

stress and the flow of sub-glacial water (the basal hydraulic gradient is controlled primarily by the surface slope²⁴). This likely sequence of events raises the possibility that the shutdown of flow of ice and basal water through ISCO contributed to the eventual stagnation of the trunk region of ice stream C about 100 years later. Others have also suggested that the slow-down of ISC was a result of re-routing of ice²⁵ or basal water²⁶ away from the main trunk of the ice stream.

Of particular consequence are implications for the future. On the basis of the present-day geometry (ice thickness about 1.1 km, surface slope about 1.8×10^{-3}), measured surface velocities toward WIS2 (up to 20 m yr^{-1}) are two orders of magnitude faster than those expected from deformation of the ice column alone²⁷. Most of the speed today is a result of basal motion, which is not surprising because fast flow requires a lubricated bed, and liquid water has been detected in boreholes that have been drilled to the bed in the region⁸. Basal meltwater production will increase if flow continues to accelerate¹⁰, which could lead to streaming velocities in the near future. The mass balance of the Ross ice streams is now positive¹, but flow of 600 m yr^{-1} through such a hypothetical tributary (WIS3—1.1 km thick and 30 km wide) would discharge about $20 \times 10^{12} \text{ kg yr}^{-1}$ and effectively eliminate the present imbalance not only of ISC, but also of the entire Ross drainage system. □

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Lateralization of magnetic compass orientation in a migratory bird

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Lateralization of brain functions, once believed to be a human characteristic, has now been found to be widespread among vertebrates^{1–3}. In birds, asymmetries of visual functions are well studied, with each hemisphere being specialized for different tasks^{4–8}. Here we report lateralized functions of the birds' visual system associated with magnetoperception, resulting in an extreme asymmetry of sensing the direction of the magnetic field. We found that captive migrants tested in cages with the magnetic field as the only available orientation cue were well oriented in their appropriate migratory direction when using their right eye only, but failed to show a significant directional preference when using their left eye. This implies that magnetoreception for compass orientation, assumed to take place in the eyes alongside the visual processes^{9–11}, is strongly lateralized, with a marked dominance of the right eye/left brain hemisphere.

In birds, fibres of the optic nerves cross over completely and interhemispheric commissures are comparatively small. As a consequence, visual input from the right eye is predominantly processed by the left hemisphere and vice versa. Studies testing monocular birds with one eye occluded suggest a division of functions between the two hemispheres, with the left eye/right hemisphere being specialized for geometric aspects of visual cues and novelty⁸, whereas the right eye/left hemisphere predominantly processes object vision^{5,6,12}. These studies concerned tests performed in the small-scale surroundings of laboratories. However, recent studies with pigeons homing over distances of up to 40 km revealed that monocular birds using their right eye performed



Figure 1 A robin ready for monocular testing. Left, view of the covered eye; right, view of the open eye. J.T. took the photographs.

consistently better than those using their left eye, thus suggesting a superiority of the left brain hemisphere also in processes involving flight control, navigation and homing^{13,14}. The differences were mostly small, with one exception: in the only release conducted under overcast conditions, the difference in initial orientation and homing performance between the two groups was markedly increased¹³. This seemed to point out a possible involvement of the avian magnetic compass.

In birds, magnetic compass orientation is based on light-dependent processes assumed to take place in the eyes^{9–11}. Certain macromolecules are raised by photon absorption to singlet-excited states, forming radical pairs. By hyperfine coupling, singlet pairs are interconverted into triplet pairs. The triplet yield depends on the alignment of the molecules in the ambient magnetic field and could thus be used to detect directions⁹ (for details on the proposed mechanism, see ref. 9). Behavioural studies with passerines—using migratory orientation as a criterion of whether birds are able to obtain directional information from the magnetic field—showed that magnetoreception requires light from the blue–green part of the spectrum, with excellent orientation under near-monochromatic green light with a peak wavelength of 565 nm^{10,11,15}. Therefore, to test for a possible lateralization of the magnetic compass, we recorded the orientation behaviour of European robins, *Erithacus rubecula*, in cages under green light, testing the birds under binocular as well as under the two monocular conditions (left or right eye occluded).

For the monocular tests, one eye of the robin was covered with a cap so that light could reach the other eye only (see Fig. 1). Binocular and both types of monocular tests took place in the local geomagnetic field of Frankfurt am Main. The birds were additionally tested monocularly right-eyed in a magnetic field with the vertical component inverted, that is, inclination pointing upwards instead of downwards, to check whether they were using the magnetic inclination compass typical for birds^{15–17}.

We obtained two recordings of each bird in each of the four test conditions. The means of their two headings, α_b , together with the vector lengths based on the two headings, r_b , are given in Table 1. Under the binocular control condition, the birds significantly preferred their seasonally appropriate northerly migratory direction (Fig. 2a). The same is true when they were tested monocularly right-eyed in the local geomagnetic field (Fig. 2c); this distribution is statistically indistinguishable from control. In the monocular right-eyed condition, birds reversed their headings when the vertical component of the magnetic field was inverted (Fig. 2d), indicating the use of an inclination compass. There is no difference in variance

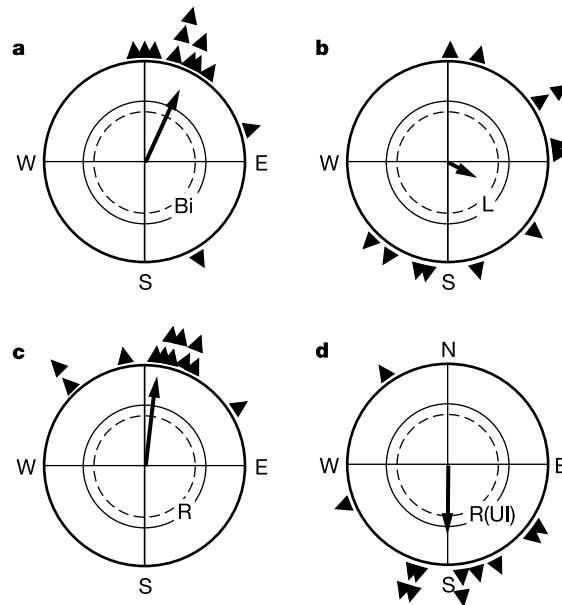


Figure 2 Orientation behaviour under monochromatic green light with the magnetic field as the only cue. The mean headings of the 12 birds are indicated as triangles at the periphery of the circle; the grand mean vector is represented by an arrow proportional to the radius of the circle (for numerical values, see Table 1). The inner circles are the 5% (dotted) and the 1% (solid) significance border of the Rayleigh test²⁵. **a**, Binocular control (Bi) tested in the geomagnetic field. **b**, Monocular left eye (L) tested in the geomagnetic field. **c**, **d**, Monocular right eye tested in the geomagnetic field (**c**; R) and in a magnetic field with the vertical component inverted, so that the inclination was pointing upwards (**d**; R(U)).

between this sample and the control sample or the right-eyed tests in the local geomagnetic field, although the preferred direction is significantly different ($P < 0.001$). In all three conditions, the mostly long vectors (r_b) indicate an excellent agreement between the headings of the two tests per bird (Table 1; see note on r_b in Methods). Together, these data suggest that being forced to use their right eye only did not adversely affect the birds' ability to orient with the help of their magnetic compass.

When the same birds were tested with their right eye occluded, however, the variance increased significantly. They failed to show a significant directional preference (Fig. 2b), with their mean head-

Table 1 Orientation performance of individual birds under test conditions

| Bird | Binocular control (GF) | | Monocular left eye (GF) | | Monocular right eye (GF) | | Monocular right eye (UI) | |
|----------|------------------------|--------------|-------------------------|--------------|--------------------------|--------------|--------------------------|--------------|
| | α_b | r_b | α_b | r_b | α_b | r_b | α_b | r_b |
| R1 | 72° | 0.97 | 57° | 0.39 | 9° | 0.99 | 199° | 0.98 |
| R2 | 27° | 0.94 | 213° | 0.21 | 316° | 0.84 | 200° | 0.91 |
| R3 | 4° | 1.00 | 225° | 0.66 | 58° | 0.70 | 174° | 1.00 |
| R4 | 151° | 0.91 | 16° | 1.00 | 15° | 0.94 | 325° | 0.08 |
| R5 | 17° | 0.91 | 191° | 0.89 | 21° | 1.00 | 195° | 0.92 |
| R6 | 35° | 0.97 | 165° | 0.38 | 13° | 0.96 | 130° | 0.98 |
| R7 | 16° | 1.00 | 196° | 0.47 | 5° | 1.00 | 154° | 0.98 |
| R8 | 16° | 1.00 | 56° | 0.81 | 26° | 0.98 | 196° | 0.99 |
| R9 | 359° | 1.00 | 129° | 0.60 | 23° | 0.85 | 125° | 0.99 |
| R10 | 24° | 0.89 | 81° | 0.60 | 349° | 0.81 | 164° | 0.13 |
| R11 | 25° | 0.97 | 1° | 0.60 | 318° | 0.48 | 173° | 0.92 |
| R12 | 354° | 0.84 | 85° | 0.76 | 11° | 0.82 | 249° | 1.00 |
| $n = 12$ | 25° | Median r_b | (119°) | Median r_b | 7° | Median r_b | 181° | Median r_b |
| | 0.81*** | 0.97 | 0.31 (NS) | 0.60 | 0.89*** | 0.90 | 0.70** | 0.98 |

α_b and r_b are the direction and length of the mean vectors on the basis of the two recordings of the bird under the respective condition. The two bottom lines give the data of the second-order statistic: the direction and length of the grand mean vectors calculated on the basis of the directions of the 12 birds is given under α_b , with asterisks at the vector lengths indicating significance by the Rayleigh test (**, $P < 0.01$ and ***, $P < 0.001$; NS, not significant—here, the grand mean direction is given in parentheses; see also Fig. 2); the medians of r_b are given below. There is no statistical difference in the variance of α_b and in r_b between binocular control and the two monocular right eye conditions, whereas the α_b values of the monocular left eye condition are significantly more scattered ($P < 0.01$, Mann–Whitney U -test) and the r_b values are significantly shorter ($P < 0.01$, Wilcoxon test) than those recorded under control conditions. GF, geomagnetic field condition; UI, upward inclination condition.

ings scattered around the circle. (These headings seem to suggest a certain (nonsignificant) preference of a northeast–southwest axis. The distribution of the 24 headings on which the 12 mean headings are based, however, do not support bimodality, as the axial vector, 0.05, is even shorter than the unimodal vector, 0.19.) At the same time, the vector lengths (r_b) of the individual birds, with a median of 0.60, decreased significantly (see Table 1). These findings indicate that birds with monocular use of their left eye failed to orient, which implies that they were not able to derive the relevant directional information from the geomagnetic field.

Previous findings on the wavelength dependency of magneto-reception^{10,11} were always open to the argument that the observed disorientation under light of longer wavelengths was an unspecific response, as yellow and red light might have influenced the birds' motivation. Our present data make this type of explanation highly unlikely; they clearly indicate an involvement of the eye, in particular the right eye, in magnetoreception.

The performance of the birds when using only the right eye is indistinguishable from their binocular performance, whereas use of only the left eye obviously prevents normal magnetic orientation—this observation indicates a strong lateralization of the avian magnetic compass. It suggests that the processes leading to the perception of directional information from the magnetic field in birds occur almost exclusively in the right eye. As a consequence, the first steps of processing magnetic compass information must be expected to take place predominantly in the left hemisphere of the avian brain.

Such pronounced asymmetry may seem odd in animals whose organization is generally characterized by bilateral symmetry. However, the nature of the geomagnetic field as a stimulus does not require bilaterally symmetrical sensors, because, unlike in audition or vision, there is no need to survey large parts of the environment or to derive directional information from minute time differences between the left and right sensor. Birds could perceive the direction of the geomagnetic field with a non-paired sensory organ, provided it is built in an appropriate way; that is, shaped to include all axial directions⁹, a condition that could be satisfied by the hemispherical shape of one eye.

Electrophysiological evidence indicates that magnetic input is processed by neural structures of the accessory optic system, where single-unit responses to changes in the direction of the magnetic field have been recorded from the nucleus of the basal optic root in pigeons and passerine species. Similar responses have been recorded from the tectum opticum^{18–20}. Both of these midbrain structures feed into the nucleus rotundus^{21,22}, a thalamic relay activated after stimulation with changes in the direction of the ambient magnetic field²³. Tectum opticum, nucleus rotundus and the forebrain ectostriatum comprise the tectofugal system. In pigeons, lateralization of object vision depends on this tectofugal visual system²⁴, which displays numerous morphological asymmetries that are linked to visual lateralization at the behavioural level⁶. For instance, lateralization of object vision, in contrast to a number of other known lateralized functions, has a corresponding anatomical substrate. At the same time, its neuronal pathways are at least in part shared by magnetoreception for directional information. This raises an intriguing question about the origin of these neuronal asymmetries: did they emerge in connection with the one-sided system of magneto-reception in birds so that the superiority of the right eye/left hemisphere in object vision has been induced by already existing structures, or vice versa? Whatever the case, our findings provide evidence of lateralized reception of information for compass orientation, which is associated with a fairly strong hemispheric specialization. Given the basic need for orientation, this may open new perspectives for the understanding of why and how cerebral asymmetries have evolved. □

Methods

Test birds

European robins are small passerines that migrate at night. The test birds had been mist-netted in the garden of the Zoological Institute in Frankfurt am Main (50° 08' N, 8° 40' E) in September 2000; they were kept in an indoor bird room over the winter in a photoperiod simulating the local one until December, when it was reduced to a light/dark cycle of 8/16 h. After New Year, it was increased in two steps to a light/dark cycle of 13/11 h. This induced premature zugunruhe (migratory restlessness) so that testing took place between 8 January and 13 February 2001.

Test procedure

The robins were accustomed to wearing the eye covers—small spherical aluminium caps covering the eye, fixed to the bird's head with adhesive tape (Leukoplast; see Fig. 1)—by wearing them three times for about 90 min on each side before the tests. A pseudo-random sequence determined what bird was subjected to which treatment on a given day. Birds to be tested monocularly received their eye cap immediately before the test; it was removed again at the end of each test. Birds assigned as binocular controls received no treatment.

The tests began when the light went out in the birds' housing cages, and lasted approximately 75 min. Testing followed standard procedures^{10,11}. The birds were tested one at a time in funnel-shaped cages (35 cm upper diameter, 20 cm high) lined with typewriter correction paper; scratches were left in the coating as the birds moved. The cages were covered with an opaque plexiglas cover and placed in aluminium cylinders the top of which carried 24 green LEDs (peak frequency 565 nm, wavelength (λ)/2 at 553 and 583 nm, respectively). The light passed two diffusers before reaching the bird with an intensity of 2.1 mW m⁻².

Most tests took place in the local geomagnetic field of the Frankfurt am Main test site (46,000 nT, 66° inclination); the birds were also tested with their left eye covered in a magnetic field of equal intensity, but with the vertical component inverted (46,000 nT, -66° inclination) produced by a pair of Helmholtz coils.

Data analysis and statistics

The scratches were counted by experimenters that were blind to the test condition, and from the distribution of scratches the heading of the bird in that test was determined. One recording under control conditions with fewer than the standard limit of 35 scratches was excluded from the analysis because of too little migratory activity; this recording was repeated. From the two headings per test condition, the mean heading α_b and a vector length r_b of each bird were calculated (for details, see ref. 11), the latter indicating how well the headings of the two tests coincide. Note that the vector length, r , resulting from two data points, does not change linearly with increasing angular distance, $\Delta\alpha$, between the two points, but follows the function $r = \cos(\Delta\alpha/2)$. Therefore, long vectors are over-represented, with the median at 90° being 0.71 and the quartiles at 45° and 135° being 0.92 and 0.38, respectively.

The mean headings (α_b) of the twelve birds in each condition were combined to the grand mean vector, which was tested for directional preference using the Rayleigh test²⁵. The Watson Williams test was used to test for differences in direction and the Mann Whitney *U*-test was applied to the angular differences from the mean to test for differences in the variance²⁵. The vector r_b values were compared with those obtained under control conditions using the Wilcoxon test for matched pairs of data.

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Moving visual stimuli rapidly induce direction sensitivity of developing tectal neurons

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During development of the visual system, the pattern of visual inputs may have an instructive role in refining developing neural circuits^{1–4}. How visual inputs of specific spatiotemporal patterns shape the circuit development remains largely unknown. We report here that, in the developing *Xenopus* retinotectal system, the receptive field of tectal neurons can be ‘trained’ to become direction-sensitive within minutes after repetitive exposure of the retina to moving bars in a particular direction. The induction of direction-sensitivity depends on the speed of the moving bar, can not be induced by random visual stimuli, and is accompanied by an asymmetric modification of the tectal neuron’s receptive field. Furthermore, such training-induced changes require spiking of the tectal neuron and activation of a NMDA (*N*-methyl-D-aspartate) subtype of glutamate receptors during training, and are attributable to an activity-induced enhancement of glutamate-mediated inputs. Thus, developing neural circuits can be modified rapidly and specifically by visual inputs of defined spatiotemporal patterns, in a manner consistent with predictions based on spike-time-dependent synaptic modification.

Spontaneous and experience-evoked activities in the developing brain can influence the refinement of developing nerve connections into mature neural circuits. In the visual system, rearing kittens with

an artificial squint leads to failure in the development of binocular response properties of striate cortex neurons⁵. Blockade of spontaneous waves of retinal activity also disrupts eye-specific segregation of retinal inputs to the lateral geniculate nucleus^{6,7}. Synchronizing retinal inputs by strobe light or electrical stimulation affects formation of normal receptive field properties in various systems^{8–10}. Furthermore, an instructive role of visual inputs is indicated by the appearance of visual modules in the auditory cortex of the ferret after rewiring of retinal inputs^{11,12}. In the present study, we found a rapid and specific modification of receptive field properties of tectal neurons by the visual input of a defined spatiotemporal pattern, in a manner consistent with hebbian synaptic modification as a mechanism for activity-dependent changes in visual circuits^{13,14}.

The effect of visual experience on the receptive field properties of tectal neurons was examined in developing *Xenopus* tadpoles. Patterned visual inputs were used to stimulate the retina, and tectal cell responses were monitored with *in vivo* perforated whole-cell recording methods (Fig. 1a). First, we mapped the receptive field of the tectal neuron by random and sequential flashing of a white square at various locations on the retina (see Methods). The integrated charge of stimulus-evoked compound synaptic currents (CSCs) was measured within a defined window for the more prominent ‘off’ responses (Fig. 1b). The measured value at each location was represented in grey scale as one element of an 8 × 7 grid that covered the total area of the projected visual image on the retina (Fig. 1c). This analysis based on CSCs reveals a large receptive field (50–80% of the retina, *n* = 12) of tectal neurons at these early stages (42–45), consistent with a diffuse retinotectal connectivity during early development^{15,16}.

To examine the effect of patterned visual inputs on the receptive field property of tectal neurons, we stimulated the retina with white moving bars (20-μm wide, speed 0.3 μm ms⁻¹) in four orthogonal directions (right, down, left and up, Fig. 2a) and recorded the responses of tectal cells evoked by moving visual stimuli. In all tectal cell responses (voltage-clamped at -70 mV, *n* = 20), we found no

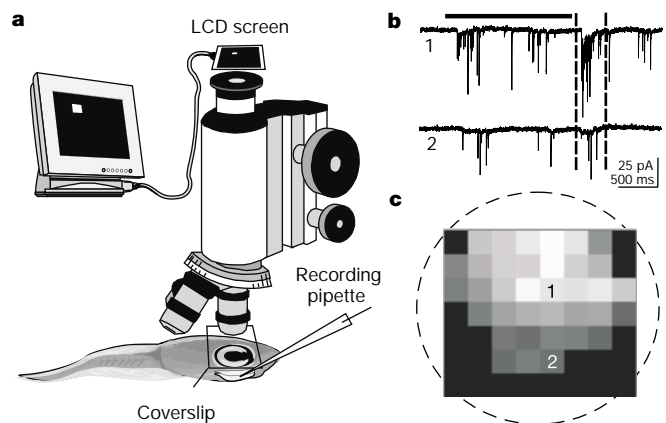


Figure 1 Mapping the receptive field of developing *Xenopus* tectal neurons. **a**, Diagram of the experimental set-up, depicting the recording of a tectal neuron in the exposed tectum. **b**, Traces shown are samples of compound synaptic currents (CSCs) evoked by the flashing of a white square (for 1.5 s, bar) within the receptive field at two locations (marked 1 and 2). Recording was made in voltage clamp at the reversal potential of Cl⁻ current (-45 mV) to reveal glutamate-mediated inputs. **c**, The receptive field was assayed by measuring the integrated charge of the ‘off’ response of CSCs within a defined window (dotted lines in **b**). The value of CSC charge is represented by linear grey scale (black = average basal activity without light stimulus) as a corresponding element in the 8 × 7 grid covering the projection area. The dashed circle marks the approximate position of the retina.

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