Orientation in birds: Concluding remarks

A brief definition of the research field's position

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For those interested in problems of avian migration an exceptionally large body of information will be appearing in 1990. In addition to this multi-author review on avian orientation in Experientia, proceedings of a specialists' meeting, held in Tutzing, in southern Germany, during October 1988, entitled *Bird Migration: The Physiology and Ecophysiology* will soon be published by Springer. Lastly, towards the end of the year, an updated students' text book on *Bird Migration* by P. Berthold will be published by the Wissenschaftliche Verlagsgesellschaft, treating the main aspects of avian migration in short overviews. Thus, three reviews will be available during the course of this year and will cover practically the whole field of bird migration.

The present multi-author review on avian orientation does demonstrate the enormous progress that has been made in analyzing orientation mechanisms over the past few years, but at the same time it unveils our considerable ignorance. The answer to the most pressing question – how displaced birds can reorient themselves rapidly more or less precisely homeward and subsequently navigate successfully to their home area – still appears more mysterious than certain. Undoubtedly, Papi's hypothesis on olfactory navigation, based on an impressively extensive amount of pigeon studies and also supported by quite a number of investigations by other experimenters, seems to be a step in the right direction. But at present, it hardly appears to be the solution to the whole mystery. With respect to cases in which anosmic pigeons demonstrate a residual orientation, or even a good orientation, towards home comparable to that of controls or starlings, subjected to bilateral cutting of the olfactory nerves, which demonstrate a homing success of half that of controls, Papi himself suggests that "there may be an auxiliary mechanism which helps to fix the homeward direction..." and "it is possible that a non-olfactory auxiliary mechanism based on information picked up en route functions in some cases...". What is such an auxiliary mechanism – does it just support olfactory navigation in critical cases or is it an essential but explained part in a redundant system of orientation and navigation mechanisms? Wallraff in his extremely careful conceptual approaches to avian navigation systems concluded: "At the present stage, any conceptual approach to the mechanism underlying olfactory navigation is necessarily speculative; its heuristic value cannot be assessed yet." These uncertainties are due to a large extent to the fact that almost nothing is known about the physical substrate and the physical environment on which olfactory navigation is thought to be based. But Wallraff surely is also correct in concluding further that it is certainly less constructive to dismiss olfactory navigation as 'unfeasible'. In my opinion, it appears best and least dangerous at present for further studies to consider the concept of olfactory navigation as a working hypothesis and to keep one's eyes open for alternatives, for possibly undiscovered navigation mechanisms. Waldvogel in his most recent review on olfactory orientation by birds (in: *Current Ornithology*, D. M. Power ed., Plenum Publ. Corp., New York 1989) concluded in a similar way: "The issue of whether odors form the basis of a compass or navigational map in birds (especially homing pigeons) remains unsettled, although in my opinion the bulk of the evidence is currently against an essential role for odors in avian navigation".

In the historically 'classic' domain of our research field – the study of the sun compass orientation – substantial problems are still open and new questions have arisen. As Schmidt-Koenig pointed out, such basic questions as how the sun compass may function in equatorial and transequatorial migrants still remain to be solved – and the same holds true for the magnetic compass in migrants crossing the equator, like those the Wiltschkos have been studying. It is an interesting challenge for ecophysiologists in equatorial countries, who are now starting to perform an increasing amount of basic research. Even more surprising is Schmidt-Koenig's conclusion that "even the most convincing results obtained in the laboratory do not provide evidence that the demonstrated capacities (of the sun compass) are also used in migration or homing". In the case of homing in pigeons, field experiments caught up with laboratory studies a long time ago, but not with respect to migratory species. Although the sun compass was originally studied by Kramer in migratory starlings, later work has overwhelmingly concentrated on homing pigeons, and very little is known about the use of the sun compass by migrants. From Able's and the Wiltschkos' contribution one can expect a reactivation of relevant experiments with respect to problems deriving from 'information around sunset'. It is clear that 'sunset cues' appear to be highly informative for nocturnal migrants. But, as the Wiltschkos pointed out, at present, it is still open "whether sunset cues are part of the sun compass or whether they represent an independent system indicating west". Likewise, the significance of the orientation by polarized light around sunset is also unclear. Very recent tests with warblers have shown that these birds changed their reaction relative to the e-vector significantly when the natural one was replaced by an artificial one, and "these findings lead to the question whether tests with polarizers reflect the natural situation realistically". Whatsoever the meaning of sunset cues might be, their importance favors the idea of checking sunrise factors for their possible significance for diurnal migrants. In this context it has to be emphasized that orientation mechanisms by no means have to be considered to be restricted to migratory species, as Schmidt-Koenig and Terrill pointed out. The recently discovered example that the resident American scrub jay uses the sun compass to directionally retrace formerly built seed caches supports the view that sun compass orientation can also be used by nonmigrants for everyday tasks, and may therefore be studied in a large variety of species.

Able pointed out how easily a study on orientation problems may be erroneously directed to artefacts created by the investigator himself. This may happen when using polarizers as shown above, or also in many other procedures, for instance by simply hand-raising experimental birds and affecting the development of the nervous system with the altered early sensory experience.

There is now some evidence for details of the ontogenetic development of redundant, multi-faceted orientation mechanisms in migrants, i.e. the development of the star compass largely independently from magnetic influences, its later calibration, modification and final stabilization, as well as interactions between the magnetic and the sun compass. As Able stressed, however, all this is based on information from very few species and should therefore be treated with caution. He concluded, for instance: "The hierarchical approach has been a useful paradigm for dealing with the problem of multiple cues in orientation, but in fact it may turn out to be overly simple".

Considerable progress has been made with respect to the study of the magnetic compass. There is now evidence for its existence in 11 nocturnal migrants (8 European, 3 American; R. Wiltschko, Habilitationsschrift, Univ. Frankfurt, in prep.) and in the homing pigeon. Comparable to the uncertainty concerning the physical substrate and environment in the case of olfactorial navigation, the sensory basis for magnetic orientation is still largely obscure. As Griffin pointed out in the preface, "perhaps the data reported in the chapter by Semm and Beason mark the beginning of such a rounded body of mutually reinforced evidence that will at last constitute a fully convincing explanation of avian (magnetic) orientation". Semm's and Beason's conclusion that "it might well be that the photoreceptors are also the postulated magnetoreceptors for the magnetic compass" is a strong challenge for further practical work in this direction. They concluded further that "two different types of magnetoreceptors have been postulated and [that] there is some preliminary electrophysiological evidence that birds may have two independent magnetic systems". The severing of the posterior part of the ophthalmic nerve in the upper beak area "implies that two different magnetic systems with different receptors are present in the bird's central nervous system". These conclusions are in my opinion of considerable theoretical importance with respect to the possibility of magnetic navigation. In this context it should be noted that a migratory salamander, the American eastern red-spotted newt, is thought to use an axial magnetic compass mechanism for compass orientation similar to that demonstrated in migratory birds, but has in addition a "distinct magnetoreception pathway with polar response properties ... in homing ... possibly linked in some way to the navigational map" (Phillips, J. B., Science *233* (1986) 765). Could similar mechanisms also be involved in avian navigation? On the other hand, there are possibly sensory limitations restricting the capacity of magnetic orientation which most plausibly explain typical cases of disorientation and catastrophic mortality in migrants faced with total cloud, fog, rain, etc., as discussed by Alerstam in his review. Nevertheless, orientation based on the geomagnetic field is most simple with respect to a primarily innate mechanism and provides a reliable reference system of spatiotemporal constancy. Finally, it appears rather unlikely that avian navigation should be based on single mechanisms when compass orientation is most probably derived from a redundant system. All these findings and reflections should, in my opinion, prevent us from rushing to conclude that magnetic navigation in birds could not be a working hypothesis for further studies.

Terrill offers in his review for the first time both a comprehensive as well as a detailed hypothesis for the possible evolutionary steps during avian migration, in general, and for orientation behavior in particular. The proposed evolutionary processes from residency through facultative migration and facultative and obligate partial migration over short distances to obligatory migration over long distances may have occurred independently several or even many times in birds. Unlike migratory behaviour, orientation and navigational abilities and mechanisms appear to be phylogenetically more primitive and probably have (apart from the star compass) evolved essentially prior to the main avian speciation. This may facilitate orientation research in birds. Terrill is presumably right in emphasizing that intratropical migration represents an ideal testing ground for studies of rather basic orientation behavior which so far may have been greatly overlooked.

The hypothesis of vector-navigation, demonstrated in my chapter, is now generally accepted as a basis for migratory orientation in birds, expressed as an endogenous, genetically determined time-and-direction program (see Wallraff's and the Wiltschkos' reviews in this issue). This general acceptance, however, should not make one blind to the fact that we still do not know whether the genetically controlled time-and-direction programs are merely a rough orientation framework for birds inexperienced in migration or whether these programs lead migrants in a more detailed fashion to their unknown winter quarters. The accumulating evidence of a general migration with intermittent strategies in steps, at least in a large number of small bird species, allows for a cautiously affirmative suggestion that inherited programs may lead migrants more continuously, step-by-step, to their wintering areas. Extensive analyses of field data will be necessary to elucidate the individual courses of migratory journeys and to solve this problem.

The broad overviews presented by both Alerstam and Richardson demonstrate in an encouraging way that the gap between formalistic laboratory and experimental orientation research and ecological relationships can be bridged. For instance, in the large field of sophisticated relationships between avian orientation and wind, after a long series of often contradictory publications "we are beginning to find a few patterns in this variable behavior", as Richardson states, and "it now appears that optimum behavior may range, depending on circumstances, from total tolerance of (wind) drift to total compensation". It seems likely that careful tests of Alerstam's models for optimum migration strategies will help to settle quite a number of conflicting views on spatially and temporally varying orientation behavior. It is highly likely that new techniques, above all satellite telemetry, will soon add new insights into the individual courses of migratory journeys. The first steps in this promising field have been taken (for review, see Nowak and Berthold, J. Orn. *128* (1987) 405). On the computer screen in the French center of ARGOS in Toulouse (a far-reaching cooperative venture for the satellite-based location of various items), unpublished tracks of albatrosses can be seen which are based on about five contacts per day and demonstrate the oceanic flights of the birds for about eight weeks from the Kerguelen Islands. These tracks show impressively where future orientation studies may obtain optimal information on the behavior of migrants under natural conditions.

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