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0014-4754/90/070753-03$1.50 + 0.20/0

Depolarization of natural skylight disrupts orientation of an avian nocturnal migrant

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Received 22 August 1989; accepted 1 November 1989

Summary. Given a view of clear evening skies, migratory blackcaps (Aves: *Sylvia atricapilla*) orient appropriately in the absence of meaningful information from the geomagnetic field. When the intensity of natural skylight polarization patterns was reduced with pseudodepolarizers by over 90%, test birds were disoriented, and their migratory restlessness in autumn was drastically reduced.
Key words. Orientation; skylight polarization; bird migration; pseudodepolarizer; *Sylvia atricapilla.*

Nocturnal avian migrants often take off for migratory flights during the twilight period after sunset but before total darkness. At that time of day skylight polarization reaches its maximal intensity and, with a band of maximal polarization running perpendicular to the sun azimuth through the zenith, it provides a prominent potential compass cue for organisms able to perceive it[1-3]. In addition to the geomagnetic field, visual, sun-related information has been demonstrated to provide an important directional reference for nocturnal migrants during take-off[4,5]. Despite some early failures to demonstrate the ability of birds to perceive the plane of polarization of linearly polarized light[6], it has now been firmly established that birds are able to differentiate e-vector directions[7-9]. It was possible to influence predictably the directional choices of migratory birds in funnel-shaped orientation cages[10] by covering them with polarizers; the birds tended to orient parallel to the artificial e-vector, no matter which way it was turned[9,11-14]. These findings indicate that birds may use e-vector information as a compass for migratory orientation.

Two points, however, remain to be resolved: a) Does sun-related visual information used by nocturnal migrants consist of the azimuth of the sunset point, the polarization patterns, or both? b) What role do natural polarization patterns (as opposed to artificially imposed ones) play in the orientation system? Polarizers produce a highly artificial visual stimulus[9], and the birds oriented parallel to the e-vector rather than keeping an angle as they did (in control tests) with respect to the natural band of maximal polarization[13]. Such experiments do not prove that natural skylight polarization patterns have any significance in bird orientation. This can only be demonstrated by depolarizing the skylight as seen by the birds, and at the same time preventing orientation by the geomagnetic field. I here report results of the first such experiment, which provide evidence that birds can indeed use *natural* skylight polarization patterns for orientation, independently of the horizon glow of the setting sun.

Material and methods

Experiments were conducted with the blackcap (*Sylvia atricapilla*, Sylviidae), a widespread Palearctic nocturnal migrant which was previously shown to respond to e-vector manipulations during sunset orientation tests[13]. Thirty birds (27 juveniles, 3 adults) were caught prior to migration during July to mid-September and were housed in individual cages in Frankfurt am Main (FRG). Cages were placed in an outdoor aviary until late September, and again ten days prior to the spring tests and from then on, so that the birds could see parts of the natural sky. Orientation tests were performed during 15 September to 30 November 1986, and 8 April to 18 May 1987, with birds chosen at random from a pool of 29 in autumn and 14 in spring. Individuals used in spring had wintered indoors at Frankfurt in a photoperiod corresponding to the natural one of their winter range.

Aluminium orientation funnels (top diameter 35 cm, height 15 cm) lined with typewriter correction paper (Tipp-Ex) were covered either with clear plexiglass (controls) or with plexiglass plus a double-layer of a commercially available pseudodepolarizer (Hostaphan = polyethylene terephthalate, Hoechst AG, Wiesbaden). Two sheets of Hostaphan (each 0.18 mm thick) were taped

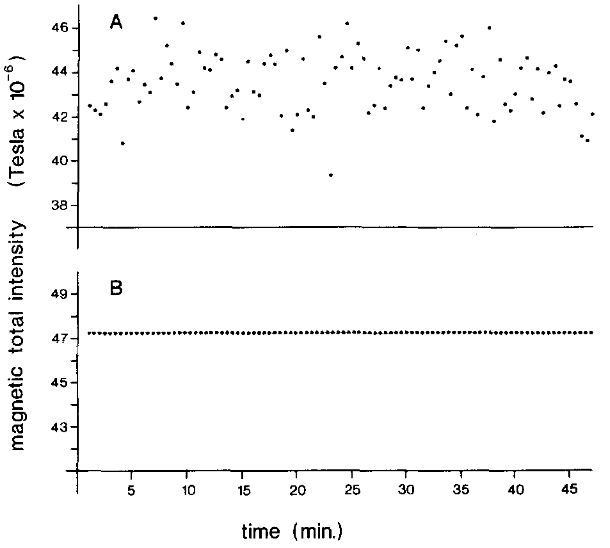

Figure 1. Magnetic total intensities measured at 30-s intervals at Frankfurt test site *A* and at an undisturbed control site *B*. Mean values (but not range) around which intensities fluctuated at *A* depended on the exact location on the site. Measurements were taken at the time of the experiments.

together with their fast axes at 45° (for the functioning of pseudodepolarizers, which consist of linear chromatic wave retarders, see Shurcliff[15]). Polarized light passing through this arrangement was depolarized by over 90% (91.8% at 625 nm)[12] while light intensity was reduced by 10–15% between 400 and 800 nm. Below this range, transmission declined to 65% at 360 nm and then steeply to near zero at 310 nm. Optically the sheets were clear and allowed the birds an unobstructed view of the sky. Funnels were set up on clear evenings only (with no peripheral shields) on the flat roof of our institute building after local sunset (birds did not see the sun) and were retrieved when major stars became visible (about 50 min later). Control and depolarizer tests were always run simultaneously. Extensive measurements with a G-866 recording magnetometer (EG&G Geometrics) showed that the magnetic field at this site was greatly disturbed (fig. 1); it fluctuated at random between 42000 and 54000 nT with average inclinations between 64° and 78°. The fluctuations were caused by the building's air conditioning system (which was running permanently) and made the field unsuitable for magnetic orientation. At this site, birds were disoriented in tests under overcast skies but well oriented under clear skies[16]. It was thus not necessary to use Helmholtz coils to prevent the birds from orienting magnetically. At magnetically undisturbed sites, both wild-caught and hand-raised blackcaps orient well without a view of the clear sky[16, 17].

Data analysis and statistics

Funnel papers were divided into 24 sectors and scratches left by the birds counted on a light screen. This yielded a reliable measure of directional preferences as well as amount of activity. Recordings with less than 25 scratches were scored as 'inactive'. Statistical treatment follows Batschelet[18]. A directional heading was calculated by vector addition irrespective of the concentration of the hopping activity (for treatment of axially bimodal distributions see Helbig and Wiltschko[13]). Data were pooled for each experimental condition and a mean vector was calculated and tested for significance using the Rayleigh test. The non-parametric Mann-Whitney test was used to compare deviations from the overall mean direction and amounts of activity (numbers of scratches) between two samples.

Results

During both seasons the blackcaps were significantly oriented in seasonally appropriate directions, i.e. WSW in

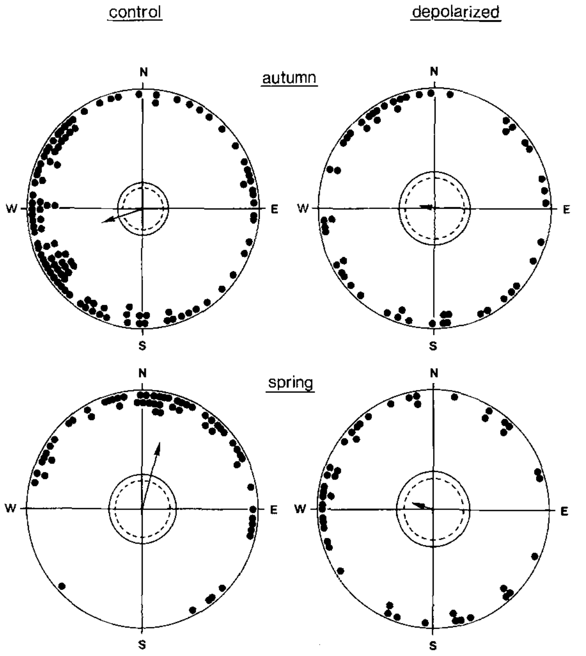

Figure 2. Directional choices of blackcaps in autumn (n = 29 birds) and spring (n = 14 birds) under clear plexiglass (control) and under pseudodepolarizers (depolarized). Inner circles = 5% (dashed) and 1% (full) significance level of Rayleigh test. Data see table.

Activity and orientation of blackcaps in orientation funnels covered with depolarizer and plexiglass only (controls) resp. n = number of tests; r = length, α = direction of mean vector

Condition	n active	n inactive	n axial	No. scratches (median)	r	α
Autumn						
Depolarized	53	24[a]	10	101[b]	0.15[n.s]	279°
Controls	110	17	12	160	0.37[c]	253°
Spring						
Depolarized	45	12[d]	11	79[d]	0.20[n.s]	285°
Control	60	20	15	83	0.56[c]	15°

[a] Significantly more inactive tests than in control conditions ($p < 0.005$, chi^2) [b] For active tests significantly fewer scratches than in controls ($p < 0.01$; Mann-Whitney test) [c] Significant directional preference ($p < 0.001$, Rayleigh test) [n.s] No directional preference ($p > 0.05$, Rayleigh test); headings significantly more scattered than in controls ($p < 0.01$, Mann-Whitney test) [d] No differences between depolarizer and controls tests (chi^2 & Mann-Whitney test, resp.)

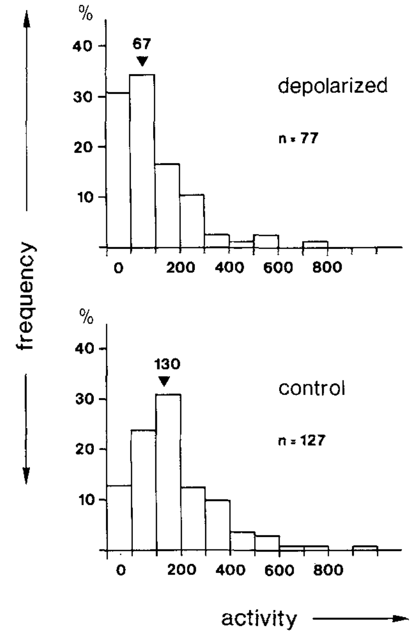

Figure 3. Frequency distribution of number of scratches produced per test by blackcaps in autumn. Depolarized = 77 tests under pseudodepolarizers; control = 127 tests under plexiglass covers. Black triangles = median numbers.

autumn and NNE in spring (fig. 2, table). This roughly corresponds to migratory directions in this species known from ringing recoveries[19]. Under depolarizers the birds' behavior differed from that of the controls in two ways: a) The distribution of directional choices was significantly more scattered and did not differ from random in either season. b) The hopping activity per test was significantly reduced compared to that of controls in autumn, but not in spring (table; fig. 3). Under depolarizers in autumn, tests without any activity were not only more frequent, but those birds displaying activity also produced significantly fewer scratches than under control conditions.

Spring activity was lower overall ($p < 0.001$; Mann-Whitney test), which would tend to obscure a possible influence of depolarizers on migratory motivation. The effect of depolarizers in every way resembled that of total cloud cover at the same site[16], although the birds were still able to see the clear evening sky and the horizon glow of the setting sun.

Discussion

These results are the first to provide direct evidence that avian migrants are able to use the natural polarization patterns at dusk as a compass reference. In the absence of useful magnetic information, blackcaps even seemed to depend on polarization, since the sunset horizon glow did not suffice for meaningful orientation. Surprisingly, the amount of autumnal migratory restlessness displayed during the tests was significantly depressed under depolarizers. This might indicate an unspecific effect on the motivation to migrate caused by the lack of a prominent orientation factor.

Previous tests with depolarizers were performed in the natural geomagnetic field and did not seem to influence the birds' orientation as compared to controls, nor were effects on the amount of migratory activity reported[14]. It is thus unclear whether those test birds used the sunset horizon glow or the magnetic field as a back-up compass reference. Moore and Phillips[12] used a very different experimental set-up to test for the relative importance of the sun versus polarization patterns in yellow-rumped warblers; the view of the (maximally polarized) zenith sky was covered and the birds were looking out through side windows. When incoming light was depolarized and the setting sun was shifted with mirrors, the birds shifted their orientation as if using a sun compass (the magnetic field was not altered). While supporting a role of skylight polarization in orientation, these results are not strictly comparable with mine, because the birds could not see the zenith with its band of maximal polarization but, on the other hand, were allowed a view of the setting sun.

In summary, the evidence from experiments with migratory birds points to an important role of skylight polarization patterns in the orientation system, whether or not the sunset horizon glow is involved as an additional cue. As is the case with the sun compass in homing pigeons[20], the polarization compass is likely to be an ontogenetically secondary mechanism, which has to be learnt and calibrated against some primary reference, most likely the geomagnetic field[21–23]. Among vertebrates the ability to perceive e-vector directions has been reported for fish[24], amphibians (in which it may relate to extraocular perception[25, 26]), reptiles[27], birds[7, 8], and mammals including man[28]. The sensory mechanisms by which birds (or other vertebrates) perceive e-vector directions are not known, but the behavioral significance of this capacity has been clearly demonstrated. As with the classic studies of polarization orientation in honey bees, it may be a long way from the demonstration of behavioral relevance[29] to the elucidation of underlying sensory mechanisms[30].

Acknowledgments. This study was supported by the Deutsche Forschungsgemeinschaft (program SFB 45) and a scholarship from the Konrad-Adenauer-Stiftung.

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0014-4754/90/070755-04$1.50 + 0.20/0

Interpreting animal wall-following behavior

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Received 24 July 1989; accepted 8 December 1989

Summary. Using computer simulations and behavioral experiments with the American cockroach, we found that active vs passive (barrier-directed) wall-following can be readily distinguished and quantified by incorporating a range of convex curves into test arenas. Although previously considered strongly thigmotactic, more than 50% of running American cockroaches depart convex curves with diameters less than 1 m. A new framework for evaluating wall-following behaviors is presented.

Key words. Thigmotaxis; wall-following; cockroaches; orientation.

Wall-following is commonly taken as diagnostic of 'thigmotaxis', which is currently defined[1, 2] as the orientation of an animal in space by touch. The wall-following paths produced by thigmotactic animals are thought to be generated by minimizing departures from a surface once contact is established and a propensity to turn back quickly if contact is lost[3-5]. However, using Weston's[6] computer simulations of animal movement, we can generate a pattern of wall-following very similar to that of a thigmotactic animal simply by restricting the circular standard deviation of permissible turn angles for an otherwise random mover in a bounded arena (fig. 1A–C). These movement simulations convincingly demonstrated that the apparent wall-following paths of straight running movers in an arena bounded by straight or concave walls (fig. 1B, C) could easily be confused with true thigmotaxis. We suspect that this confusion abounds in the behavioral literature, including work of our own[7].

In light of the simulation results, we reasoned that incorporating convex curves into the walls of an arena (e.g. the hourglass arena, fig. 2A) should help differentiate active from passive wall-following. A highly thigmotactic animal (active wall-follower) would be expected to hug the wall when following both convex and concave curves (fig. 2A, path 1), while a pseudothigmotactic animal (passive wall-follower) would be expected to depart from the convex curves (fig. 2A, paths 2 and 3). Furthermore, the strength of an animal's thigmotactic response could be quantified by scoring the percent of runs along convex curves of varying radii that result in departures.

We tested these predictions using a laboratory strain of the American cockroach (*Periplaneta americana* L.), an animal considered strongly thigmotactic[8], but previously studied only in circular arenas. In our own preliminary studies of cockroaches using a 1 m diameter circular arena, walking *P. americana* (n = 10) spent 74% of their time in contact with the arena wall, and when running rarely departed (i.e. moved more than 1 antennal length) from the wall. While these data are consistent with Bell's[8] observations that *P. americana* is strongly thigmotactic, they do not exclude passive wall-following. We report here: 1) the results of two experiments which demonstrate that moving American cockroaches are not strongly thigmotactic and 2) a new conceptual framework for evaluating the wall-following behavior of animals.

Materials and methods

Hourglass arena experiment. The arena (fig. 2A) was constructed by cutting a hole of desired shape in a 65 × 120 cm sheet of 2 cm thick plywood. A 15 cm high wall of flexible, Mylar™ plastic was glued to the sides of the cut-out. This movable arena was set on a sheet of heavy brown wrapping paper (changed for each experi-