

Magnetic Compass of European Robins

Abstract. *The magnetic compass of European robins does not use the polarity of the magnetic field for detecting the north direction. The birds derive their north direction from interpreting the inclination of the axial direction of the magnetic field lines in space, and they take the direction on the magnetic north-south axis for "north" where field lines and gravity vector form the smaller angle.*

In recent years more and more evidence is reported that birds are affected by magnets and by magnetic fields (1). In our previous experiments we could change the direction that birds selected in Kramer cages by changing the direction of the magnetic field, in closed rooms as well as outdoors (2, 3). The importance of the magnetic total intensity became evident. Migratory orientation is possible only in a rather narrow intensity range. This range can be enlarged to a certain extent by acclimating the bird to weaker or stronger fields (3, 4).

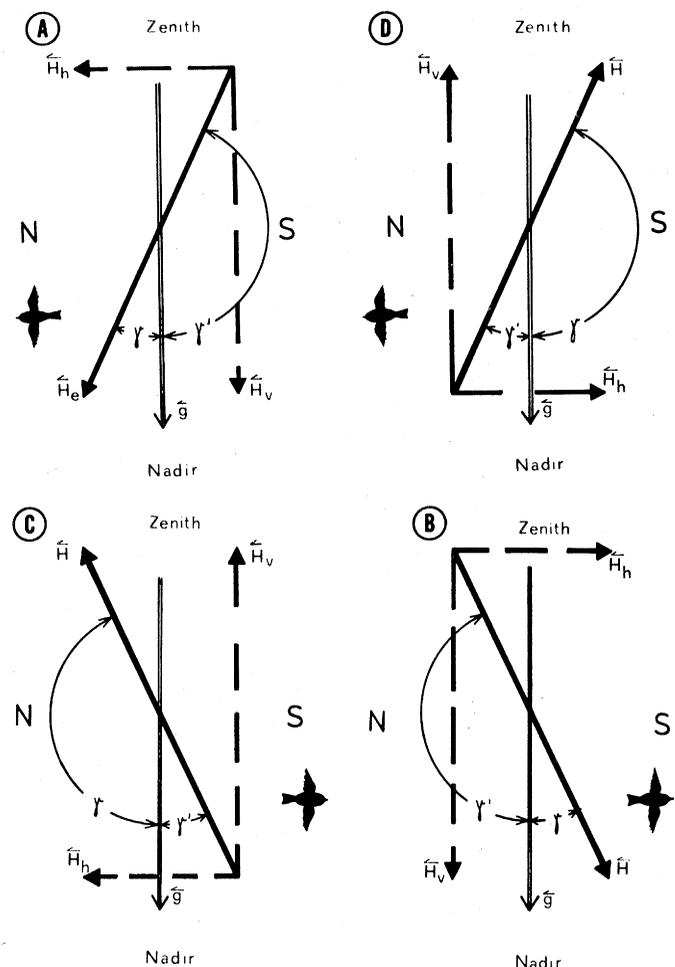
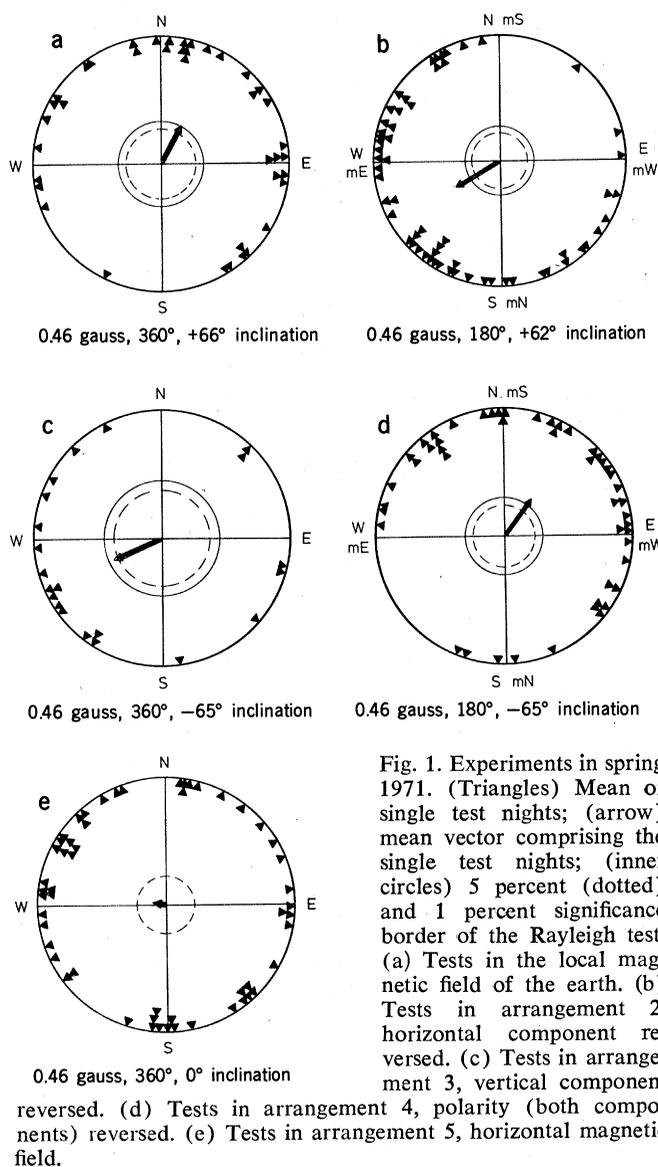
The test series described below was made in the spring of 1971 between 8 January and 12 May to determine the influence of inclination.

Our test bird is the European robin (*Erithacus rubecula*), a night migrating species. All our test birds were kept in rooms with the natural local magnetic field of the earth. Eleven were caught during the spring migration of 1971, and they were kept in a room with the natural photoperiod; 16 others had been caught during the autumn migration of 1970, and they were brought into a light-dark period

(L/D = 13/11) at the end of December, so that we had birds exhibiting migratory restlessness (Zugunruhe) at the beginning of January (5).

We measured the spontaneous directional preferences of the nocturnal migratory restlessness of our birds with octagonal registration cages (1 m in diameter, 35 cm high) that contained eight radially positioned perches. The movements of the test bird on the perches were recorded electromechanically on a paper tape, which was processed by a computer. In each registration cage we tested one bird a night. The registration method is described in detail in (3).

The earth's magnetic field in Frankfurt is 0.46 gauss; magnetic north is at 360°, and the inclination is +66°. The different magnetic fields used in this study were produced with Helmholtz coil (2 m in diameter, 1 m clearance). To control the tests and to pre-



vent unnoticed irregularities of the test rooms from affecting the outcome of the experiments, a test series in which we expected a direction to be preferred and a test series in which we expected random movements, or two test series in which we expected two different directions to be preferred, were performed alternately in the same test room.

As in our previous experiments, we used the frequencies of activation of the individual perches as the criteria for directional preference. The mean directions for each night are comprised in the mean direction α_m and in the concentration a_m of a series, according to the procedure outlined by Batschelet (6). The directional concentration a_m is tested by the Rayleigh test for directional preference, and differences in mean directions of different series are tested with the Watson and Williams test (6).

1) In test arrangement 1 we used the natural local magnetic field of the earth (0.46 gauss, magnetic north 360° , inclination $+66^\circ$; Fig. 2A). The results are given in Fig. 1a; in 40 test nights, α_m was 29° north-northeast. As controls we used the tests performed in test arrangement 3.

2) In test arrangement 2 we inverted the direction of the horizontal component of the magnetic field, so that magnetic north was now in geographic south (Fig. 2B), while the total intensity and inclination remained about the same as in the earth's magnetic field (0.46 gauss, magnetic north 180° , inclination $+62^\circ$). The birds changed their preferred direction correspondingly; the results are given in Fig. 1b; in 60 test nights, α_m was 240° , geographic west-southwest, magnetic east-northeast. These data and the data obtained in the earth's magnetic field are from different statistical populations ($P < .001$). As controls we used the tests performed in test arrangement 5.

3) In test arrangement 3 we inverted the direction of the vertical component of the magnetic field, so that the inclination was changed from $+66^\circ$ to -65° , while the total intensity and north direction remained the same (0.46 gauss, magnetic north 360° , inclination -65°). The vertical component of this magnetic field was now directed upward, toward the sky, whereas the horizontal component pointed toward north, as in the earth's magnetic field (Fig. 2C). The results are given in Fig. 1c; in 21 test nights,

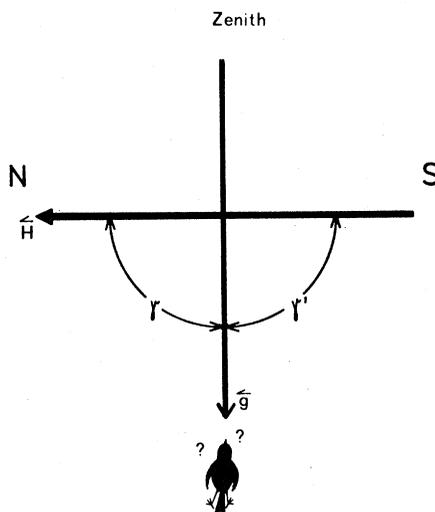


Fig. 3. Arrangement 5; the symbols have the same meaning as in Fig. 2.

α_m was 246° , geographic west-southwest, magnetic west-southwest. While the difference between the directional preference in this magnetic field and that in the earth's magnetic field is statistically significant ($P < .001$), we cannot find any statistical difference between the directional preferences in this magnetic field and in test arrangement 2. These findings confirm the results of a test series conducted in spring 1970 in the same test arrangement (4).

4) In test arrangement 4 we inverted both components of the magnetic field, so that the horizontal component pointed toward south and the vertical component pointed upward (0.46 gauss, magnetic north 180° , inclination -65°), that is, we inverted the polarity of the magnetic field, while keeping the same axial direction of the magnetic field lines (Fig. 2D). The results are given in Fig. 1d; in 49 test nights, α_m was 37° , geographic northeast, magnetic southwest. This directional preference does not differ from the birds' preference in the earth's magnetic field, whereas the Watson and Williams test shows a statistically significant difference ($P < .001$) from the outcome of the tests in arrangements 2 and 3. (As controls we used a test series in a magnetic field with a total intensity outside the intensity range birds can use for orientation: 0.32 gauss, magnetic north 360° , inclination $+60^\circ$. In 38 test nights α_m was 94° , and a_m was 0.145, with $a = 0.28$ at $P = .05$.)

5) In test arrangement 5 we produced a magnetic field with horizontal field lines; that is, this magnetic field had only a horizontal, but no vertical

component (Fig. 3). The total intensity and the north direction were the same as in the earth's magnetic field (0.46 gauss, magnetic north 360° , inclination 0°). In this test arrangement the birds seemed to be unable to orient themselves; the means of the 55 test nights show a random distribution (Fig. 1e).

One might expect birds to use a magnetic compass working by the polarity of the magnetic field, like the ordinary magnetic compasses used by surveyors or sailors. But our findings do not fit this hypothesis. We would have to expect the same preference in test arrangements 1, 3, and 5, since in all these test arrangements the polarity points toward north (Fig. 2A and C and Fig. 3). Instead we find opposite preferences in arrangements 1 and 3, and in arrangement 5 we cannot find any preference at all. The direction the birds take for "north" does not depend on the polarity of the magnetic field.

Another parameter is the axial direction of the magnetic field lines, which is identical in the local magnetic field of the earth and in arrangement 4 (Fig. 2A and D), and also in arrangements 2 and 3 (Fig. 2B and C). Since the birds' preference is the same in the earth's magnetic field and arrangement 4, and in test arrangements 2 and 3, we must assume that the direction which is "north" for the birds depends on the axial direction of the magnetic field lines.

But the axial direction of field lines, without their polarity, can provide only a north-south axis for the birds' orientation system. Yet birds select their migratory direction according to the season, unequivocally, and not axially, and so they must use still another source of information to determine where "north" lies on the north-south axis given by the magnetic field lines.

One possibility is that this further information is their knowledge of up and down, and that they interpret the inclination of the magnetic field lines in space. In the northern hemisphere we have a dip toward the ground, that is, the angle between the downward direction (direction of the gravity vector) and the magnetic field lines is smaller than 90° in the north. If the bird compares the two angles between the magnetic field lines and the downward direction (we call the one between the magnetic vector and the gravity vector γ and its supplement angle γ' ; see Fig. 2), he can determine

north by selecting the smaller one. In all our experimental magnetic fields the birds took the direction in which the smaller angle was formed by the field lines and the gravity vector for "north."

In test arrangement 5 the magnetic field had no vertical component and, correspondingly, no inclination (Fig. 3). In this field the two angles γ and γ' were equal, so that the birds were unable to decide which end of the north-south axis of the magnetic field lines was "north." They were disoriented, and we could no longer find a significant directional preference.

A compass system that uses the axial direction of the magnetic field lines and their inclination will fail at the magnetic equator, where the field lines are horizontal; it will lead the birds in a wrong direction after they have crossed the equator and are flying in the southern hemisphere, where the smaller angle between the field lines and the gravity vector lies in the south. Our experimental species, the European robin, has all his wintering areas north of the magnetic equator and will never encounter these situations, but most bird migrants cross the magnetic equator twice a year. Experiments with long-distance migrants will have to show whether they have a similar compass system and, if they do, what other orientation aids they use to find their way across the magnetic equator.

On the whole this magnetic compass represents a highly flexible direction-finding system. Its ability to adjust to

a varying intensity range makes it independent of any secular variation in total intensity, and the fact that it does not use the polarity of the magnetic field means that it is not affected by the reversals of the polarity of the earth's magnetic field that have taken place several times since the phylogenetic origin of birds (7).

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5. Previous experiments showed no difference in the orientation behavior of robins kept in the natural photoperiod and robins whose migratory restlessness was induced earlier by photoperiodic treatment [see (3)].
6. E. Batschelet, *Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms* (American Institute of Biological Sciences, Washington, D.C., 1965).
7. See S. K. Runcorn, in *The Earth's Crust and Upper Mantle*, P. J. Hart, Ed. (Geophysical Monograph 13, American Geophysical Union, Washington, D.C., 1969), p. 447.
8. This work was supported by the Deutsche Forschungsgemeinschaft in the program SFB 45. The computer work was carried out by the Zentrales Recheninstitut der Universität Frankfurt. We also thank H. Golle, C. Siebert and C. Birkmüller for help in conducting the experiments, and J. R. King and F. W. Merkel for critically reading the manuscript.

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Angiotensin I: Metabolism by Plasma Membrane of Lung

Abstract. (8-L-[¹⁴C]phenylalanine)angiotensin I is metabolized in one passage through blood-free lungs. Approximately 20 percent of the radioactivity emerges as angiotensin II, the remainder as lower homologs. Radioactivity is not retained by the lungs but has the same volume of distribution and mean transit time as blue dextran, a compound unlikely to leave the intravascular space. Plasma membrane fractions of lung are capable of converting angiotensin I to angiotensin II. These data, taken together, indicate the circulating angiotensin I is metabolized by enzymes of the luminal surface of pulmonary endothelial cells.

We have postulated that circulating angiotensin I and bradykinin, like the adenine nucleotides, are metabolized by enzymes located on the luminal surface of pulmonary endothelial cells (1-3). Our hypothesis is based on the findings that angiotensin I, bradykinin, and the adenine nucleotides disappear during a single passage through the lungs (4). Disappearance is accounted for by enzymatic degradation, and not by tis-

sue uptake nor transfer to extravascular spaces. The metabolites of these compounds are recovered in quantitative yields in the pulmonary venous effluent, neither the parent compounds nor the metabolites being retained by the lung. Furthermore, the metabolism does not depend on enzymes of blood nor secretion of soluble hydrolase enzymes (1-3).

In the case of adenosine 5'-monophos-

phate (5'-AMP), we have shown that the relevant metabolic enzymes are located within endothelial caveolae intracellularly open to the vascular lumen (3). The close parallels of the disappearance of angiotensin I, bradykinin, and 5'-AMP suggest that they are metabolized by similar mechanisms (1, 3). In the present investigation we have extended studies of the kinetics of disappearance of (8-L-[¹⁴C]phenylalanine)angiotensin I during circulation through the lungs and have examined plasma membrane and attached caveolae of lung for their ability to metabolize angiotensin I. The fate of angiotensin I, and therefore the subcellular localization of its metabolic enzymes, in the pulmonary circulation may be of physiologic significance as one of the metabolites is angiotensin II, the most potent hypertensive substance known (1, 2).

The first series of experiments were performed using Sprague-Dawley rats (0.2 to 0.3 kg). The rats were anesthetized with intraperitoneal injections of chloral hydrate (300 mg/kg). The trachea was cannulated and the lungs were ventilated with a Harvard (model 680) respirator. The aorta was ligated just above the aortic valve, and the lungs and heart were removed as a unit. The lungs were perfused via the pulmonary artery with Krebs-Henseleit solution aerated with O₂ and CO₂ (95:5) and heated at 37°C. The perfusion solution was pumped at 6 ml/min, at pressures of less than 25 mm-Hg. The venous effluent was collected from a cannula placed in the left atrium.

Our perfusion method is efficient in removing blood elements, and it does not cause damage detectable by electron microscopy (5). In particular, those structures most sensitive to mechanical damage and variations in pH, electrolytes, and nutrients, such as the mitochondria, cell membranes, and cell junctions, are well preserved. Furthermore, we have found no evidence by gravimetric or electron microscopic techniques of interstitial edema.

When the venous effluent became free of blood (2 to 3 minutes), blue dextran and (8-L-[¹⁴C]phenylalanine)angiotensin I (100 μ C/ μ mole) were added to the pump line for constant infusion. Blue dextran (molecular weight > 2 million) was used as a compound unlikely to leave the vascular space during a single circulation, and therefore provided a basis for estimating apparent mean transit times and intravascular volumes (6). The venous effluent was collected, dropwise, into scintillation