76 Wallraff, H. G., Relevance of atmospheric odours and geomagnetic field to pigeon navigation: What is the 'map' basis? Comp. Biochem. Physiol. *76A* (1983) 643–663.

77 Wallraff, H. G., Theoretical aspects of avian navigation, in: Acta XVIII Congr. int. Ornith., pp. 284–292. Eds V. D. Ilyichev and V. M. Gavrilov. Nauka, Moscow 1985.

78 Wallraff, H. G., Navigation mit Duftkarte und Sonnenkompass: Das Heimfindevermögen der Brieftauben. Naturwissenschaften *75* (1988) 380–392.

79 Wallraff, H. G., Simulated navigation based on unreliable sources of information (Models on pigeon homing, part 1). J. theor. Biol. *137* (1989) 1–19.

80 Wallraff, H. G., Simulated navigation based on assumed gradients of atmospheric trace gases (Models on pigeon homing, part 2). J. theor. Biol. *138* (1989) 511–528.

81 Wallraff, H. G., Long-distance navigation of homing pigeons based on airborne olfactory signals, in: Olfaction and Taste X, in press. Ed. K. B. Døving.

82 Wallraff, H. G., Navigation by homing pigeons. Ethol. Ecol. Evol. *2* (1990) in press.

83 Wallraff, H. G., and Gelderloos, O. G., Experiments on migratory orientation of birds with simulated stellar sky and geomagnetic field: method and preliminary results. Oikos *30* (1978) 207–215.

84 Wallraff, H. G., and Kiepenheuer, J., Migración y orientación en aves: observaciones en otoño en el Sur-Oeste de Europa. Ardeola (Madrid) *8* (1963) 19–40.

85 Wallraff, H. G., and Neumann, M. F., Contribution of olfactory navigation and non-olfactory pilotage to pigeon homing. Behav. Ecol. Sociobiol. *25* (1989) 293–302.

86 Wallraff, H. G., and Sinsch, U., The role of 'outward-journey information' in homing experiments with pigeons: new data on ontogeny of navigation and general survey. Ethology *77* (1988) 10–27.

87 Williams, T. C., and Williams, J. M., The orientation of transoceanic migrants, in: Physiological and Ecophysiological Aspects of Bird Migration, in press. Ed. E. Gwinner. Springer, Berlin.

88 Wiltschko, R., and Wiltschko, W., Relative importance of stars and the magnetic field for the accuracy of orientation in night-migrating birds. Oikos *30* (1978) 195–206.

89 Wiltschko, R., and Wiltschko, W., Pigeon homing: olfactory orientation – a paradox. Behav. Ecol. Sociobiol. *24* (1989) 163–173.

90 Wiltschko, R., Wiltschko, W., and Keeton, W. T., Effect of outward journey in an altered magnetic field on the orientation of young homing pigeons, in: Animal Migration, Navigation, and Homing, pp. 152–161. Eds K. Schmidt-Koenig and W. T. Keeton. Springer, Berlin 1978.

91 Wiltschko, W., and Wiltschko, R., The interaction of stars and magnetic field in the orientation system of night migrating birds. I. Autumn experiemtns with European warblers (gen. *Sylvia*). Z. Tierpsychol. *37* (1975) 337–355.

92 Wiltschko, W., and Wiltschko, R., The interaction of stars and magnetic field in the orientation system of night migrating birds. II. Spring experiments with European robins (*Erithacus rubecula*). Z. Tierpsychol. *39* (1975) 265–282.

93 Wiltschko, W., and Wiltschko, R., A theoretical model for migratory orientation and homing in birds. Oikos *30* (1978) 177–187.

94 Wiltschko, W., and Wiltschko, R., The role of outward journey information in the orientation of homing pigeons, in: Avian Navigation, pp. 239–252. Eds F. Papi and H. G. Wallraff. Springer, Berlin 1982.

95 Wiltschko, W., and Wiltschko, R., Magnetic orientation in birds, in: Current Ornithology, vol. 5, pp. 67–121. Ed. R. F. Johnson. Plenum Press, New York 1988.

96 Wiltschko, W., and Wiltschko, R., Magnetic orientation and celestial cues in migratory orientation. Experientia *46* (1990) 342–352.

97 Yeagley, H. L., A preliminary study of a physical basis of bird navigation. J. appl. Phys. *18* (1947) 1035–1063.

98 Zink, G., Der Zug europäischer Singvögel: Ein Atlas der Wiederfunde beringter Vögel, Vol. 1–4. Vogelzug-Verlag, Möggingen 1973–1985.

99 Zink, G., Richtungsänderungen auf dem Zuge bei europäischen Singvögeln. Vogelwarte *29*, Sonderheft (1977) 44–54.

100 Zink, G., Räumliche Zugmuster europäischer Singvögel, in: Acta XVII Congr. int. Ornith., pp. 512–516. Ed R. Nöhring. Verlag Dtsch. Ornith.-Ges., Berlin 1980.

101 Zuur, B., Nearest neighbour distances in day and night migrating birds: A study using stereophotography. Vogelwarte *32* (1984) 206–218.

0014-4754/90/040379-10$1.50 + 0.20/0

Experimental studies of the development of migratory orientation mechanisms

K. P. Able

Department of Biological Sciences, State University of New York, Albany (New York 12222, USA)

Summary. Recent experimental studies (since ca 1985) on the ontogeny of orientation mechanisms in migratory birds are reviewed. The processes and interactions are synthesized into a framework that may help identify critical research questions. Birds that grow up in the earth's magnetic field develop the ability to perform appropriate migratory orientation even in the absence of any experience with relevant visual cues. In two species, large changes in direction during the course of migration seem to be controlled by an endogenous time program. In one of these, the pied flycatcher (*Ficedula hypoleuca*), the correct magnetic orientation seems to occur only when the magnetic fields appropriate to the latitudes encountered en route were experienced at the proper seasonal time. The magnetic compass may be modified by visual experience with either the daytime or night sky. Celestial rotation may be the calibrating reference in this case, as it is in the development of the star compass. Young Savannah sparrows (*Passerculus sandwichensis*) learn to perform compass orientation at sunset based on polarized skylight. This compass capability seems to be calibrated by magnetic directions. Some problems of experimental design and the interpretation of results from experiments on development are discussed.

Key words. Migration; orientation; bird; ontogeny; magnetic compass; star compass; polarized light.

Introduction

By the early 1970's, students of bird orientation were faced with the fact that their subjects possessed multiple mechanisms for determining compass directions. These capabilities appeared to be related one to another in complex ways that could not be resolved by simple experiments involving the manipulation of one orientation stimulus at a time[1, 21, 27]. Serious attempts to understand the development of orientation behavior in migratory birds, which began at that time, were motivated primarily by the hope that an examination of the steps by which individuals acquire orientation ability would elucidate the relationships among the multiple mechanisms found in adult birds. In our applications of the ontogenetic approach, we have remained more interested in its potential to answer specific questions about the mechanisms of bird orientation than in what it might tell us more generally about the development of behavior. Nonetheless, a number of studies have revealed interesting details of ways in which experience with specific stimuli interacts with apparently innate rules in the development of complex compass capabilities.

We recently reviewed what was known about the development of orientation and navigation behavior in migratory birds and the homing pigeon (*Columba livia*)[7]. Here I will concentrate on experimental studies that have been done since that time (ca 1985). In keeping with the theme of this review volume, I will concentrate on migratory birds, largely ignoring work on homing pigeons. My goal will be to synthesize what we know into a general framework outlining the processes and interactions that take place during the ontogeny of orientation mechanisms. That framework, however, must be viewed as a hypothesis in need of testing rather than as a representation of fact. Even now, the number of studies, and especially the number of species examined, is very small. Whereas there are a number of common themes that seem to transcend orientation and navigation mechanisms across a wide array of taxa[3], there is some evidence, and every reason to expect, that the details of the mechanisms and their development may vary from species to species. Thus it is imperative to recognize the weaknesses of the foundation upon which generalizations are made. At the same time, such a synthesis may be useful in identifying critical areas for future research.

Capabilities that develop with limited experience

On their first migration, the young individuals of many passerine species migrate separately from experienced birds. They need to be able, with whatever equipment they may develop in 2–3 months in their natal area, to successfully find their way into the winter range of their population and to stop migrating once they have reached it. As discussed by Berthold elsewhere in this review, there is much evidence that in some species the distance and direction of the first migration are controlled by a heritable, endogenous program[22]. By this so-called vector-navigation, the young bird would fly in a compass direction or directions for a distance that would bring it within the appropriate wintering area. Here I will examine only the orientational aspects of the problem.

Birds, hand-raised under laboratory conditions where they are deprived of experience with any visual information that might be used in orientation, nonetheless develop an ability to show more or less appropriate migratory orientation at the proper time. In the four species studied in detail (garden warbler, *Sylvia borin*; blackcap, *S. atricapilla*; pied flycatcher, *Ficedula hypoleuca*; Savannah sparrow, *Passerculus sandwichensis*), this orientation was based on the earth's magnetic field as indicated by tests performed in shifted fields[5, 15, 18, 23, 36, 37].

Growing up in the ambient magnetic field and under a L:D cycle seems to provide sufficient conditions for the development of this capability, which Able and Bingman[7] termed the primary magnetic compass. No manipulations have been performed to determine the necessary conditions. The orientation of birds raised and tested in this way is often deficient. Savannah sparrows and blackcaps exhibit axial orientation that is appropriate to their migratory track, but seem ambivalent in their night-to-night choice of one of the two directions[5, 13, 15]. In Savannah sparrows, wild-caught adults exhibit unimodal orientation[14, 15], so presumably some experience obtained by birds in nature is responsible for refining bimodal into unimodal orientation.

The migration routes of many species involve large changes in direction that might require a change in orientation on the part of the bird. There are some situations where a bird might be able to traverse a curved migration path by maintaining a fixed orientation heading and taking advantage of consistent spatial changes in wind patterns as Williams and Williams[33] have proposed for migrants flying over the western North Atlantic Ocean. Other cases seem to require that the bird change its heading en route.

A classic study of this phenomenon was conducted by Wiltschko and Gwinner[23, 36] on the garden warbler. German populations initially migrate SW to Iberia and then turn SSE and move to their winter range in sub-Saharan Africa. Held under a constant 12:12 L:D cycle in the ambient magnetic field of Germany, the birds tended to orient SW in early autumn, shifting to SE late in the season. Their magnetic orientation changed in direction and timing consistent with the hypothesis that an endogenous circannual rhythm controlled the changes in the bird's preferred direction relative to the magnetic field, quite independent of exogenous factors.

A different and more complicated situation seems to obtain in the pied flycatcher. It has a migration route similar to that of the garden warbler, but does not continue south of the equator. When hand-raised, visually naive pied flycatchers were tested throughout the autumn in the magnetic field of central Europe, they showed SW orientation early in the migration season, but hopped randomly in orientation cages later, when their free-flying conspecifics would have been in northern Africa[11]. A second group of birds lived and was tested in a series of magnetic fields that simulated the decreasing total intensity and angle of inclination that would be experienced during the southward migration. These birds showed oriented hopping throughout the entire season and shifted from SW to SE at approximately the correct time (and in the correspondingly correct magnetic field)[10, 12]. These remarkable data suggest a complex interaction between an endogenous temporal program and an external cue (some parameter of the magnetic field): only when the appropriate magnetic field condition (presumably indicating latitude) is experienced at the proper time does appropriate orientation occur. Further experiments will be necessary to discover how the magnetic field controls the behavior.

This is, of course, only one study of a single species. However, taken with the data on the garden warbler and other species, a picture emerges that a quite substantial amount of ecologically appropriate orientation behavior can develop in birds whose experience is limited to growing up in a magnetic field with properties similar to that of the earth.

Effects of experience with visual cues on development of the magnetic compass

In the real world young birds are exposed not only to the magnetic field, but also to a variety of other stimuli, including celestial cues that are used in orientation. Because a functional magnetic compass develops in the absence of any experience with visual orientation cues, as described above, it was surprising to find that this primary magnetic compass may be modified during the first three months of a bird's life by exposure to unnatural relationships between magnetic and geographic directions (i.e. raising them in a situation of large magnetic declination)[15, 18].

In experiments on Savannah sparrows and pied flycatchers, the birds lived outdoors within large Rubens coils that shifted magnetic N and from within which they had an unobstructed view of the sky both during the day and at night. When tested in autumn with controls that had been reared entirely indoors, the experimental birds oriented in a direction that differed by approximately the magnitude of the shifts in magnetic directions. The two groups developed different preferred magnetic directions that corresponded to the same geographic direction in the rearing environments[7]. These studies showed clearly that the magnetic compass is malleable during early development, modifiable by some frame of reference containing information about true geographic directions. Because the birds that grew up in the shifted field were exposed to both day and night skies, it was not possible to identify the cue or cues involved in calibrating the magnetic compass.

Recently, we have conducted experiments with Savannah sparrows that were designed to discover the calibrating reference[5]. Birds raised entirely indoors oriented NNW-SSE when tested in the magnetic field only (no visual cues). Birds raised outdoors, exposed to both the daytime and night sky in a normal magnetic field, showed N-S magnetic orientation. Three groups were given experience with the natural sky only within a magnetic field in which magnetic N was shifted counterclockwise to geographic ESE: one group saw only the daytime sky, one group saw only the clear night sky, and the third saw both day and night skies. The birds of all three groups that grew up in the shifted field oriented NE-SW, significantly different from the birds raised indoors. As before, this magnetic direction corresponded to geographic NW-SE within the coils in which the birds obtained their visual experience. Surprisingly, these results showed that experience with either the clear daytime or night sky is sufficient to effect this modification. This would seem to require one of two general explanations: 1) there are multiple independent routes by which the magnetic compass may be modified (e.g., by both the stars and the sun); or 2) the mechanism is unitary and based on some factor common to both the day and night sky (e.g., celestial rotation). Further experiments will be required to identify precisely the cues involved.

Ontogeny of the star compass

Compared to the magnetic compass, relatively little recent work has been done on the development of stellar orientation. Emlen's classic study of the ontogeny of the star compass in the indigo bunting (*Passerina cyanea*)[20] showed that configurational star patterns acquire directional meaning from the axis of stellar rotation. Based on an internal rule of unknown basis, the pole star is defined as northward. Once learned, rotational information is no longer required and the static relationships among stars are sufficient for meaningful orientation.

Wiltschko et al.[35] recently replicated this basic finding in studies on garden warblers. The experimental design employed a flat disc with small light spots simulating artificial 'stars' in an arbitrary pattern. During their first summer, groups of birds viewed this rotating disc from four eccentric positions so that each group experienced a different relationship between the center of rotation of the disc and magnetic north. Tested in autumn under the stationary disc in a vertical magnetic field (no directional magnetic information, so that the bird's response to visual cues alone can be assessed), the birds that observed rotation oriented in a direction more or less opposite the center of rotation that they observed. The same birds showed no orientation with respect to the magnetic directions they had experienced during their training[34]. A control group that was reared under a stationary disc showed no orientation when tested in the absence of a directional magnetic field.

Whereas the available evidence is not voluminous, it is quite consistent in showing that the ability to use the stars as a compass is learned. Most data also indicate that the development of stellar orientation proceeds independent of influence from other orientation cues (e.g., magnetic directions)[15, 16, 34]. There is, however, some indication that things may not always be so straightforward. Liepa (in Katz et al.[26]) raised great reed warblers (*Acrocephalus arundinaceus*) under a normally rotating planetarium sky. One group lived in the ambient magnetic field and another lived in a vertical (non-directional) field. The birds were tested under a stationary planetarium sky and in the magnetic field condition in which they had grown up. The group that was exposed to the planetarium sky in a directional magnetic field showed SSE orientation whereas the group reared in the vertical magnetic field was random. A third group reared under a stationary sky and in a normal magnetic field was also random. These results clearly suggest some involvement of magnetic information in the ontogeny of the star compass in this species. There are no other directly comparable data. Bingman[16] raised some pied flycatchers in a vertical magnetic field, but they lived outdoors where they were exposed to both day and night skies. In tests performed under clear, starry skies in a vertical magnetic field, the birds of this group showed southward orientation similar to the other groups in the experiment. Once again, the data are simply too few to permit reasonable guesses as to whether these apparent inconsistencies are due to species differences, details of experimental design, or simple error in some of the studies.

Development of mechanisms of sunset orientation

At least for a number of North American bunting species, orientation information obtained around the time of sunset seems to be of primary importance in choosing the migratory direction[8, 29, 30]. There is strong experimental evidence that the relevant cues are visual and unavailable when the sky is overcast. Both the sun itself and skylight polarization patterns have been implicated in the orientation behavior[2, 4, 24, 28–30], but their relative roles have been difficult to discriminate in experiments performed on adult migrants. The available data suggest that polarized light is the primary cue[4, 31], but it is impossible to experimentally replicate the natural skylight polarization patterns and the stimulus used in all the tests was unnatural in several respects that could affect its salience.

We have recently conducted experiments with Savannah sparrows designed to examine the ontogeny of the migratory orientation performed at sunset[6]. The outdoor visual experience of these sparrows was limited to the clear daytime sky, which they viewed from Emlen funnel orientation cages covered with sheet polariods in the ambient magnetic field. One group always looked at the sky through polaroids aligned with their transmission axes perpendicular to the sun's azimuth (90° group), a relationship that roughly simulates the polarization pattern in the natural sky. In the second group the polaroids were aligned with their E-vector axis rotated 45° clockwise from the sun's azimuth, and in the third group the E-vector axis was always rotated 45° counterclockwise from the sun's azimuth. By creating these experimental relationships between potential orientation cues (the sun, E-vector of polarized light, and magnetic directions), we could assess whether the birds had learned compass directions and to which cue they were responding.

Initially, we tested the birds at dusk under a solid overcast sky wherein the natural patterns of polarized skylight are absent. This enabled us to record orientation in cages covered with polaroids aligned in all compass directions to ask if the birds showed orientation relative to the E-vector of polarized light and if the rearing groups differed in a predictable way. Each group exhibited axial orientation in directions with respect to the imposed E-vector that would have corresponded to N-S during their rearing experience. This was a different direction for each group and so it appears that the birds learned these relationships during their exposure to the sky in their first summer. We also tested these birds under clear skies in cages covered with depolarizers to assess their orientation behavior in response to sunset direction alone. Under these conditions, the birds failed to show orientation in a migratory direction and instead hopped on average directly toward the brightest part of the horizon where the sun had set. Finally, we tested the birds under clear, natural dusk skies so that they could see the natural skylight polarization patterns and the position of the setting sun simultaneously. For the 45° clockwise and 45° counterclockwise groups, this pattern represented an abnormal relationship between sun azimuth and the E-vector of polarized light. If the birds used the sun itself as their primary directional cue, all the groups should have oriented in the same, presumably southerly direction. If, on the other hand, the birds relied on polarized light patterns as their compass, the groups should differ in ways predicted by the relationship they observed during rearing. In fact, the results were consistent with orientation based on the E-vector of polarized light. These experiments were consistent with the hypothesis that the sparrows had learned an approximately N-S axis with respect to the E-vector of polarized skylight.

The birds might have developed this ability in one of two ways. The orientation might be learned based on some internal set of rules analogous to those involved in the establishment of the star compass through observation of the axis of stellar rotation[19, 32]. On the other hand, the stimulus might be calibrated by some other directional cue. We tested the calibration hypothesis by rearing groups of birds similar to those described above, within large coils that shifted the direction of magnetic N. In autumn, we tested them under the natural clear dusk sky in a vertical magnetic field. The orientation of the groups was most consistent with the hypothesis that the E-vector of polarized skylight provided the orientation stimulus of first choice and that the polarized light pattern had been calibrated by magnetic directions.

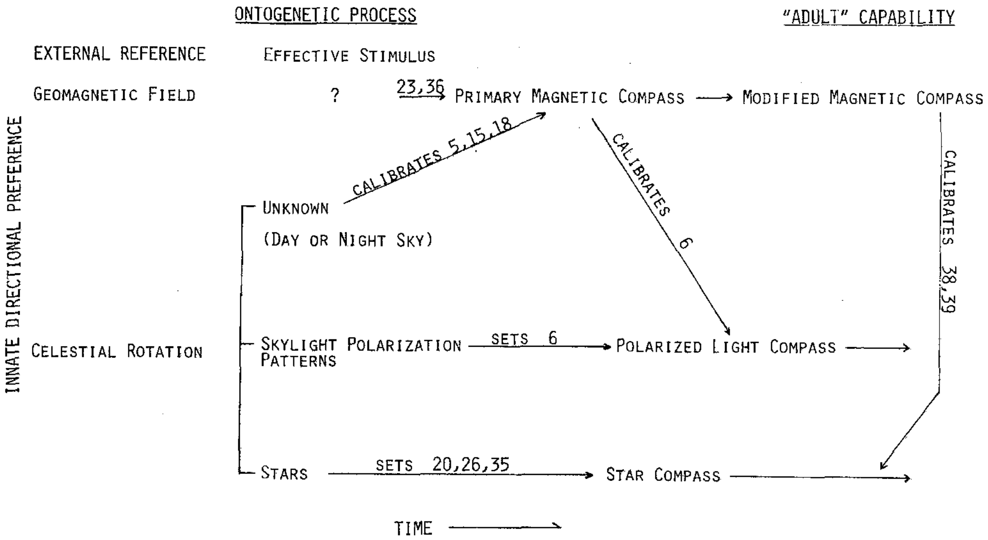
These experiments seem to show that the development of the compass mechanism used to perform migratory orientation at sunset involves learning during the first three months of life. The results support those from adult birds in indicating that polarized skylight provides the primary orientation information, but cannot be regarded as conclusive. Even though some of the orientation tests were performed under the natural sky (no polaroids used), the early visual experience of the birds was limited to viewing the sky through polaroids that could have affected the potency of that stimulus during development. That the polarized light compass seems to derive directional information from the magnetic field is reminiscent of the apparent calibration of the pigeon's sun compass by magnetic directions[40,42].

Synthesis of interactions of cues during development

In the development of any compass orientation mechanism, a stimulus must become imbued with directional information. This process may involve the transfer of information from an independent stimulus or stimuli, or it may be based on aspects of the primary cue itself. The figure summarizes current evidence of the relationships and interactions among orientation cues during the development of migratory orientation. Nearly all of these relationships should be considered tentative as most are based on unreplicated studies of single species. Among adult birds we have a good deal of evidence of inter-specific differences in at least the relative weighting of orientation mechanisms, and we should expect the development of those mechanisms to vary across species as well.

As can be seen, all of the known compass mechanisms employed by migratory birds appear to be subject to modification by experience. As Wiltschko[41] has noted, the heritable migratory direction seems to be represented at least twice in birds: relative to celestial rotation and relative to magnetic directions. At least two orientation mechanisms, the magetic compass and the star compass, will develop to a functional level independent of any other system. The development of the star compass seems to be insulated from magnetic influences early in life (see Katz et al.[26]), but in adult migrants of some species the star compass seems to be calibrated periodically by the magnetic compass[9,17,38,39]. Whereas a magnetic orientation capability develops without any experience with visual celestial cues, it is modifiable early in life, but seems rigid later when the birds have reached migratory age.

If there is any independent, stable source of directional information during early development, it is probably celestial rotation. It appears to be central to a number of processes, acting both directly (as in the development of stellar orientation) and indirectly (e.g., via the magnetic compass). It is intuitively reasonable that celestial rotation, assessed by whatever specific stimulus, should play an important role in this process. It provides information about geographic or true compass directions, which in the final analysis are the directions of importance to a migratory bird moving over the earth. Magnetic directions, in many places, provide good approximations of geographic directions, but especially at high latitudes and in North America, declination is large. A bird might be



Diagrammatic representation of interactions during the ontogeny of orientation mechanisms in migratory birds. The relationships represent a composite of results from studies on a variety of species and must be regarded as tentative. Most are based on data from one or a very few species. Numerals refer to the references upon which the putative relationships are based.

able to calibrate its magnetic compass to adjust to that regional difference in geographic and magnetic directions, but a different correction factor would be needed when the bird moved to a region characterized by different declination. There is some suggestion that North American passerine migrants may rely less heavily on the magnetic compass in orientation than European species from regions of relatively smaller declination. At the moment, however, we have data from too few species to allow generalization.

Considerations of experimental design and interpretation of results

One of the rationales for employing a developmental approach in the study of bird orientation has been that it may provide a key to understanding the multi-layered orientation mechanisms that characterize adult birds. It is probably too soon to make a fair evaluation of its success in this regard. Clearly, there are some salient differences in the relationships among orientation cues in adult birds versus during development. The star compass, which seems to develop largely immune from any magnetic influence, is apparently calibrated by the magnetic compass during migration in several species of European night migrants. The magnetic compass, subject to modification in early life, seems to be stable thereafter. Development studies provide most of the data we have from birds tested for orientation in the presence of several orientation cues, one at a time. An interesting result, at least from studies on the Savannah sparrow, has been that the orientation direction chosen varies considerably depending on which cue is being used (NW-SE by magnetic compass, NE-SW by stars alone, SE by sunset cues alone[6,15]). Without a detailed knowledge of the migration route of a given population it is impossible to determine which, if any, of the different responses corresponds to the real migration direction. The details of migration routes are generally better known among European species and it would be interesting to have similar sets of cue-specific orientation directions from some of those birds.

Experimental studies of the ontogeny of orientation mechanisms necessarily involve controlling and manipulating the sensory experience of young birds. The experience of hand-raised birds will differ both quantitatively and qualitatively from their conspecifics growing up in the wild. In order to decipher the details of developmental interactions we have to employ a reductionist approach, often confining a bird's experience to, e.g., night sky only, daytime sky only, magnetic field only, etc. It is well known that the development of the nervous system itself is affected in important ways by the quality and quantity of early sensory experience[25]. It seems axiomatic that such effects will be manifested at the higher levels of behavioral output. If we provide a young bird with experience with one potential orientation cue, simultaneously denying it access to others, it seems likely that we may force a greater reliance on that one cue than would ordinarily be the case. There is no effective way to avoid this problem, but it becomes imperative that we evaluate the design of experiments and the interpretation of their results in light of what is known about the behavior and experience of wild birds. It would be all too easy to produce and spend our time studying an artifact of our own creation.

Our ability to control and simulate relevant stimuli also varies. For example, it is technically rather easy to produce artificial magnetic fields that precisely mimic that of the earth. Because the field within a set of magnetic coils is the resultant of the ambient earth's field and that produced by the coils, unless buffered, the artificial fields will even be subject to the regular daily and irregular variations in the geomagnetic field (though not necessarily to the same magnitude). On the other hand, the technology to simulate the pattern of polarized light in the clear sky does not exist. Available polaroids produce a stimulus that differs in many ways, both qualitative and quantitative, from the natural one[4]: the degree of polarization of the light is greater, the pattern of E-vectors much simpler, and in the type used in all bird experiments to date there is essentially no transmission in UV wavelengths. Other stimuli known to be relevant to migratory orientation in the field (e.g., wind direction) would be impossible to produce in the laboratory. The basic problem is one of stimulus salience. We may, even unknowingly, present an animal with a stimulus situation that is in some way more or less potent than the same stimulus in nature. As a result, we may, by the design of our experiment, force a response that would not occur or induce a stronger (or weaker) response than would be found in nature.

This problem is particularly critical because we are studying behavior that has to some degree a hierarchical nature. The interrelationships among cues could well be in part a function of the relative 'strengths' of the stimuli. 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. Most of our conceptions about how information flows during the development of orientation mechanisms[7,41] are based on webs of one-way interactions. The situation is complicated by the fact that we are able to examine only the final result (orientation direction in autumn) of processes that occur over three months or so. A series of sequential interactions might occur in quick succession (e.g. celestial rotation calibrates magnetic compass, magnetic compass calibrates polarized light compass,...), undetectable by current experimental procedures. We should not ignore the possibility that the development may be more complex, perhaps resulting is something more like a weighted average of several inputs than one reference imposing directionality on a series of subordinate mechanisms.

1 Able, K. P., Mechanisms of orientation, navigation, and homing, in: Animal Migration, Orientation and Navigation, pp. 283–373. Ed. S. A. Gauthreaux, Jr. Academic Press, New York 1980.

2 Able, K. P., Skylight polarization patterns at dusk influence the migratory orientation of birds. Nature *299* (1982) 550–551.

3 Able, K. P., Common themes and variations in animal orientation systems. Am. Zool. (1989) in press.

4 Able, K. P., Skylight polarization patterns and the orientation of migratory birds. J. exp. Biol. *141* (1989) 241–256.

5 Able, K. P., and Able, M. A., Ontogeny of migratory orientation in the Savannah sparrow (*Passerculus sandwichensis*): calibration of the magnetic compass. Anim. Behav., (1990) in press.

6 Able, K. P., and Able, M. A., Ontogeny of migratory orientation in the Savannah sparrow (*Passerculus sandwichensis*): mechanisms at sunset. Anim. Behav., (1990) in press.

7 Able, K. P., and Bingman, V. P., The development of orientation and navigation behavior in birds. Q. Rev. Biol. *62* (1987) 1–29.

8 Able, K. P., and Cherry, J. D., Laboratory and field studies of avian migratory orientation, in: Migration: Mechanisms and Adaptive Significance, pp. 516–525. Ed. M. A. Rankin. Contrib. Marine Sci. Suppl., vol. 27. Marine Science Inst., Univ. of Texas, Austin 1985.

9 Beason, R. C., Magnetic orientation and magnetically sensitive material in migratory birds, in: Biophysical Effects of Steady Magnetic Fields, pp. 167–172. Eds G. Maret, N. Boccara and J. Kiepenheuer. Springer-Verlag, Berlin 1986.

10 Beck, W., The influence of the earth magnetic field of the migratory behavior of pied flycatchers (*Ficedula hypoleuca* Pallas), in: Localization and Orientation in Biology and Engineering, pp. 357–359. Eds D. Varju and H.-U. Schnitzler. Springer-Verlag, Berlin 1984.

11 Beck, W., and Wiltschko, W., The magnetic field as a reference system for genetically encoded migratory direction in pied flycatchers (*Ficedula hypoleuca* Pallas). Z. Tierpsychol. *60* (1982) 41–46.

12 Beck, W., and Wiltschko, W., Magnetic factors control the migratory direction of pied flycatchers (*Ficedula hypoleuca* Pallas), in: Acta XIX Congr. Intern. Ornithol., pp. 1955–1962. Ed. H. Ouellet. Univ. of Ottawa Press, Ottawa 1988.

13 Berthold, P., Wiltschko, W., Mildenberger, H., and Querner, U., Genetical transmission of migratory behavior in blackcaps, *Sylvia atricapilla*. Experientia *46* (1990) 107–108.

14 Bingman, V. P., Savannah sparrows have a magnetic compass. Anim. Behav. *29* (1981) 962–963.

15 Bingman, V. P., Magnetic field orientation of migratory naive Savannah sparrows with different first summer experience. Behaviour *87* (1983) 43–53.

16 Bingman, V. P., Night sky orientation of migratory pied flycatchers raised in different magnetic fields. Behav. Ecol. Sociobiol. *15* (1984) 77–80.

17 Bingman, V. P., Earth's magnetism and the nocturnal orientation of migratory European robins. Auk *104* (1987) 523–525.

18 Bingman, V. P., Beck, W., and Wiltschko, W., Ontogeny of migratory orientation: A look at the pied flycatcher, *Ficedula hypoleuca*, in: Migration: Mechanisms and Adaptive Significance, pp. 543–552. Ed. M. A. Rankin. Contrib. Marine Sci. Suppl., vol. 27, Marine Sci. Inst., Univ. of Texas, Austin 1985.

19 Brines, M. L., Dynamic patterns of skylight polarization as clock and compass. J. theor. Biol. *86* (1980) 507–512.

20 Emlen, S. T., Celestial rotation: Its importance in the development of migratory orientation. Science *170* (1970) 1198–1201.

21 Emlen, S. T., Migration: Orientation and navigation, in: Avian Biology, vol. 5, pp. 129–219. Eds D. S. Farner and J. R. King. Academic Press, New York 1975.

22 Gwinner, E., Circannual rhythms in the control of avian migrations. Adv. Study Behav. *16* (1986) 191–228.

23 Gwinner, E., and Wiltschko, W., Endogenously controlled changes in the migratory direction of the garden warbler, *Sylvia borin*. J. comp. Physiol. *A 125* (1978) 267–273.

24 Helbig, A., and Wiltschko, W., The skylight polarization patterns at dusk affect the orientation behavior of blackcaps, *Sylvia atricapilla*. Naturwissenschaften (1989) in press.

25 Hirsch, H. V. B., The tuneable seer: Activity-dependent development of vision, in: Handbook of Behavioral Neurobiology, vol. 8, pp. 237–295. Ed. E. M. Blass. Plenum Press, New York 1986.

26 Katz, Y., Liepa, V., and Viksne, J., Orientation research in the Latvian SSR in 1982–1985, in: Acta XIX Congr. Intern. Ornithol., pp. 1919–1931. Ed. H. Ouellet. Univ. of Ottawa Press, Ottawa 1988.

27 Keeton, W. T., The orientational and navigational basis of homing in birds. Adv. Study Behav. *5* (1974) 47–132.

28 Moore, F. R., Sunrise, skylight polarization, and the early morning orientation of night-migrating warblers. Condor *88* (1986) 493–498.

29 Moore, F. R., Sunset and the orientation behaviour of migrating birds. Biol. Rev. *62* (1987) 65–86.

30 Moore, F. R., Sunset and migratory orientation: Observational and experimental evidence, in: Acta XIX Congr. Intern. Ornithol., pp. 1941–1954. Ed. H. Ouellet. Univ. of Ottawa Press, Ottawa 1988.

31 Moore, F. R., and Phillips, J. B., Sunset, skylight polarization and the migratory orientation of yellow-rumped warblers (*Dendroica coronata*). Anim. Behav. *36* (1988) 1770–1778.

32 Phillips, J. B., and Waldvogel, J. A., Celestial polarized light patterns as a calibration reference for sun compass of homing pigeons. J. theor. Biol. *131* (1988) 55–67.

33 Williams, T. C., and Williams, J. M., Orientation of transatlantic migrants, in: Animal Migration, Navigation, and Homing, pp. 239–251. Eds K. Schmidt-Koenig and W. T. Keeton. Springer-Verlag, Heidelberg 1978.

34 Wiltschko, W., The migratory orientation of garden warblers, *Sylvia borin*, in: Avian Navigation, pp. 50–58. Eds F. Papi and H. G. Wallraff. Springer-Verlag, Berlin 1982.

35 Wiltschko, W., Daum, P., Fergenbauer-Kimmel, A., and Wiltschko, R., The development of the star compass in garden warblers, *Sylvia borin*. Ethology *74* (1987) 285–292.

36 Wiltschko, W., and Gwinner, E., Evidence for an innate magnetic compass in garden warblers. Naturwissenschaften *61* (1974) 406.

37 Wiltschko, W., Gwinner, E., and Wiltschko, R., The effect of celestial cues on the ontogeny of non-visual orientation in the garden warbler (*Sylvia borin*). Z. Tierpsychol. *53* (1980) 1–8.

38 Wiltschko, W., and Wiltschko, R., The interaction of stars and magnetic field in the orientation system of night migrating birds. I. Autumn experiments with European warblers (gen. *Sylvia*). Z. Tierpsychol. *37* (1975) 337–355.

39 Wiltschko, W., and Wiltschko, R., The interaction of stars and magnetic field in the orientation system of night migrating birds. II. Spring experiments with European robins (*Erithacus rubecula*). Z. Tierpsychol. *39* (1975) 265–282.

40 Wiltschko, W., and Wiltschko, R., Magnetic orientation in birds, in: Current Ornithology, vol. 5, pp. 67–121. Ed. R. F. Johnston. Plenum Press, New York 1988.

41 Wiltschko, W., and Wiltschko, R., Magnetic versus celestial orientation in migrating birds. Trends Ecol. Evol. *3* (1988) 13–15.

42 Wiltschko, W., Wiltschko, R., Keeton, W. T., and Madden, R., Growing up in an altered magnetic field affects the initial orientation of young homing pigeons. Behav. Ecol. Sociobiol. *12* (1983) 135–142.

0014-4754/90/040388-07$1.50 + 0.20/0