Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms

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A newly developed flight simulator allows monarch butterflies to fly actively for up to several hours in any horizontal direction while their fall migratory flight direction can be continuously recorded. From these data, long segments of virtual flight paths of tethered, flying, migratory monarch butterflies were reconstructed, and by advancing or retarding the butterflies' circadian clocks, we have shown that they possess a time-compensated sun compass. Control monarchs on local time fly approximately southwest, those 6-h time-advanced fly southeast, and 6-h time-delayed butterflies fly in northwesterly directions. Moreover, butterflies flown in the same apparatus under simulated overcast in natural magnetic fields were randomly oriented and did not change direction when magnetic fields were rotated. Therefore, these experiments do not provide any evidence that monarch butterflies use a magnetic compass during migration.

Monarch butterflies (*Danaus plexippus*) from the eastern North American population make remarkably long migratory journeys in the fall, some of which extend more than 3,500 km from eastern Canada and the northeastern United States to Mexico. This migration was first studied by an extensive tagging program (1, 2), which eventually led to the discovery of the butterflies' overwintering areas in the Transverse Neovolcanic Mountains of Central Mexico (1–3). But how do the butterflies navigate? Because no adequate laboratory paradigm that produces and quantifies migratory flight behavior has been developed, little is known about their underlying orientation mechanisms. Recently, some evidence that monarchs may possess a sun compass has been reported (ref. 4, but see *Discussion*). Furthermore, observations that migrating monarchs still appear to fly in the migratory direction on cloudy days (5), that they appear disoriented after short periods in strong artificial magnetic fields (6), and that they contain magnetite in their thorax (7, 8) has led to suggestions that monarchs also possess a magnetic compass (1, 9). However, to date there has been no successful test of the monarch's ability to orient in the Earth's strength magnetic fields. The aims of our study were, first, to develop a robust and realistic laboratory setup that could bring monarch migratory flight behavior into the laboratory where variables influencing it can be carefully controlled, and, then, to elucidate the orientation cues used by monarch butterflies.

Materials and Methods

To accomplish our aims, we developed a flight simulator for butterflies, which is illustrated in Fig. 1. Flight in tethered insects typically is induced by directing a laminar flow of air horizontally toward their heads. Our critical modification was to direct a gentle laminar flow of air vertically from beneath the butterflies. This process also produces active flight, but without biasing the butterflies' horizontal orientation directions.

The four identical flight simulators consisted of large white translucent plastic cylinders (diameter 59 cm, height 64 cm) with a hole in the bottom through which a 16-cm diameter pipe blew air vertically toward the butterfly. The airflow, which was produced by a computer fan (Patriot PT2B3, Digi-Key, Thief River Falls, MN) controlled by a variable transformer (Superior model 10C, Tempco, Wood Dale, IL) and made laminar by passing it through hundreds of parallel drinking straws, was manually adjusted by the experimenter to the minimal flow rate necessary to produce sustained flight behavior in each butterfly. A miniature camera (VMPS-250, Circuit Specialists, Mesa, AZ) was mounted outside one of four small (8 mm) holes 90° apart in the bottom of each cylinder. Its position was varied between experiments to avoid any remote possibility that a directional bias could arise from the position of the camera. The four miniature cameras, one from each simulator, were connected to a four-way surveillance television screen (Lorex, Strategic Vista, Markham, ON, Canada, black and white 12-inch Surveillance TV SG7111). A directional recording assembly was mounted in the center of the top of the cylinder. It consisted of a commercially available optical encoder (US Digital, Vacouver, WA, E5S-360250) with a modified bearing and shaft. The standard model comes with a thick brass shaft, which is much too heavy for a butterfly to turn. We therefore disassembled the optical encoder and replaced the standard shaft with our own custom-made model, which consisted of the plastic axle used to keep track of a computer mouse's movements (obtained from the inside of a Microsoft mouse: serial mouse 50674). The teeth were ground off the axle, and the optical encoder disk from the E5S-360-250 was glued to its top. This axle was then used as our shaft, and a very low friction bearing was formed by two Teflon cylinders with holes in their centers through which the shaft was fitted. Exactly in the middle of this shaft, a 0.020-inch hole was drilled and a 15.3-cm (6 inches) tungsten rod (A-M Systems, Everett, WA, catalog no. 718000) was inserted and glued. The tungsten rod was placed inside an aluminum guide tube [length 11.5 cm (4.5 inches), inner diameter 3 mm] fitted exactly vertically to the bar on which the optical encoder was mounted. This assembly amounts to a very stable low-friction bearing, which the butterflies could easily turn.

Each butterfly had a 3-cm mounting stalk, which consisted of a section of tungsten wire (identical to the one used for the shaft), glued with beeswax to the butterfly's dorsal thorax so that its body was maintained in a horizontal orientation in the apparatus. A 1-cm long piece of clear rubber tubing with a marginally smaller inner diameter than the tungsten wires was used as a firm coupler to connect the butterfly-mounting stalk to the encoder shaft. This coupler connected the wires firmly enough to prevent any turning of the wires relative to each other. A small, 1-cm section of thin, rigid plastic tube with an inner diameter slightly smaller than the outer diameter of the rubber tube was slid over the connection to prevent any bending in the joint. Thus, the butterfly was tethered rigidly to the encoder shaft and the procedure allowed fast (a few seconds) and easy coupling and uncoupling of butterflies to the apparatus. The optical encoders were connected to a computer that recorded timed sequences of headings (four-channel program purchased from US Digital with the optical encoders).

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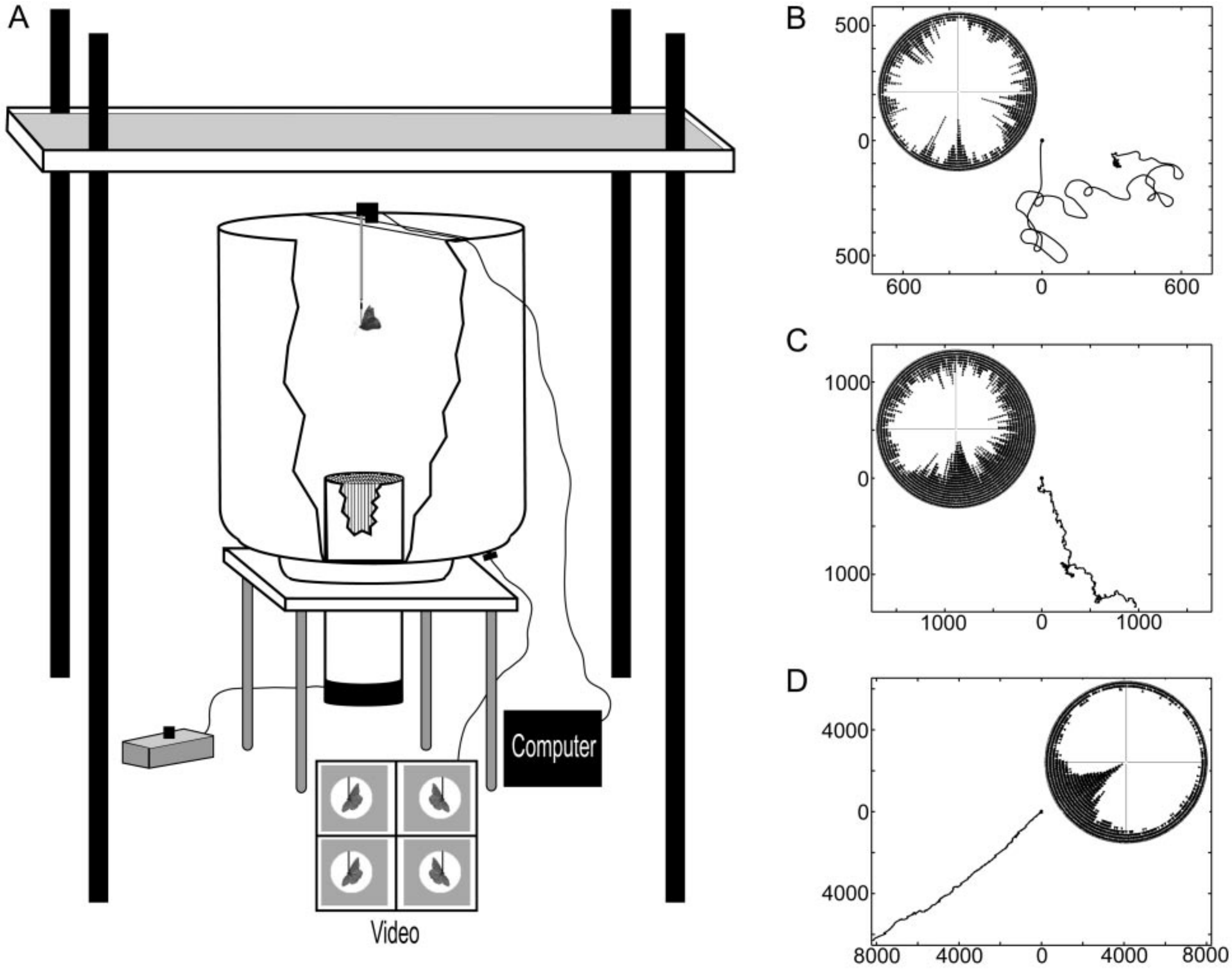

Fig. 1. (*A*) Schematic drawing of the flight simulator, the details of which are described in *Materials and Methods*. The translucent Plexiglas sky was used only in indoor experiments to simulate complete cloud cover. For clarity reasons, the overcast simulation is drawn higher above the apparatus than it was actually placed. (*B–D*) Examples of how the time resolution in our simulator data can be used to recreate the virtual path flown by the butterfly, compared with normal circular histograms of the same data. All virtual flight paths start in the center of the diagram and are directed toward the periphery. North is up. Units ≈1 m (1/5 s at speed 18 km/h). See text for details. Circular histograms show the orientation data accumulated from the periphery of the circle toward the center represented in the appropriate compass direction (north at top).

Integration of these timed sequences of directions, under the assumption of constant flight speed (a very reasonable assumption, because any given butterfly flew in a very constant manner during a given experiment), allowed us to reconstruct virtual flight paths of the butterflies. This was done by drawing a path section of 1 unit length originating in the center of a graph in the first direction recorded, then another unit path section was drawn from the end of the first one in the second direction recorded, and so on. Such reconstructed paths are illustrated in Fig. 1 *B–D* where they are presented for direct comparison to their equivalent circular histograms. Fig. 1*B* shows the circular histogram of directions and the corresponding virtual flight path of a butterfly in nonmigratory condition. The butterfly flew for only 15 min and the path looks like the normal looping flight of a foraging monarch. In contrast, Fig. 1*D* shows the reconstructed flight path of a well-oriented migratory butterfly that was stopped by us after 1 h of active flight. Fig. 1*C* illustrates that monarch butterflies in migratory condition, which show a more diffuse orientation pattern when the data were plotted as traditional circular histograms, are in fact consistently oriented when data are plotted as virtual tracks.

A total of 59 wild-captured monarch butterflies in diapause and fattened migratory condition were caught at the Northern shore of Lake Ontario during autumn migration (September 9–October 2, 2001). Because they cluster along this east-west ecological migration barrier they were fairly easy to catch and we could be almost certain that all butterflies captured were from the migratory generation. The experiments were performed at Queen's University Biological Field Station, Lake Opinicon, Ontario, Canada (44°34′N, 76°19′W) during their peak autumn migration (September 14–October 10, 2001). All procedures were approved by Queen's University Animal Care Committee in compliance with Canadian Council Of Animal Care Guidelines. After the experiments were completed, the mounting stalk was removed (by remelting the beeswax), and the butterflies were released to continue their natural migration.

Most butterflies flew continuously for at least 1 h in our simulators, and in many instances they were stopped so that other butterflies could be run. Some were allowed to fly for up to 4 h and produced flight paths extending to approximately 65 km [assuming the conservatively slow cruising speed of 18 km/h observed in wild migrating monarchs by Urquhart and Urquhart (1)], which could potentially be as long as 182 km if 50 km/h speeds observed under tailwinds are assumed (10). Video clips of monarchs flying in the apparatus can be seen as Movies 1 and 2, which are published as supporting information on the PNAS web site, www.pnas.org.

To ensure that there were no directional apparatus biases, we made extensive tests by turning the entire simulator, or each component such as the fan, the cylinder, or the recording assembly separately, by varying amounts, while butterflies were actively flying. Invariably, the butterflies did not turn their orientation with the equipment, but instead maintained constant geographical headings. Also during equipment testing, we manually turned flying butterflies toward different directions and all immediately turned back to their original geographical heading. A video clip illustrating one such test can be viewed as Movie 2.

Before the outdoor sun-compass experiments, we transferred the wild-caught monarch butterflies indoors for at least 5 days under three different conditions: (A) a light/dark cycle that exactly matched the local daylight cycle (lights on around 7 a.m., off around 7 p.m.), (B) a 6-h time-advanced condition (lights on around 1 a.m., off around 1 p.m.), and (C) a 6-h time-delayed condition (lights on around 1 p.m., off around 1 a.m.). Exact times varied in accordance with the exact sunrise and sunset times on each specific date. The average apparent azimuth movement of the sun across the sky is approximately 15°/h. At the specific latitude, date range and time ranges of our experiments, the actual 6-h azimuth movement of the sun varied between 91° and 115° (the value depends on the exact times and calendar date of each given experiment). Thus, depending on how the internal mechanism works, the two groups of 6-h clock-shifted butterflies are expected to shift their orientation circa 90° or 91°–115° in opposite directions relative to the orientation of the control group, if migrating monarch butterflies use a time-compensated sun compass.

Before commencing outdoor experiments, butterflies were placed in clear Plexiglas cages outdoors in direct sunlight for at least 15 min before testing. This process allowed them to warm up, gave them an opportunity to sense and evaluate potential orientation cues, and clearly increased their motivation to fly. For indoor magnetic-compass experiments, butterflies were warmed up with a strong heat-producing halogen lamp. To start an experiment, a butterfly was tethered rigidly to the shaft and placed in the gentle vertical airflow. Then, it was positioned precisely north while an assistant calibrated the optical encoder and started the program, which recorded the butterfly's spontaneous choice of geographic heading once every 200 ms (system resolution is 1 kHz, but observations at 5 Hz were quite adequate to generate the relevant flight paths). During experiments, the behavior of the butterflies was continuously monitored remotely via the miniature camera images, and it was noted when butterflies flew actively, glided, or stopped flying. All experiments, where the butterfly flew actively for at least 15 min, have been included in data analyses. All but four butterflies (these individuals are specially marked on the figures as gliders) flew actively all of the time until they stopped flying. When a butterfly stopped flying, it was taken out and removed from the apparatus, and its data were analyzed only up to the time flight stopped. All butterflies in each experimental group were separate individuals. None were reused.

In the sun compass experiments, clock-shifted and control butterflies were flown outdoors under sunny skies and in the natural geomagnetic field. Although the sun was directly visible to the butterflies, no geographical landmarks were within their field of view. Up to four identical cylinders (see Fig. 1*A*) were used simultaneously.

In another series of experiments to test whether monarchs use a magnetic compass, we flew butterflies indoors in a wooden

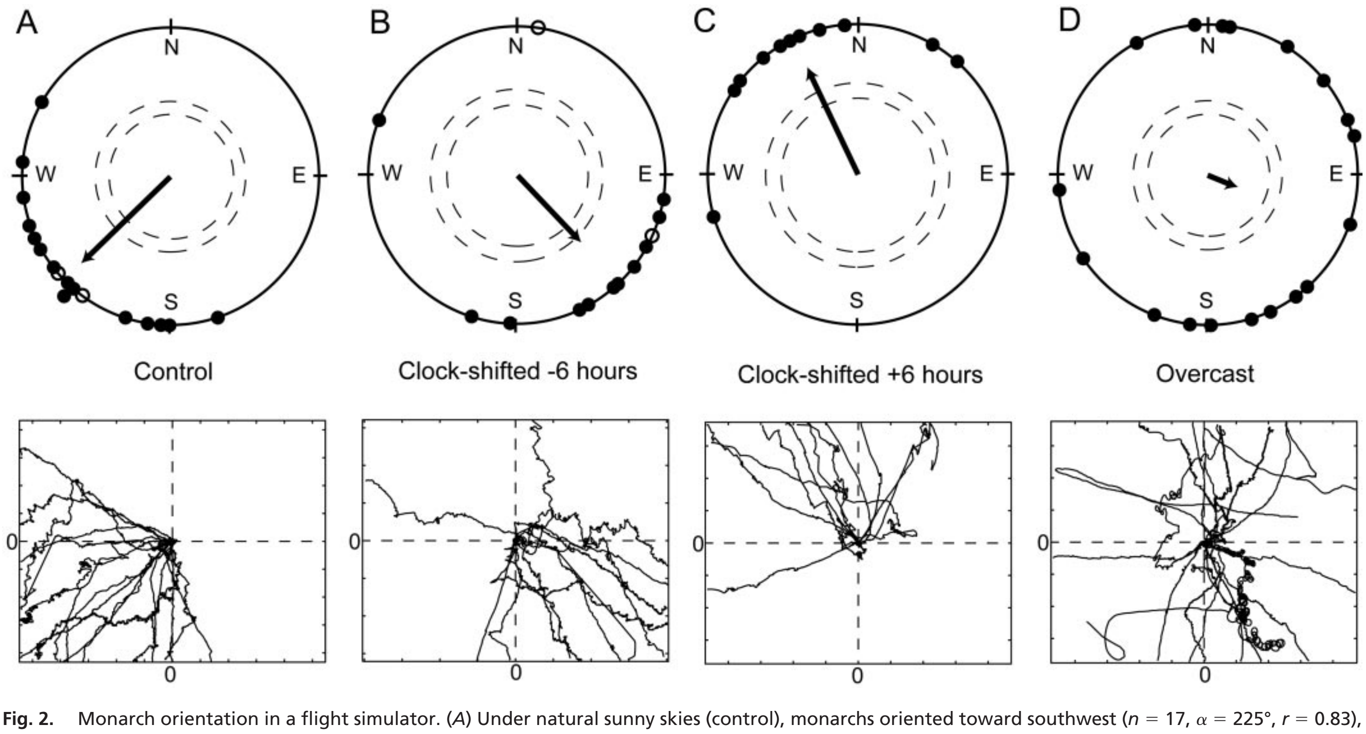

Fig. 2. Monarch orientation in a flight simulator. (*A*) Under natural sunny skies (control), monarchs oriented toward southwest ($n = 17$, $\alpha = 225°$, $r = 0.83$), consistent with the location of their Mexican wintering quarter. Butterflies clock-shifted −6 h (*B*) shifted their orientation toward southeast ($n = 13$, $\alpha = 136°$, $r = 0.62$), and those clock-shifted +6 h (*C*) oriented northwest ($n = 11$, $\alpha = 335°$, $r = 0.80$). These results are consistent with monarchs' use of a time-compensated sun compass. Butterflies tested under simulated overcast conditions (translucent Plexiglas cover) (*D*) were not significantly oriented ($n = 18$, $r = 0.21$, $P = 0.46$), suggesting that they were unable to use the natural magnetic field for orientation (see also Fig. 3). (*Upper*) The circular diagrams show the mean orientations for individuals and group mean vectors. ●, Mean orientation of each actively flapping individual. ○, Mean orientation of the four gliding individuals. ↑, The sample mean vector. The length of the sample mean vectors, *r*, indicates the angular concentration of the samples. Dashed circles indicate required length of the sample mean vectors to obtain significance at 0.05 and 0.01 levels (Rayleigh test). (*Lower*) The diagrams show the virtual path flown by each butterfly under the assumption of constant speed. (They all start in the center of the diagram and travel toward the periphery.) Distances have been normalized.

boat house (no disturbances of the natural magnetic field) under a brightly illuminated, translucent Plexiglas sky (simulating total overcast), which was placed inside a large (about 2 × 2 × 2 m) tri-axial Helmholtz coil system identical to that used previously by Mouritsen (11). First, each monarch flew for a minimum of 20 min in the natural geomagnetic field. Then, we turned the field 120° clockwise (to southeast) by use of computer-controlled constant current power supplies (Kepco, Flushing, NY, BOP100-2M) and without disturbing the flying butterfly. After another minimum 20 min, we turned the field back to normal for at least 33 min. If the butterfly was still flying, we finally turned the field 120° clockwise (to southeast) once more for a minimum of 33 min. This ABAB procedure allowed us to record both immediate and delayed magnetic responses. The heterogeneities in the artificial fields produced by this system were less than 0.01% in the area, where butterflies flew, and they are therefore smaller than the regular temporal variations in the natural magnetic field. Consequently, all properties of the artificial fields except geographical direction were almost identical to the natural geomagnetic field.

Results

The mean directions and reconstructed paths obtained under clear sunny skies are shown in Fig. 2 *A–C*. Control monarchs on local time (Fig. 2*A*) oriented in the expected southwesterly direction ($n = 17$, $\alpha = 225°$, $r = 0.83$, $P < 0.001$, 95% and 99% confidence interval: 225° ± 18° and 225° ± 24°, respectively) toward wintering sites in Mexico. Monarchs time-advanced 6 h (condition B) and tested under identical conditions (Fig. 2*B*) oriented toward the southeast ($n = 13$, $\alpha = 136°$, $r = 0.62$, $P < 0.01$, 95% and 99% confidence interval: 136° ± 36° and 136° ± 50°, respectively), while monarchs time-delayed 6 h (condition C, Fig. 2*C*) oriented toward the northwest ($n = 11$, $\alpha = 335°$, $r = 0.80$, $P < 0.001$, 95% and 99% confidence interval: 335° ± 27° and 335° ± 37°, respectively). The shifts in direction shown by the clock-shifted butterflies are highly significant [Watson–Williams two-sample test (12): control versus condition B, shift = −89°, $F_{1,26} = 44.91$, $P < 0.001$; control versus condition C, shift = +110°, $F_{1,28} = 20.85$, $P < 0.001$; condition B versus condition C, difference = 199° or 161°, $F_{1,22} = 51.89$, $P < 0.001$; also, all 99% confidence intervals do not overlap]. Furthermore, both the 89° and 110° rotation of the mean orientation vectors of the time-shifted groups were not significantly different from the expected 90° or 91°–115° shift (95% confidence intervals: 89° ± 36° and 110° ± 27°). Thus, both the direction and magnitude of the mean shifts are in very good agreement with those predicted if monarchs use a time-compensated sun compass.

The mean directions and flight paths of butterflies flown under simulated overcast conditions are shown in Figs. 2*D* and 3. Their paths during the first 20 min under simulated cloudy skies and in the Earth's natural magnetic field (Fig. 2*D*) showed random orientation ($n = 18$, $\alpha = 112°$, $r = 0.21$, $P = 0.46$). Furthermore, 11 of the 18 butterflies flown under simulated overcast continued to fly for at least 10 min in the changed magnetic field. Close inspection of these 11 normalized total flight paths (Fig. 3) shows no appropriate (120° clockwise) directional changes in response to rotations of the magnetic field. Also, no signs of directional changes were observed in the seven butterflies that stopped flying after less than 10 min in the changed field. The observed lack of appropriate directional changes is to be expected if migrating monarch butterflies do not use a magnetic compass during migratory flight.

Discussion

Our flight simulator provides a laboratory setup in which a migratory animal can orient in any geographical direction it chooses while it is actually flying. Previous orientation studies with migratory birds and butterflies involved animals walking,

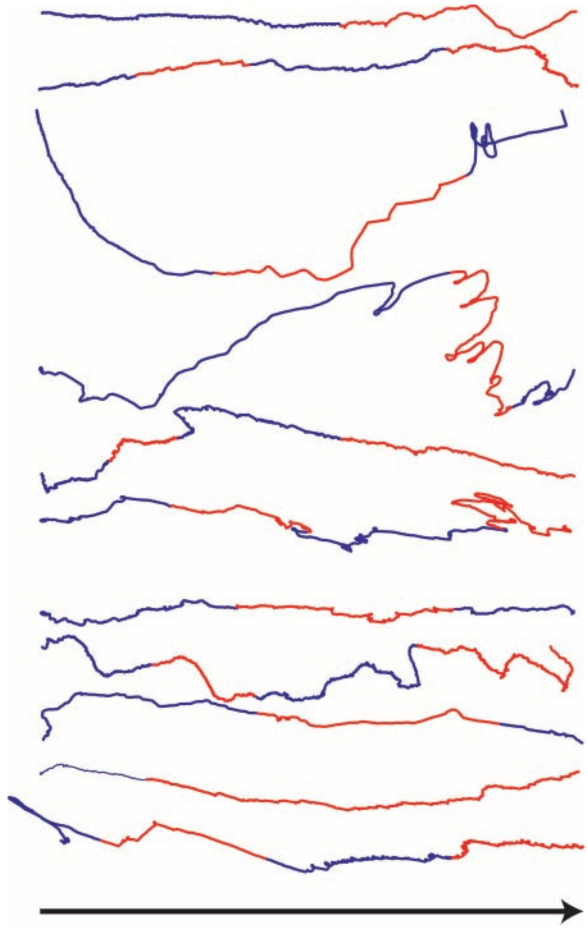

Fig. 3. Normalized virtual tracks of 11 different butterflies tested under simulated overcast conditions in a Helmholtz coil system. The tracks are drawn so that the overall mean direction of each track is from left to right; i.e., the butterflies start at the left and end at the right side. Blue traces show the virtual path flown in the unchanged geomagnetic field, whereas the red traces show the same butterfly's orientation with magnetic north turned 120° clockwise to southeast.

jumping, or flying a very short distance (0.5–1 m) in an arena (13–15), which is quite different from the migratory flight behavior that we intended to study. The true flight behavior generated in our flight simulators, which consisted of 93% sustained flapping and 7% gliding (in both flight patterns, legs were tucked and steering behavior clearly observable), also allowed us to thoroughly test for biases in the equipment. We are confident that the directions chosen by the butterflies in our flight simulator are not random directions, but accurately represent their intended flight directions, because in hundreds of forced-turn experiments, all butterflies immediately returned to their previous geographical heading. Also, turns of each separate component of our flight simulators clearly showed that there are no directional biases in any equipment component. No matter which part of the setup was turned while a butterfly was actively migrating in the setup, all butterflies kept their geographical heading. Such control tests were very difficult to perform in previous laboratory setups used for orientation experiments.

The 225° mean orientation of the control group in our experiment is in very close agreement with the 220° mean direction obtained by observing vanishing bearings of a large number of naturally migrating monarchs (5), and it is also very close to the 226° orthodrome (great circle) direction from our study site to their Mexican destination. This result further boosts

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our confidence that the flight observed in our simulator is truly equivalent to migratory flight and orientation.

The clock-shifted butterflies also show very well-oriented behavior, where both positive and negative time shifts produce strong orientation that is as well oriented as the control group. The clear and predicted directional shifts produced by clock-shifting the butterflies provide strong evidence that migratory monarchs use a time-compensated sun compass. This finding is in agreement with recent data from neotropical pierid butterflies, *Aphrissa statira* (16).

The random orientation of our butterflies under simulated cloud cover in the natural magnetic field and the lack of responses to rotated magnetic fields provide no evidence of the use of magnetic information to determine or maintain their migratory directions. Because the lack of magnetic orientation occurred in exactly the same apparatus where the butterflies showed clear time-compensated sun compass orientation, this negative result becomes particularly important. Recent research showing that polarized patterns are still available even under cloudy conditions (17) provides a plausible explanation for reports of monarch migratory orientation under cloudy skies (5).

Etheredge *et al.* (18) previously claimed that monarchs use a magnetic compass. But, half a year later, the paper was retracted: "The positive response to magnetic fields in two experiments cannot be repeated. Further experiments show the false positives in these tests result from a positive taxis by the butterflies to the light reflected off the clothing of the observers. We therefore retract our report." This makes sense, because all directional choices were based on one 1-m flight path, a very short distance, over which it would be very surprising if any significant orientation pattern would emerge. Thus, there exists no evidence that monarch butterflies use the magnetic field for orientation.

Members of the same group performed the only previous study claiming sun compass orientation in monarch butterflies (4). They recorded the body orientation of vanishing clock-shifted monarchs. The clock-shifted monarchs seen as a group did seem to turn their orientation 75° relative to controls, but their orientation was very scattered ($r = 0.29$) and significantly more scattered than the controls ($P < 0.001$; nonparametric bootstrap with 10,000 repetitions; 99.9% confidence intervals for r: natural controls, $0.78 < r < 0.94$, compared with clock-shifted butterflies, $0.0208 < r < 0.6259$, resulting in no overlap). There is no logical explanation for this finding, and there is also a peculiar increased occurrence of the heading "due south" among the controls and "due west" among the clock-shifted butterflies. Together, these facts suggest that the results in ref. 4 were biased in some way. Also, the Watson F test used to state that the mean heading of the clock-shifted butterflies is significantly different from the mean heading of the controls is not valid, because it assumes that the angular concentration, r, of both groups being compared is around 0.75 or higher (the actual r values are 0.29 and 0.67). Finally, Perez *et al.* (4) determined the orientation of the butterflies by running "behind and beneath" released butterflies while estimating the body orientation, not flight direction, of the butterflies. Consequently, the estimated headings may have been unintentionally biased, both because of the subjectivity involved in scoring body orientation of erratically flying butterflies and because butterflies, if chased by a human, will fly in any direction away from this apparent predator. This observation procedure could be particularly problematic, if the experimenters chasing the butterflies knew to which group each individual butterfly belonged and therefore also knew in which direction each released butterfly was supposed to orient. According to Wenner, quoted by Halpern (19), this was unfortunately the case in the Perez *et al.* study, and he also expressed serious skepticism regarding several other aspects of their study. Thus, there exists only questionable previous evidence of sun compass orientation in monarch butterflies.

In comparison, our experiments show that undisturbed monarchs in our flight simulator produce well-oriented sequences of migratory flight that are orders of magnitude longer than those obtained by vanishing directions (4, 5) or arena studies (15, 18). Furthermore, the orientation of our clock-shifted butterflies is just as concentrated as the orientation of the controls, and the directional concentrations ($r = 0.83$, 0.62, and 0.80) shown by our flying butterflies in the simulator are very similar to those found in free-flying migrating monarchs [$r = 0.86$ (4), $r = 0.88$ (5)]. In addition, the control direction, the directional shifts in response to both delayed and advanced clock shifts, the random orientation under simulated overcast conditions, and the lack of orientation changes in response to turned magnetic fields all lead to the conclusion that monarch butterflies use a time-compensated sun compass, but not a magnetic compass, during migratory flight.

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