Perception of the Geomagnetic Field in the Fly *Drosophila melanogaster*

Since it has become evident for several species of insects (*Isoptera*[1,2], *Blattodea*[2], *Coleoptera*[3-6], *Diptera*[2,7-9], *Hymenoptera*[10]) that their orientation patterns can be influenced by the direction of the geomagnetic field, the question arises which sensory mechanisms may be involved in the perception of magnetic fields. Until recently the physiological basis of orientation performances depending on the physical parameters of magnetic fields is completely unknown. The recent work of LINDAUER and MARTIN[10] offers some reference to an influence of the earth's magnetic field on the orientation of bees in the gravity field. By means of a special waggle dance performed on the vertical comb, bees are able to indicate a certain direction in the gravity field. But the indications of these directions systematically show small deviations, called misdirections, which disappear as the magnetic field is artificially compensated to less than 4%. Since MARKL[11] succeeded in training bees to find their way to a food source by keeping a fixed angle to gravity on a vertical screen, the same deviations from the exact directions could be found as in the waggle dance. From this result it becomes evident that the misdirections in the waggle dance are due to failures in an exact geomenotactic orientation rather than to mistakes made in transferring the sun-compass angle to the gravitational dimension. As these deviations, however, do not appear after compensation of the geomagnetic field, it seems obvious that there exists an influence of the geomagnetic field on gravity perception.

In order to get some further information on that problem we have introduced another insect species in the investigation by especially studying the influence of the geomagnetic field on the orientation of fruitflies in the gravity field. Running on a plane, which can be continuously rotated and inclined in any direction, the flies show a strongly marked negative geotactic orientation performance. In series I an inclination of 30° to the horizontal is valid for all experiments. By means of a specially constructed lift (Figure, c) the flies are individually dispensed into the centre of the iron-free apparatus. For all the flies reaching the periphery of the outer circles (C4 or C3) within 20 sec respectively 15 sec, the deviations of the runs from the zero-direction, i.e. the direction of an exact negative geotactic orientation course, are determined at different distances from the releasing point. Measuring the total intensity of the geomagnetic field by using a Foerster probe (Oerstedtmeter type 1104, Fa. Foerster) a value of 360 mOe is obtained (inclination 59.5°). Within the room, where the experiments are performed, the temporal and spatial fluctuations of this value do not exceed ± 7 mOe, i.e. $\pm 1.9\%$. Because the activity of *Drosophila* may be influenced by electrical fields[12], these influences must be eliminated by using a Faraday screen (height 16 cm, mesh width 4 cm) and controlling its effect by a cathode ray oscilloscope. During the experiments red light produced by an interference

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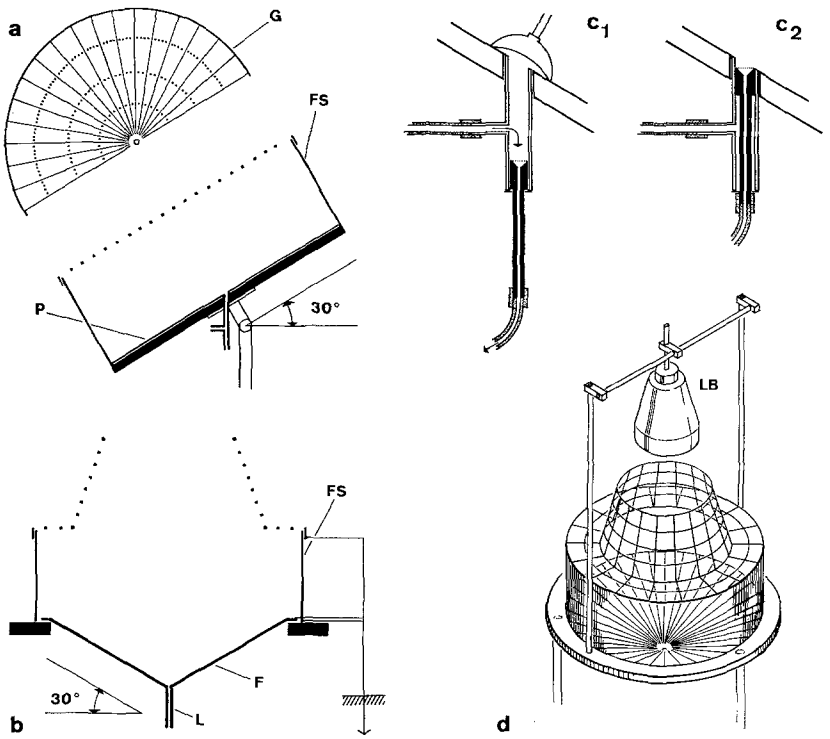

a and b, median section through the apparatus of serie I (a) and II (b). c, lift, by which the flies were individually dispensed in the centre of the apparatus a) and b). In c(1) the fly is sucked in and in c(2) lifted up. d, total view of the apparatus used in series II.F, funnel-like apparatus corresponding P in Figure a; FS, Faraday screen; L, lift; LB, red light beam for the observation of the flies (interference filter, $\lambda_{max} = 710$ nm); P, inclined plane, on which the orientation of the flies according to the gravity and geomagnetic field is measured by means of the grid G (seen from above).

filter with $\lambda_{max} = 710$ nm and $\Delta\lambda(50\%) = 10$ nm is used for illumination.

In series I the flies are exposed to 3 different experimental arrangements according to the spatial relationship between the position of the screen, in which the apparatus is inclined at 30° to the horizontal, and the direction of the geomagnetic field: 1. The line of inclination of the screen ascends to the south so that a symmetric situation is achieved with regard to the geomagnetic field (SYM). The flies exactly running in the line of inclination cross the lines of the magnetic field under the vertical angle of 29.5°; 2. and 3. The line of inclination ascends to the east (LIE) or to the west (LIW) causing the lines of the geomagnetic field to cross the fly's longitudinal axis laterally from above, when the fly strongly orientates in a negative geotactic way. As shown in the Table the mean vector of the circular distribution SYM of the flies' courses coincides with the zero-direction ($p > 0.05$), whereas in both the other positions of the plane (LIE and LIW) a significant deviation of 5.5° to the left (counterclockwise) could be found ($p < 0.01$). Statistical methods referring to circular normal distributions were used according to BATSCHELET[13]. Unimodality and symmetry of the distribution could be proved by the goodness-of-fit method basing on a χ^2-test.

In series II an apparatus is used which does not restrict the orientation of the flies to one special azimuth (S in SYM, E in LIE and W in LIW). Rather the flies are allowed to run straight upwards in all celestial directions. This was made possible by constructing a funnel-like apparatus (Figure, b and d) the walls of which are inclined at 30° to the horizontal as in series I. Leaving the platform of the lift in the centre of the funnel the flies start in any celestial direction by chance.

In the direction resembling the position SYM on the plane, there should be no deviation from the straight course to the top of the funnel whereas one expects counterclockwise deviations for the directions referring to the arrangements LIE and LIW. In preliminary experiments dealing with that problem ($n = 512$) a unimodal preference of a special direction could not be proved by using the statistical tests of KUIPER[14] and STEPHENS[15].

Now the question becomes obvious of whether flies prefer special directions with reference to the geomagnetic field when tested on a horizontal plane (series III). In the absence of any light and directed gravitational stimuli the flies do not move on the plane. Their resting positions, however, are mainly orientated in the S/N- and E/W-directions as it has also been proved for *Musca, Calliphora* and *Sarcophaga*[2,8]. The differences between the values obtained for the sectors around the directions N/S and E/W and those around NE/SW and SE/NW is highly significant ($p < 0.0005$).

By means of series I we were able to show an influence of the geomagnetic field on the direction of the geotactic orientation. The same is true for bees performing their waggle dance on the vertical comb. One of the numerous values presented in the work of LINDAUER and MARTIN[10] can be directly correlated to our own findings on flies: When bees have to signal the direction straight upward on the eastern side of a comb, which is vertically orientated in the direction N/S, they deviate from the exact direction by nearly 5° to the left (Figure 3: 360°). The stimulus configuration is just the same as in our experimental set up described as LIW, where a deviation of 5.4° to the left was obtained. Two other arrangements (Figure 5: 170°, Figure 8: 185°, black points[10]) resembling our configuration SYM show no deviations as is true for *Drosophila*. Even in the mollusc *Nassarius* deviations to the left occur, when the lines of the geomagnetic field fall at right angles to the long axis of the snail[16].

The deviations of the negative geotactic courses of the flies from the zero-direction (series I)

Stimulus pattern[a]	Distance from the centre of the screen [cm]	Deviation from the zero-direction [degrees][b]	Length a of the mean vector $(0 \leq a \leq 1)$	n
SYM	7	—2.2	0.92	319
	13	—1.2	0.92	319
	19	—0.7	0.93	319
	25	—0.7	0.93	297
	mean deviation:	*—1.2*	*0.92*	
LIE	7	—6.9	0.91	247
	13	—6.2	0.91	247
	19	—4.7	0.92	247
	25	—3.9	0.93	237
	mean deviation:	*—5.4*	*0.92*	
LIW	7	—4.7	0.91	210
	13	—6.3	0.89	210
	19	—5.1	0.91	210
	25	—5.8	0.92	193
	mean deviation:	*—5.5*	*0.91*	

[a] The line of inclination ascends to the south (SYM), to the west (LIW) or to the east (LIE). [b] +, to the right; —, to the left.

Zusammenfassung. Die negativ geotaktische Orientierung von *Drosophila melanogaster* auf einer 30° geneigten Ebene zeigt eine signifikante Abweichung nach links (5.5°), wenn die Linien des Erdmagnetfeldes lateral zur Fortbewegungsrichtung der Fliegen einfallen. Auf einer horizontalen Ebene bevorzugen die Fliegen als Ruhestellungen die N/S- und W/E-Richtungen.

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