SYMP06: The geomagnetic field and its role in bird orientation

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For animals that are able to perceive the geomagnetic field, it represents an omnipresent, reliable source of navigational information. Its vector quality provides directional information, while the spatial gradients of total intensity and/or inclination may provide information on position. The symposium is devoted to presenting various aspects of magnetic orientation and magnetoreception. A first point concerns whether and how free-flying migrants and homing seabirds make use of magnetic cues on long-distance flights. A second focus will be orientation cues used by migrants in cage experiments for spatial and temporal orientation, emphasising the ecophysiological conditions. The last part will concentrate on questions of magnetoreception.

SYMP06-1 Are free-flying migrants guided by geomagnetic cues?

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Caged migrants have been shown to be able to use the geomagnetic field for migratory orientation, but at the same time studies have shown that birds can show appropriate migratory orientation even in the absence of magnetic cues. However, studying the importance of the geomagnetic field for the orientation of free-flying migrants remains extremely difficult primarily due to difficulties in following free-flying birds for long distances and in manipulations of the magnetic field and the uncertainties on the exact location of the goal area. To elucidate the importance of the geomagnetic field for long-distance migrants, we investigated whether migratory tracks of raptors tracked by satellite-based radio telemetry followed geomagnetic courses. More than 70 individual raptors, mostly peregrines on autumn migration in America, but also honey buzzards and ospreys on autumn migration between Europe and Africa, were used for analysis. Overall birds did not follow constant geomagnetic courses, but most tracks curved more than expected from constant geographic courses also. When removing position readings close to the coast (American birds) or obviously curved portions (European birds) there was no such general turn of directions between positions, but it was not possible to distinguish between geographic and geomagnetic courses due to the wide scatter in directions between positions. Consistent deviations from constant compass courses are thus probably caused by topographical features, such as the distribution of land and sea. However, the parts unaffected by the oceans of long, rather straight tracks indicated geographic rather than geomagnetic courses.

SYMP06-2 Orientation in petrels

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During the breeding period petrels make foraging excursions covering thousands of kilometres over featureless oceans. Magnetic information seems the most suitable way to explain their remarkable orientation capacities. To our knowledge, three main experiments have been performed to investigate the role of magnetic cues in petrels' orientation. In all these experiments birds had magnets glued on the head. Satellite tracking of white-chinned petrels released at about 300 km from the colony location, did not show impaired homing capacities. Black-browed albatrosses showed unaffected foraging performances. Wandering albatrosses equipped with satellite transmitters, or GPS loggers, did not show anomalous foraging tracks. Therefore, it doesn't seem that disturbing magnetic perception affects petrels' orientation abilities. These birds should rely on alternative orientation mechanisms.

Olfactory orientation, demonstrated to date in homing pigeon, could make intuitive sense in petrels: they have highly developed olfactory neuroanatomy; some species use olfactory cues to search food at sea; burrowing petrels use olfaction to find the colony and to recognise their own burrow. Could these findings be extended to a possible role of olfaction in orientation? In the ocean, air and water currents are roughly regular. Odours may be transported by winds far from their sources and organised in roughly monotonic gradient fields, making a good reference system for olfactory navigation. Despite such an olfactory landscape might be limited in extension, and petrels could rely on it only at a limited, but huge, distance from their targets, this suggestion opens a new challenge in the study of petrels' orientation mechanisms.

SYMP06-3 Tracks of foraging albatrosses equipped with magnets

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The foraging excursions of waved albatrosses, *Phoebastria irrorata*, during incubation are ideally suited for navigational studies because they navigate between their Galápagos breeding site and one specific foraging site in the Peruvian upwelling-zone along highly predictable straight-line routes. We used satellite telemetry to follow free-flying albatrosses after abolishing magnetic orientation cues by attaching magnets to strategic places on the birds' heads. All experimental birds, as well as sham manipulated and control birds, were able to navigate back and forth from Galápagos to their normal foraging sites at the Peruvian coast over 1000 km away. The three treatments did not differ in the routes flown or in the duration and speed of the trips. Consequently, if the magnetic sensor is located in the head region, as current evidence suggests, magnetic information does not seem to be required for these birds to navigate successfully.

SYMP06-4 Orientation of juvenile barn swallows (*Hirundo rustica*) during autumn migration

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Contrary to night migrants, the migratory orientation of very few day migrating species has been studied so far, and thus data are needed to outline a satisfactory comparative picture.
In this study the migratory orientation of juvenile barn swallow (*Hirundo rustica*), a typical diurnal migrant, was tested for the first time in Emlen funnels during autumn migration. Our aims were to verify the suitability of this species for cage experiments, and to investigate the role of visual and magnetic cues during the first migratory journey. Tests took place the morning following the capture day and each bird was tested only once.

Wild-caught swallows were displaced to the testing site and randomly assigned to four different experimental conditions: clear sky or simulated overcast, in local or shifted magnetic field (magnetic North = geographical West).

Under clear sky swallows tended to orient phototactically toward the best lit part of the funnel and failed to respond to the shift of the magnetic field. In overcast conditions swallows did not orient in the seasonally expected direction but they changed their directional choices accordingly to the shift of the magnetic North. Furthermore, their orientation seemed to depend on the site where they were tested.

These results show that barn swallows have to be added to the small list of diurnal migrants, for which a magnetic compass has been described. Moreover, the site-dependent variability of their directional preferences under simulated total overcast suggests the hypothesis that swallows could at least partially compensate for the imposed displacement.

SYMP06-5 Orientation in the high arctic: experiences from field experiments with migratory passerines

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Birds and other animals use the Earth's magnetic field and celestial cues for orientation during migration. Inherited magnetic compass courses are selected based on the angle of inclination, making it difficult to orient in near vertical fields found at high geomagnetic latitudes. We have performed orientation cage experiments at different sites in high Arctic Canada with adult and young white-crowned sparrows *Zonotrichia leucophrys gambelii* to investigate birds' ability to use the Earth's magnetic field and celestial cues for orientation in naturally very steep magnetic fields at and close to the North Magnetic Pole. We performed experiments during the natural period of migration at night in the local geomagnetic field under natural clear skies and under simulated total overcast conditions. The experimental birds failed to select a meaningful magnetic compass course under overcast conditions at the North Magnetic Pole, but could do so in geomagnetic fields deviating less than 3.0° from the vertical. At all sites migratory orientation was successful when celestial cues were available. Cage experiments with juvenile white-crowned sparrows at a breeding site in Northwestern Canada demonstrated shifts in orientation following shifts of the magnetic field and compass calibrations between celestial and geomagnetic cues. We have also studied the effects of long-distance lateral displacements on the birds' navigation performances in both Canada and in Russia.

SYMP06-6 Magnetic cues trigger extensive fuel deposition in a trans-Saharan migratory bird species, the thrush nightingale *Luscinia luscinia*

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Long-distance migration is a common life-history trait in birds and some species even migrate for more than six months of the year. The main fuel for migratory flights is fat, deposited at stopover sites en route. Large fuel loads entail increased flight costs as well as increased predation risk and birds are most often found to accumulate rather small fuel deposits. Many long-distance migrants have to pass stretches of sea and desert where fuelling is not possible. The passage of the Saharan desert involves flight distances of at least 1500 km, and a safe passage requires that an extensive fuel load has been accumulated in advance. How this strategic fuelling is governed has so far not been fully understood. First-year thrush nightingales caught in the early phase of autumn migration and exposed to a magnetic field simulating a migratory movement to northern Egypt increased more in fuel load than control birds experiencing the ambient magnetic field in southeast Sweden. This finding indicate that geomagnetic information is involved as an external cue when birds decide where to accumulate extensive fuel loads in preparation for crossing the Saharan desert. The non-random geographical distribution of ringing recoveries, found in several trans-Saharan migrant species in the eastern Mediterranean area, further supports the idea that an external cue is involved.

SYMP06-7 The avian magnetic compass – an ancient mechanism?

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Magnetic compass orientation has been studied only in a limited number of birds, yet some unexpected features of this mechanism are shared by all species studied so far: (1) The avian magnetic compass is an „inclination compass“, based on the inclination of the field lines rather than on their polarity. (2) It is light-dependent and shows the same wavelength-dependency in passerines and homing pigeons, working only in the presence of light from the blue-green part of the spectrum. (3) It was found to be lateralized to the right eye / left hemisphere of the brain. These features, found in passerine species and homing pigeons alike, suggest that the avian magnetic compass may be an ancient mechanism, having evolved this way in the ancestors of modern birds.

SYMP06-8 Light-dependent orientation in European robins

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Magnetic compass orientation in birds is dependent on both wavelength and intensity of light. Avian magnetoreception seems to be possible under a specific wavelength-composition of light only, and

shifts in orientation have been observed at high light intensities. The underlying biophysical and physiological mechanisms of such a light-dependent magnetoreception system are still unknown and therefore behavioural studies examining the orientation of birds under different lights give valuable indications of how such a system might work.

We investigated the light dependence of the avian magnetic compass by performing orientation cage experiments with European robins exposed to lights of different wavelengths and intensities. The birds were tested under 560.5 nm green, 567.5 nm green-yellow and 617 nm red monochromatic light of a very narrow wavelength range (half bandwidth of 10 nm, compared to half bandwidths ranging between 30 and 70 nm in other studies) in three different intensities. They were oriented into the seasonally expected migratory direction under green, completely disoriented under green-yellow and showed shifted orientation under red. Based on these results we propose that birds possess a light-dependent magnetic compass based on magnetically sensitive, antagonistically interacting spectral mechanisms.

SYMP06-9 Retinal photopigments as possible transducers for the avian magnetic compass

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Magnetic compass orientation in migratory birds has been shown to require light from the blue-green part of the spectrum. The sensory mechanisms for the detection of the geomagnetic field, however, have yet to be identified. Theoretical models of magnetoreception suggest that birds perceive the direction of the magnetic field by specialized retinal photopigments. A possible candidate could be cryptochrome, a photopigment with an absorption spectrum of 300–500 nm. We used retinal total cDNA of European robins (*Erithacus rubecula*) as a template for amplification of cryptochromes expressed in the eyes of passerine birds. We identified and sequenced two independent PCR products. Temporal and spatial expression analysis of these genes in the retina by quantitative PCR and in situ hybridization are in progress.

SYMP06-10 A first structural candidate for magnetic field reception in homing pigeons

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By an interdisciplinary approach of neurobiology, geophysics and material sciences, we are able to present for the first time nervous terminals in the upper beak of homing pigeons as putative magnetic field sensors, which are characterized by two essential intracellular component parts. (1) The nervous terminals contain chains of tiny aggregates of SPM-nanocrystals, which are aligned along the cell membrane. Any modification of magnetic field intensity changes both, the arrangement and shape of the SPM-clusters. (2) Non-crystalline iron platelets, connected by a dense fiber network, build an intracellular „backbone“ of the terminal, and may additionally enhance sensitivity of the receptor by some log units, by focussing magnetic field lines to the SPM-clusters. The fine-structural findings match older data on behavior and neurobiology of magnetoreception of birds, but they could also be ascertained by theoretical calculations and model experiments. The paper introduces details of our ideas concerning primary magnetoreceptor processes.