resting cicada is approached within about a meter, it responds first by moving sideways to the far side of its perch or by flying away. Males usually escaped by flying upward, whereas females often escaped by first flying slightly downward, perhaps because of heavier weight due to eggs. During cooler days, or with stronger wind and cloudy skies, both flight and singing activities were reduced. Under these environmental conditions, both sexes often escaped from visually detected disturbances by diving down to the ground. During feeding, and especially during egg-laying, the animals had a much higher threshold for visual disturbances.

Flight Posture

Based on several hundred observations, during straight and slightly ascending or descending flights, both sexes kept a body angle of 10° to 45°, head up with respect to gravity. When turning, this angle was even increased to 55° or more, but few accurate data from the field are available. When banking and landing, body angles were frequently above 45° or even 55°, for they usually landed in a steep head-up attitude, throwing the fore legs forward and spreading and lowering the hind legs a bit. During takeoff, the animals usually jumped from the substrate as they spread their fore wings from their mesonotal wing-catches, dropped a short distance and often side-slipped a bit, then flew away free from interfering branches.

Flights and Phonoresponses

In our experiments with caged males that were blinded, controls and those with only the three ocelli covered exhibited a combined total of 85 flights and 29 associated disturbance squawks during 30 minutes of observation. Males with both compound eyes and ocelli covered flew only 22% as often (combined total, 19 flights) and produced only 41% as many associated disturbance squawks as controls (combined total, 12). Controls sang 41 calling songs, while males of the three test groups combined sang only 75% as many songs, and most of those calling songs were produced by males with only the eyes covered and whose cage was closest by 10 m to the strongest—and sometimes synchronized—chorus during three of the observation periods, indicating a strong acoustical influence. In experiments with males both deafened and blinded, test animals combined only flew an average of 23% as often and produced 18% as many associated disturbance squawks, produced 75% as

many courtship sounds, and sang 45% as many calling songs as controls. In both sets of experiments, males with the compound eyes covered walked less and fell frequently, unlike controls. Additional covering of the ocelli greatly decreased walking. Lowered locomotor activity (flight and walking) was accompanied by reduced singing activity, but abolishing acoustic and visual input did not prevent singing.

Flight and Phonotaxis

In tests with shortened buzzes from *M. cassini* calling songs repeated more rapidly than in nature, undisturbed free-flying females from nearby vegetation responded in 100% of 13 experiments (with 20 thirty-second periods of playbacks, totaling 10 minutes). The 26 responding females had a mean response time of 30.8 s from start of playbacks (range 2–120 s). They landed on the outside of the screened cage and stayed there for about 5 s after the playbacks ceased, then flew about 8 m to the largest nearby trees with the strongest competing chorus. Nearly all responding females took off from vegetation no more than 1.2 m high, and flew short distances between landings (\bar{x} = 3.9 m, range = 2–8 m, N = 9, SD = 2.5 m). They turned in flight directly toward the caged tree and sound source from a distance of about 3 m, then flew closely past it and looped back to land on the net.

None of the essentially equal number of free-flying undisturbed males from nearby vegetation flew to the caged shrub during these tests. By contrast, during control periods without playbacks, totaling 20 minutes, only 2 females and 1 male approached, and these three animals arrived only during times when the males within the caged shrub were vigorously chorusing. The males within the shrub usually stopped singing immediately when the playback started, and those few which sang were unable to match their songs to the repetition rates of the playbacks.

Compound Eyes and Ocelli

The compound eyes are situated on cranial enlargements which project laterally and horizontally (Fig. 1). A corona of nearly erect long setae is borne on the cranial margin adjacent to a compound eye. The eyes are red in color in living animals, slightly asymmetric in shape (horizontal:vertical axes, 0.8:1.0), with similar curvatures in both vertical and horizontal planes. The smooth ocular surface is divided into equal-sized facets arranged in a regular, homogeneous hexagonal pattern (Fig. 1 C). The number of facets, determined by first calculating the total surface area of the whole eye and then dividing that by the area computed for a single facet ($700 \mu\text{m}^2$), was estimated at 13,000 facets for males and 14,000 for females. Morphometric measurements showed slightly smaller heads in males (Fig. 4), while overall size of compound eyes between sexes was not greatly different (Fig. 5).

The reddish, domed ocelli are borne dorsally on the vertex, and their nearly circular elevations form a triangular arrangement (Fig. 1A). All three ocelli possess single, simple lenses with reticulate surfaces. The anterior, median ocellus is slightly smaller in males than in females (for males, $\bar{x} \pm SD$, $250 \pm 23 \mu\text{m}$ for the longitudinal axis, 220 ± 22 for the transverse axis; for females, 280 ± 47 and $250 \pm 31 \mu\text{m}$, respectively). The lateral ocelli are nearly the same size (for males, 260 ± 20 and $220 \pm 16 \mu\text{m}$; for females, 270 ± 21 and $250 \pm 21 \mu\text{m}$, respectively, for longitudinal and transverse axes). For both sexes, data were obtained from measurements of 10 animals. The median ocellus is surrounded by a narrow cuticular depression and tilts somewhat forward because the vertex behind it is slightly elevated; more so in females

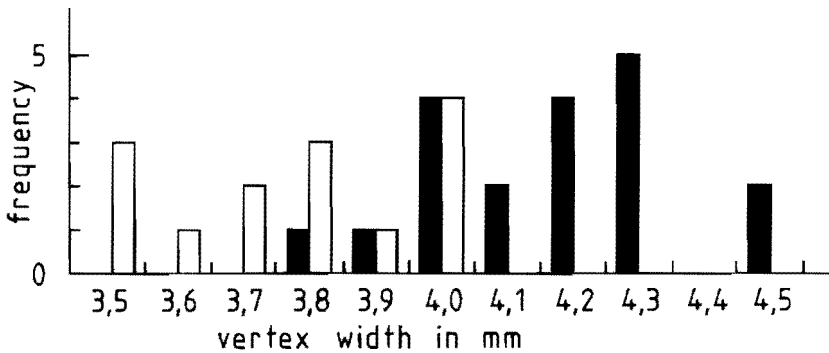


Figure 4. Histogram of head sizes in males (open) and females (filled columns) of *Magicicada cassini*, calculated from width of the vertex between inner compound eye margins. N = 14 males, 20 females.

than in males. The lateral ocelli are oval and directed slightly postero-laterally by the slightly raised antero-medial adjacent cuticle of the vertex.

Binocular Field of View

The lack of data for binocular and monocular fields of view for cicadas prompted our attempt to measure these fields. Clearly visible principal pseudopupils (stippled areas in Figs. 1 A and B) cover regions on the surface of the compound eyes of about 10 to 12 facets in diameter (Fig. 1 D). The pseudo-

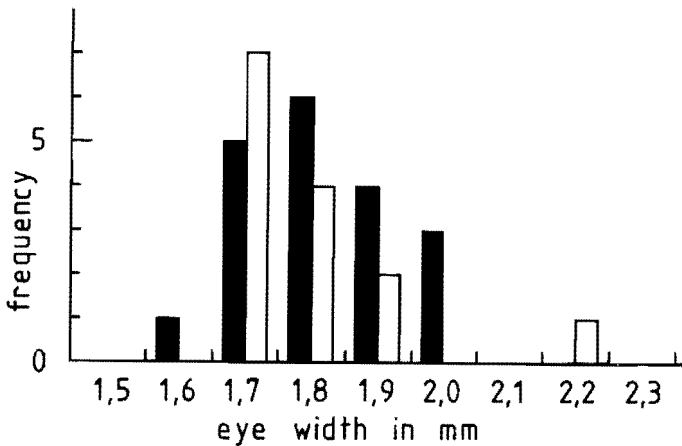


Figure 5. Histogram of sizes of compound eye widths in males (filled) and females (open columns) of *Magicicada cassini*, calculated from total head width across eyes minus vertex width divided by 2. N = 14 males, 20 females.

pupils are almost circular and slightly smaller in diameter in the dorsal and fronto-dorsal parts, but more ellipsoid and slightly larger in the frontal and especially fronto-ventral parts of the eyes, indicating a slightly lower curvature and a larger optical radius in these latter regions. Caudally, pseudopupils were more ellipsoid and elongated.

As diagrammed for visual far field measurements from three males and three females projected onto a sphere (Fig. 6), the binocular field of view is similar in both sexes. The binocular overlap extends from the front and narrows to about 30° dorso-caudally and to about 40° ventro-caudally, leaving a binocularly blind area of about 70° caudally. The most expanded binocular areas cover the dorso-frontal and the fronto-ventral regions with a slight reduction mid-frontally. Interommatidial angles were not measured, thus we have no information about differences in spatial resolution in different parts of the eye. Furthermore, the fields of view of the three ocelli are unknown, but should be quite large.

Preflight Behavior

Cicadas most commonly take off from a tree branch or other vegetation, and rather rarely from the ground (as simulated by our horizontal platform). When placed on the platform, all controls (N = 11), those with all three ocelli covered (N = 5), those with the field of binocular overlap covered (N = 4), and those with the monocular fields covered (N = 5), started to walk immediately, and after a few steps took off. Out of 25 animals tested, 19 clearly turned into the wind before takeoff. Those that walked longer and reached an edge of the platform moved along it until takeoff, without regard to wind direction.

Behavior on the platform was different for the 27 animals tested with both compound eyes covered (with and without the ocelli covered), or with just the bottom halves covered. They rested on the platform much longer, and walked more slowly than controls; after reaching an edge, they also walked along it. Takeoff was delayed from the few seconds typical in control animals to several minutes in these animals. With both dorsal halves of the eyes covered but with the ocelli not covered, 6 out of 10 additional cicadas tested raised the anterior part of the body during walking.

The 12 animals tested with only one compound eye covered (without ocelli covered) slightly inclined their bodies toward the side of the normal eye when resting on the platform. During walking, they circled toward the side of the uncovered eye, either continuously or in bouts of rather straight courses. Circling continued after they reached an edge, and also takeoff was delayed.

Flight Courses After Takeoff

Controls, and animals with only the three ocelli covered (Fig. 7), took off and flew at low altitudes (<5 m) and for short distances (<15 m) to nearby shrubs and trees, where they landed. Similar flight and landing strategies were seen in deafened animals with normal vision (N = 8, not shown in a figure). The distribution of flight courses during times with no nearby male chorus did not correlate with wind direction or sun position, but rather correlated with the location of nearby shrubs which probably provided optical landmarks. The ranges of flight distances for undisturbed normal animals that we recorded are comparable to those reported for *Magicalcicada septendecim* (Karbon 1981, Maier 1982, White et al. 1983).

One might expect that animals prevented from form vision (or even totally blind) would not take off for flights. However, as documented in Fig. 8, all 13 animals tested with both compound eyes covered, and all six tested with compound eyes and ocelli covered, took off and then made a dramatic change

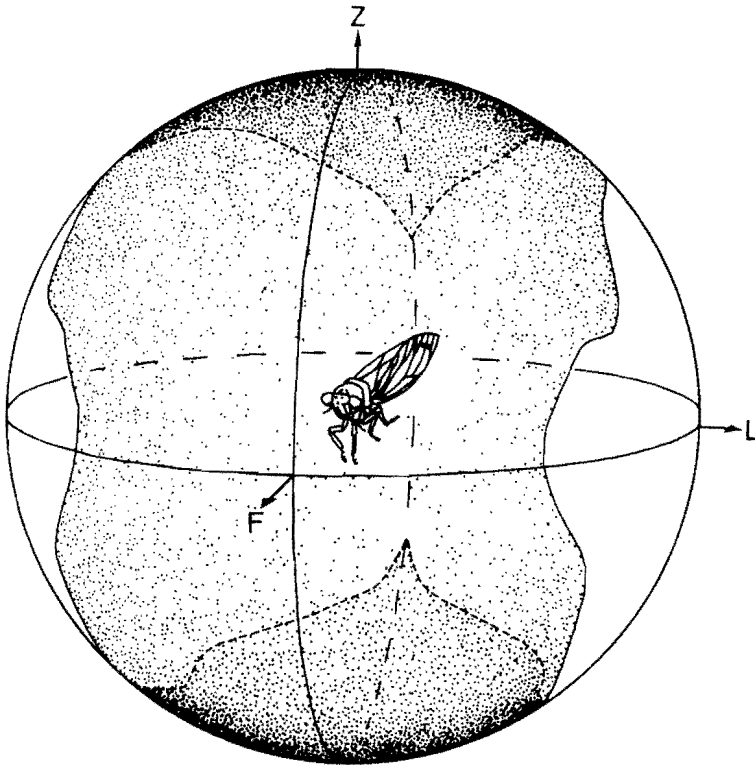


Figure 6. Global (three dimensional) diagram of the binocular field of view of *Magici-cada cassini* males or females. Light stippling with solid boundaries represents anteriorly directed binocular fields; darker stippling and dashed boundaries represents caudally directed binocular fields; unshaded parts of the globe represent monocular visual fields. F, frontal point originating from the equator; L, lateral point; Z, zenith. The cicada diagram in the middle orients the fields of view.

in flight course. These animals increased their flight altitude very rapidly (often to more than 15 m within several seconds), and reached heights of more than 30-50 m. They passed beyond the tallest trees and kept flying for long distances (more than several hundred meters) until they became lost to view. Only two animals landed within sight, but they flew low and may have crashed into a shrub or tree. Again, there was no clear correlation with either wind direction or sun position. At least at the beginning of flight, when these animals could be closely watched, the body was tilted head up by 10° to sometimes 30° , and no obvious change in flight performance or aerodynamic stability was evidenced. However, one could see these animals frequently drifting more than controls in stronger winds aloft. Some of them changed altitude by alternating short passages of horizontal or even descending flights followed again by upward directed flying. Our experimental design did not

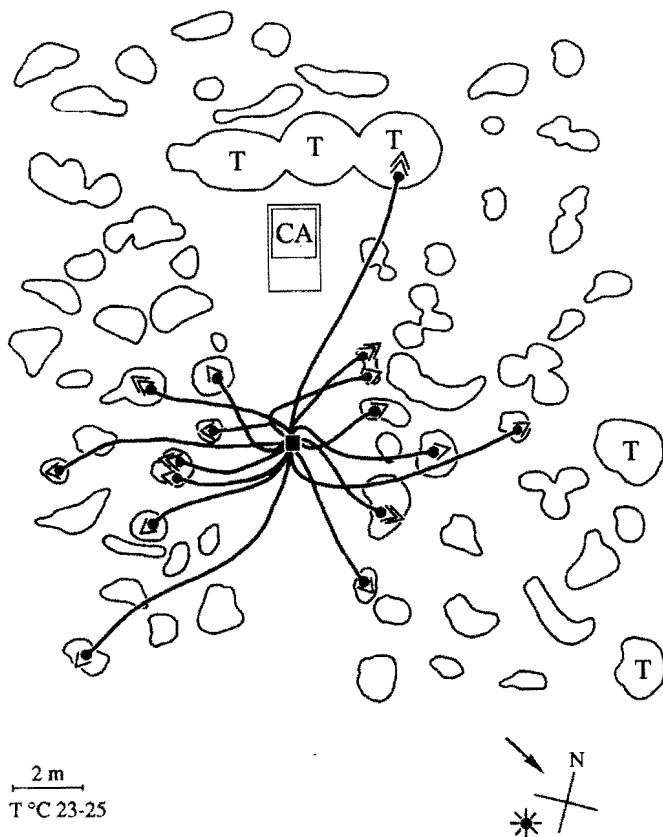


Figure 7. Experimental area, seen from above, with shrubs (without symbols), trees (T), car (CA) and the platform (black central square). Flight courses (solid lines represent flight altitudes of less than 5 m; dashed lines on other figures altitudes of more than 5 m) and landings (o) for every animal are indicated. Controls (\rightarrow) (N = 11), animals with the three ocelli covered ($\rightarrow >$) (N = 5). Inset, lower right: compass coordinates, wind direction (arrow) and sun position (☀). Inset, lower left: map scale and temperature. Wind speed range = 0.9-1.3 m/s.

allow measuring small changes in flight parameters, especially when the cicadas flew further away.

In flight, just as on the platform, animals with one compound eye covered (but the ocelli not covered) followed the general rule "turn to the side most stimulated", as documented in Fig. 9. Out of 12 animals tested, 11 took off to high-altitude long-distance flights for which no landings could be observed. The other cicada circled continuously at low altitude, then crashed into the front of the parked car. During flight, cicadas frequently circled to the side of

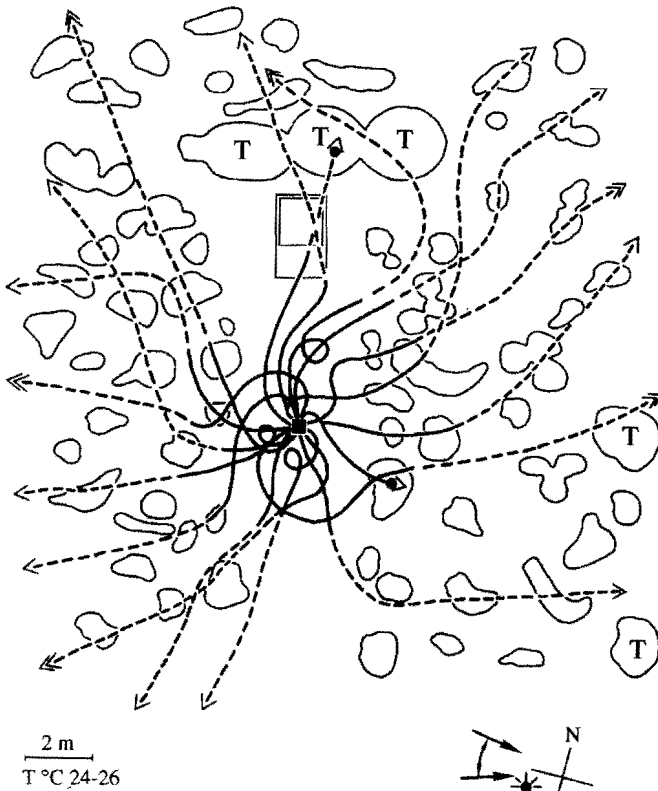


Figure 8. Flight courses of *M. cassini* with both compound eyes completely covered (\rightarrow) (N = 13), and with additional covering of the three ocelli (\rightarrow >) (N = 6); further explanations as for Fig. 7. Wind speed range = 0.9-1.3 m/s.

the normal eye at lower altitudes in the beginning of flights. At higher altitudes, later in the flights, the animals flew rather long straight courses.

As expected (Fig. 10), 6 out of 8 animals tested with only the frontal halves painted over took off to high-altitude and long-distance flights for which no landings were observable. The other two animals flew rather low and landed. In contrast, 8 out of 9 animals tested with only both caudal halves covered (again with ocelli not covered) coursed at low heights and landed in nearby shrubs, as did the controls, indicating the importance of both frontal fields of view.

Six out of 8 animals tested with both ventral halves covered (and the ocelli not covered, Fig. 11) flew high and far and could not be seen landing; the other 2 animals behaved somewhat like the controls. In contrast, 8 out of 10



Figure 9. Flight courses of *M. cassini* with only one compound eye completely covered and with the three ocelli not covered. Right eye covered (\rightarrow) ($N = 7$), left eye covered ($\rightarrow >$) ($N = 5$). Further explanations as for Fig. 7. Wind speed range = 0.4-1.3 m/s.

animals with only both dorsal halves covered (the ocelli not covered) flew low and landed like the controls (cf. Figs. 7 and 11).

As shown in Fig. 6, an expanded binocular field of view exists dorso-frontally to fronto-ventrally. Surprisingly, there were no differences in flight courses between animals either with these binocular regions covered or with only their monocular fields covered (Fig. 12). All except one animal took off for high-altitude and long-distance flights, indicating that input through the fronto-ventral quarters of the eyes involves both binocular and monocular regions.

Gluing the short, stiff antennae of these cidas in resting position by covering them completely with aluminum paint, but leaving eyes and ocelli normal, did not affect takeoffs, flight courses, flight speeds, or landings.

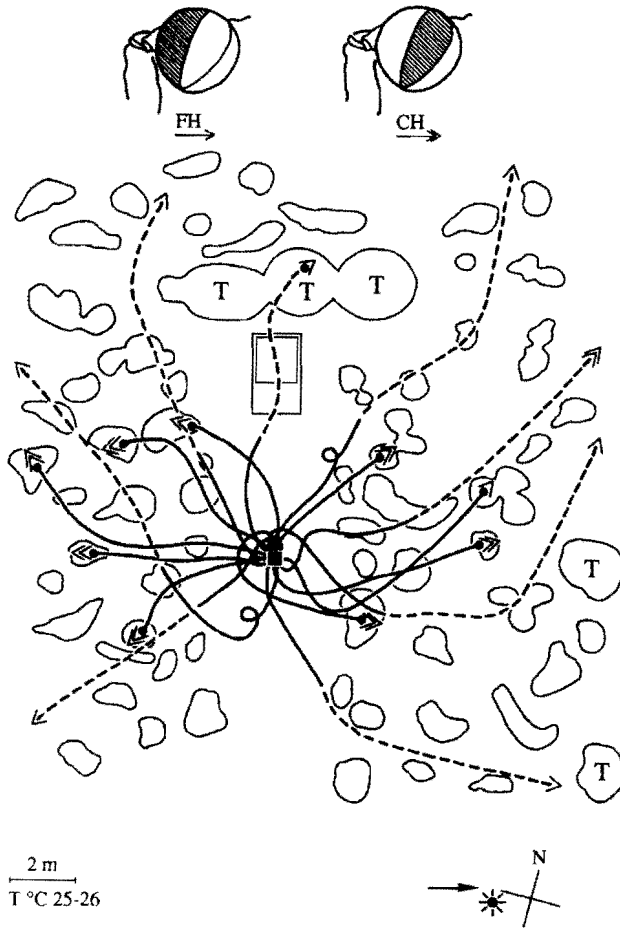


Figure 10. Flight courses of *M. cassini* either with only the frontal halves (FH) (—>) (N = 8), or only the caudal halves (CH) (->>) (N = 9) of both compound eyes covered. Uppermost, outlines comparing the paint-covered (shaded) portions of only a left eye, including a part of the vertex, postclypeus, and antennal base, viewed laterally, front of head to the left; further explanations as for Fig. 7. Wind speed range = 0.4-0.9 m/s.

DISCUSSION

There are no other studies addressing the simultaneous interaction of visual and phonotactic orientation during flight that is so common in cicadas. Our results suggest that these animals adjust their flight altitude and landing behavior to the special optical scenario of the habitat. Perhaps the most surprising discoveries obtained by watching flight behavior and landings of *M. cassini* are that (1) animals completely prevented from form vision make high-altitude and long-distance flights without obvious changes in flight perfor-

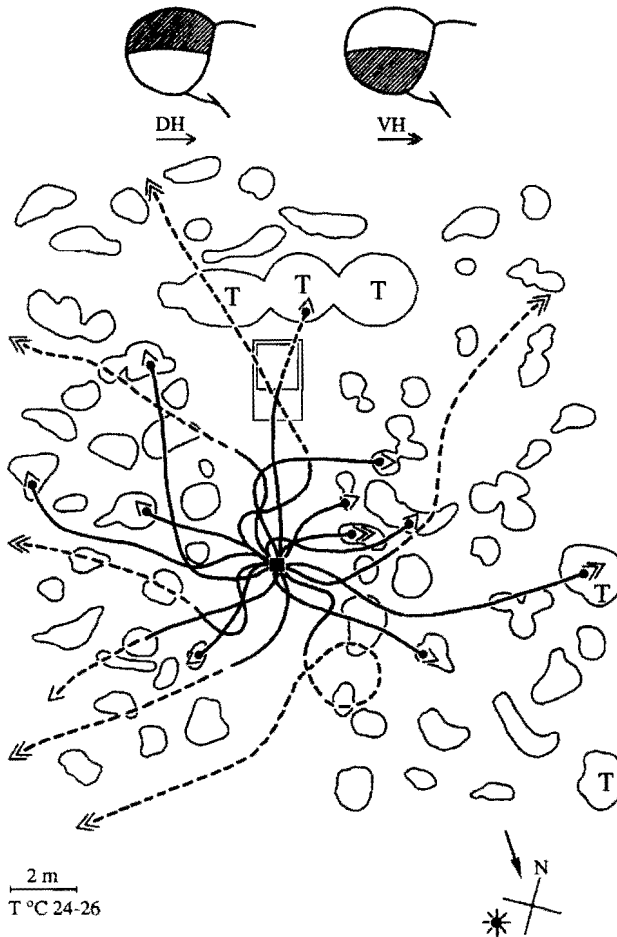


Figure 11. Flight courses of *M. cassini* with either dorsal halves (DH) (\rightarrow) (N = 10), or ventral halves (VH) (\rightarrow) (N = 8) of both compound eyes covered. Uppermost, outlines comparing the paint-covered (shaded) portions of only a left eye, including a part of the top and front of the head surrounding the eye, viewed frontally; further explanations as for Fig. 7. Wind speed range = 0.4-0.9 m/s.

mance and aerodynamic stability, (2) visual input from the fronto-ventral areas of both eyes is required for low-level and short-distance flights with normal landings to occur, and (3) only the frequency/intensity sweep of a male's calling song buzz is required for phonotactic orientation by females to occur during bush-hopping flights.

Calling of *Magiciada* males, especially synchronized chorusing, attracts other conspecifics by flight phonotaxis (Alexander & Moore 1962, Dunning et al. 1979, Williams & Smith 1991). The approaching males join the chorus and

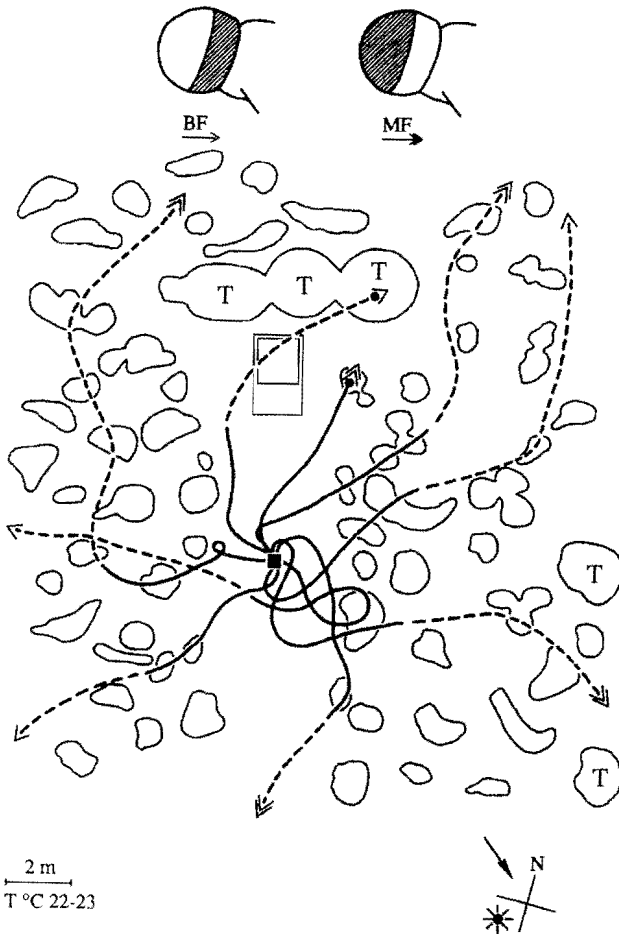


Figure 12. Flight courses of *M. cassini* either with only the field of binocular view (BF) (->) (N = 4), or only the field of monocular vision (MF) (->>) (N = 5) of both eyes covered. Uppermost, outlines comparing the paint-covered (shaded) portions of only a left eye, including a part of the top and front of the head surrounding the eye, viewed frontally; further explanations as for Fig. 7. Wind speed range = 0.9-1.3 m/s.

start to sing and to synchronize. Females fly to the chorus trees where they are within courtship and copulation range of many males. Such complex potentially "selfish herds" may minimize the probability of any one of the three species within a brood being reduced in numbers beyond a point of no return by the numerous general predators which attack them (Alexander & Moore 1962, Hamilton 1971, Williams & Smith 1991, Moore 1993). Our phonotactic tests revealed insight into the orientation, movements, and heights involved in females flying to choruses of males. Doolan and Young (1989)

found, in choice experiments, that females of *Cystosoma saundersii* (Westwood) in Australia flew equally well from long-range to broadcasts of natural songs and experimental songs, even with temporal patterns altered, but not with carrier frequency altered; while at short-range, with non-choice broadcasts, they found that females made courtship responses only to those experimental songs with temporal patterns similar to those of normal calling songs, even though carrier frequency at short-range could vary widely. Villet (1991) found, in field experiments with broadcasts of complete calling songs of seven sympatric African cicadas in five genera, that responses were elicited only from conspecific cicadas: silent males were stimulated to sing in five of the species, females flew to nearby the loudspeaker in another species, while both males and females landed nearby the loudspeaker in the seventh species.

Vision affects locomotion and associated sound production in *M. cassini* males, perhaps first affecting locomotor activity. These results parallel the observation that males with normal vision completely stop their singing and associated flying behavior as soon as clouds suddenly obscure the sun, and just as suddenly start again upon reappearance of the sun (Alexander and Moore 1962). Heath (1967) reported a mean minimum body temperature for level flight in *M. cassini* in Oklahoma of 20.85°C; and for spontaneously flying males a mean of 29.08°C, and for females 27.13°C. The data for females may be comparable, but for males the mean from our work (31.9°C) is near the upper limit of range for Heath's, suggesting less regulation of body temperature during flight in males than previously thought. Heath et al. (1971) suggested differing maximum voluntarily tolerated thoracic temperatures before seeking shade for all three sympatric 17-year cicadas in Brood V (*septendecim*, 31.3°C; *septendecula*, 32.6°C; *cassini*, 33.3°C), for *septendecim* in Brood VI (31.5°C), and for *cassini* in Brood IV (31.0°C). Toolson and Toolson (1990) determined a minimum thoracic temperature of 24.5°C for sustained flight in the allopatric 13-year cicada *M. tredecim*, sibling to *septendecim*, found no statistically significant differences in thoracic temperatures of males and females, and established mean thoracic temperature in the field for both sexes of 33.0°C ± 0.19°C, averaging 2.7°C ± 0.21°C above ambient. Bartholomew and Barnhart (1984) reported for the first time non-flapping warm-up of cicadas before flying in the laboratory (tethered *Fidicina mannifera* [Fabr., in Panama], but we did not detect any warm-up in *M. cassini*, and it seems unlikely that such a warm-up is involved in singing males of most cicadas. The means and extremes of thoracic temperatures during unrestrained flight in nature for *M. cassini* were higher, and wingbeat frequencies lower, in our study than for the larger tropical cicadas in the study by Bartholomew and Barnhart.

The black curtain covering the platform heated up during longer-lasting experiments, which may have facilitated faster walking and takeoff even in animals with eyes and ocelli completely covered. Flight behavior originating from the platform was not significantly different from that seen in animals in nature which took off from a branch. Therefore, abolishing form vision did not prevent flight behavior of these cicadas, and their demonstrated aerodynamic stability suggests cues in addition to visual ones. Cicadas flying backward have never been reported; therefore, one might expect our result that covering only the front halves of the compound eyes (with the ocelli not covered) affects flight behavior in a manner similar to covering the whole eyes, given the great reduction in visual information until after landmarks are passed. We have commonly witnessed fly-by landings, as described here, with all species of *Magiccicada* from several broods (Moore unpublished).

We found behavioral evidence for the significance of different eye regions in flight orientation during landing. Body posture during low-altitude flight, with the head tilted slightly upward, suggests that cicadas certainly gather optical landmark information for flying and landing mainly from the fronto-

ventral regions of the eyes. The confirmations are surprisingly clear (Fig. 11), but there are no external ommatidial specializations. Perhaps because of the absence of regular landmarks typical of the usual low altitude flights, high altitude flights follow rather long and straight courses. Cicadas apparently are able to compensate for visual asymmetries in the absence of landmarks. Moreover, visual input from both compound eyes is required for low level flights and normal landings. There is no evidence in cicadas suggesting a role for ocelli in minimizing delay of visual response, in augmenting visual response in the absence of sharp horizontal borders, or in following horizons after ablation of both eyes, as shown in Orthoptera, Diptera, and Odonata by Taylor (1981). Kastberger (1990) showed that ocelli help control phototactic alertness and minimize disturbance in flight course control in honeybees, as well as also shortening photokinetic reaction times compared to the response with compound eyes alone as known for grasshopper locusts; again, functions not indicated for cicadas.

The compound eyes of *Magicicada cassini* are normal apposition eyes. Each ommatidium has a eucone crystalline cone formed by four Semper cells, and each crystalline cone is surrounded proximally by two primary pigment cells (with large pigment granules) and distally by twelve secondary pigment cells (with smaller granules). Eight receptor cells form a closed rhabdom which is attached to the tip of the crystalline cone; no rhabdomeres are eccentric. At the light microscope level, no specialized ommatidia can be found in the dorsal rim area of the eye, suggesting no sensitivity to natural plane polarized light. No details of fine structure of the rhabdomeres are available (T. Labhart, pers. comm.). In the absence of adequate information on the optics of single facets or of facet assemblies, on the receptor arrangement, and on the organization of the large optic ganglia, a meaningful comparison with work on other insects, for example on Diptera, Hymenoptera, and Orthoptera (see Wehner 1981), is not yet possible. Furthermore, we need studies of tethered flight of cicadas for analyzing optomotor and fixation properties under closed loop conditions as studied in Orthoptera (Taylor 1980), Hymenoptera (Wehner 1981), and in Diptera (Reichardt and Wenking 1969, Reichardt and Poggio 1976, Wagner 1986a-c). Such studies may throw light on some of the control mechanisms acting in free flight, especially when considering complex flight strategies as documented for hoverflies (Collett and Land 1975a,b, 1978; Collett 1980a,b) and for *Musca* (Wagner 1986a-c).

Quantitative estimates of binocular overlap based on principal pseudopupils show an impressively large binocular window. A similar shaped but smaller binocular field of view was measured in honey bee (*Apis mellifera* L.) workers by Sommer (1977), Wehner and Flatt (1977), and Seidl and Kaiser (1981), as well as in the desert ants *Cataglyphis bicolor* Fabr., *C. fortis* (Forel), and *C. albicans* (Roger) by Wehner (1983) and Wehner and Srinivasan (1984). Frantsevich and Pichka (1976) compared sizes and shapes of binocular fields of view in a variety of insect species and related them to natural history and behavior. They pointed out that insects hunting for small, movable prey, or those which detect small mates against the sky, possess a rather small binocular overlap; for example as reported by Beersma et al. (1977) for males of *Calliphora* blowflies. In contrast, those insects which detect targets (for instance, landing sites by cicadas) against a highly complex visual background may have larger binocular fields of view, such as the expanded fronto-ventral areas of the Asian stalk-eyed fly *Cryptodiopsis whitei* (Curran) in tropical rainforests (Motte and Burkhardt, 1983), or the frontal areas of the cricket *Gryllus bimaculatus* DeGeer in grass-covered temperate soil surfaces (Honegger, 1980). This relationship certainly fits the normal bush-hopping flight of *Magicicada*. The two expanded regions of binocular overlap in *M. cassini* may

serve the same purpose, and may even act in concert to optically integrate surroundings, depending on flight altitude and attitude.

The results here partly parallel earlier findings of Chen and Young (1943) on vision and flight in the Chinese cicada *Cryptotympana atrata* Fabr. (as *pustulata*) (Platypleurinae), a species which surely differs in ecological demands and flight strategies. The results obtained by Chen and Young for flights and landings of Chinese cicadas (1) with only the three ocelli covered, (2) with both compound eyes coated but with the ocelli not covered or only partly covered, (3) with only one compound eye painted over (even in details of results), (4) with only the upper (dorsal) halves of the compound eyes covered, (5) with the lower (ventral) halves covered, and (6) with either the inner (including the binocular overlap) or the outer (probably most of the monocular field of view) regions covered, are in complete agreement with our data.

Several of the experiments of Chen and Young we did not duplicate, others we could not confirm with *M. cassini*. All of our animals took off spontaneously; nearly all of theirs were thrown into the air. Their rare spontaneous flights were of short distance (a few feet), followed by dropping down to the ground. *Cryptotympana atrata* refused to fly with both the compound eyes and the ocelli covered, perhaps the greatest difference from the results obtained with *M. cassini*. Their conclusion that form vision is a necessary requisite for takeoff and sustained flight behavior in insects was not confirmed for *M. cassini*. Also in contrast, we were unable to detect significant changes in flight posture or in time courses of "spontaneous changes" in orientation of the longitudinal axis of the body in free flights by animals completely prevented from form vision. Compared to controls, blinded *M. cassini* individuals seemed to fly normally with similar flight speeds; furthermore, aerodynamic stability remained normal. Despite light intensities reduced to 0.04%, our animals may not have been totally blind, but we doubt that our animals could detect the horizon. Our findings are paralleled by Wagner's (1986a-c) studies of flight performance and visual control of flight in free-flying *Musca domestica* L., where flight activity was reduced but otherwise normal in terms of flight performances and maneuvers, even in completely blinded house flies.

We agree with Wagner (1986b) that visual input is not the only source for controlling flight maneuvers. Other, non-visual sensory inputs must act or compensate during free flight, as well known in Acrididae (Rowell 1988). In the Diptera, possible candidates are the halteres (Sandeman 1980, Sandeman and Markl 1980), which act as velocity detectors (Hengstenberg 1984). In *Magicicada*, studies of motor and neural patterns associated with flying, and of functions of special sensors (Klein et al. 1987, 1988), have just started. The small and rather stiff antennae in cicadas apparently have little effect on the control of flight behavior, in contrast to the striking effects shown for antennae in locusts (Gewecke 1972, Rowell 1988). Halteres are of course not present in cicadas, but there are many long hair-like sensilla on the head, legs, sides, and other surfaces of the body, and most probably also sensors on the wings.

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