HISTORICAL PERSPECTIVES

ORIENTATION AND NAVIGATION: A PERSPECTIVE ON FIFTY YEARS OF RESEARCH

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The study of animal navigation is based on a singular but unassailable fact: birds and many other animals have the ability to return to precise, previously occupied locations. In birds, this ability may be expressed over distances sometimes approaching global scale. Homing has been known and exploited in pigeons since the time of the early Greeks; among "wild" birds, the advent of large-scale banding quickly revealed that site fidelity was widespread among migratory species (Stresemann 1961, Baker 1980, 1984, and Mead 1983, provide accounts of the historical roots of migration and orientation studies). Rigorous studies of the mechanisms of bird migration and navigation did not get underway until well into the Twentieth Century, most of them in the years since World War II.

Studies of birds have played a leading role in advances in understanding of animal orientation and navigation in general. This has been conspicuously the case in other areas of biology as well; ecology, ethology, behavioral ecology, and evolutionary biology come immediately to mind. In part, this is no doubt a result of the fact that ornithology has a long tradition. In the specific case of orientation and navigation, it also seems likely that the conspicuous and dramatic nature of the homing feats and migrations of birds has been a compelling magnet drawing generations of students to attempt to explain phenomena which seemed utterly mysterious to their predecessors, the product of a sixth sense. What we have learned about the orientation behavior of birds and other animals has revealed many similarities in mechanisms (as well as some interesting, apparently adaptive, differences) (Able 1991a). Just as the homing pigeon provides a reasonable model system for studies of bird navigation, so studies of birds continue to provide leading insights about orientation that generalize to other taxa.

What follows is a selective and surely biased review of the conceptual advances and empirical results that I believe have been instrumental in shaping the field of orientation and navigation studies over the last forty years or so. I have made no attempt at a detailed historical chronology. As in any field, many ideas and lines of investigation that seemed promising at the time subsequently led nowhere. Some of these may emerge as important in the future, but to my mind they have not played a major role in bringing the field to where it is now. Therefore, I will focus on those branches of the discipline's evolution that lead directly to our current understanding. To the extent that they can be determined, I have tried to cite the origins of important ideas and the first empirical demonstrations of important results, but space does not permit a review or even enumeration of all of the confirmations, replications, refutations and extensions. Over these forty years, the field and its literature have grown so much that reviews of only a small subset of the field can now run to scores of pages and hundreds of references.

ENDOGENOUS PROGRAMS AND VECTOR NAVIGATION

The means by which a young, inexperienced bird is able to reach the overwintering area of its species or population on the first migration is of fundamental importance not only to the individual migrating bird, but also to our understanding of orientation and navigation. This problem is especially demanding in the case of species in which young individuals do not migrate in company with experienced birds from whom they might receive information about how to reach the winter quarters. That young birds might be born with information concerning the course and timing of at least the first migration was suggested long ago (e.g., Stresemann 1934). The first empirical evidence for the existence of endogenous migratory programs, as they have come to be called, was provided by Gwinner (1967) (Fig. 1). Subsequently, the details of these programs have been studied extensively by Gwinner and Berthold and their colleagues in Andechs and Radolfzell, respectively.

These studies have revealed a remarkable richness in the detail of the endogenous programs. In nocturnal migrants, both the nightly amount of *Zugunruhe* and its seasonal duration are correlated with migration distance when comparisons are made across species as well as between populations and sexes (Holberton 1993) of the same species that vary in the extent of migration. Orientation direction, which appears to be coded independently with respect to both celestial rotation and

the geomagnetic field, is programmed similarly. In some species, large changes in orientation direction during the course of migration take place spontaneously at approximately the appropriate time during the period of *Zugunruhe*. All of these characteristics of the migratory program exhibit a high degree of heritability as demonstrated by cross-breeding experiments, mainly on various populations of the Blackcap (*Sylvia atricapilla*) (reviewed in Berthold 1991). The execution of the migratory program has been termed vector navigation (Schmidt-Koenig 1973) and can in theory take a first-time migrant from its natal area to a point within the winter range of its population on an appropriate time schedule.

Berthold and his colleagues have emphasized the sufficiency of these migratory programs to enable a young bird to successfully complete its first autumn migration. Yet in the field, migrants must encounter many contingencies that could cause problems for vector navigation. Migration might be accelerated, retarded or stopped altogether by ambient weather conditions encountered enroute. Cross-winds, storms or other poor weather may disrupt orientation and cause birds to become displaced from the normal route of migration. In either case, some adjustment or correction to the time-based program will be necessary. Much less attention has been paid to the extent and nature of such interactions between environmental variables and the endogenous programs (Terrill 1991).

In the case of orientation, the data available from the very few species that have been studied are not in agreement concerning the control mechanisms. In the Garden Warbler (*Sylvia borin*), Gwinner and Wiltschko (1978) were the first to show that hand-raised birds exhibited appropriately oriented magnetic migratory activity, including the expected SW to S shift in direction, when held in the magnetic field of Frankfurt throughout the migration season. Similar results have been obtained from the western German population of the Blackcap (Helbig et al. 1989). In the Pied Flycatcher (*Ficedula hypoleuca*), however, the situation seems more complicated. The well-known shift in direction from SW to SE that occurs in the field was observed in the orientation cage only when the birds were subjected to a series of changing magnetic field conditions that simulated those that would be experienced during southward migration (Beck and Wiltschko 1982). This remarkable study, which has not to date been replicated, suggests a complex interaction between the endogenous temporal program controlling migration and an environmental cue: only when the appropriate magnetic field (presumably indicating latitude) is experienced at the proper time does proper orientation occur.

There are yet other ways in which presumably innate migratory programs may be influenced by environmental variables. Simulating a crossing of the magnetic equator appears to reverse the response of the birds to field inclination (Wiltschko and Wiltschko 1992, Beason 1992), as expected if an inclination compass is going to work effectively in a trans-equatorial migrant. Although the classic displacement experiments of Perdeck (1958) and other data suggest that first-time migrants do not compensate in a navigational way for lateral displacements experienced during migratory

FIGURE 1.   Eberhard Gwinner (center) talking with Verner P. Bingman (left) and Sidney A. Gauthreaux, Jr. (right) in Zagorsk, Russia, during the 18th International Ornithological Congress, 1982. Gwinner's work on circannual rhythms has provided insight into the endogenous control of timing and orientation of bird migration. (Photo by K. P. Able.)

flight (but see Rabøl 1985), young birds that experience wind drift subsequently exhibit compensatory orientation responses in coastal situations (Evans 1968, Able 1977), and perhaps inland as well (Gauthreaux 1978).

It is clear that to a substantial degree vector navigation in young migratory birds has a genetic basis. It is no surprise that being discovered and studied primarily in the cradle of classical ethology, the "innateness" of the behavior has been emphasized. Modern studies of behavior have shown repeatedly that gene-environment interactions characterize the development of all complex behavior. Theoretical considerations suggest that barring extreme circumstances, vector navigation alone could bring first-time migrants to an appropriate wintering area (Gwinner 1968), but until the questions are asked experimentally, we will not know to what extent these endogenous programs are open to environmental influences that may act not only during migration, but also during early development. Such lability can be discovered only if our initial assumptions do not prevent us from looking for it.

SITE-FIDELITY: THE PHENOMENOLOGICAL BASIS OF THE STUDY OF NAVIGATION

Whereas birds on their first migration are surely heading for an unknown goal, in very many species, all subsequent migrations involve a return to a known locale: the natal region or the previously occupied overwintering area. Banding has shown unequivocally that many migrants return with pinpoint precision to previously occupied places. This behavior appears analogous and perhaps homologous to the homing behavior of pigeons and other birds displaced by man. It has

FIGURE 2. Hans Wallraff (ca. 1979) has done fundamental theoretical and empirical work on homing navigation in pigeons. His work provides the strongest evidence that pigeons can determine the homeward direction based solely on information perceived at distant, unfamiliar release sites. In recent years he has been a strong proponent of olfactory navigation. (Photo courtesy of H. G. Wallraff.)

been termed site fidelity (Gauthreaux 1982) and it is the phenomenon that provides the basis for the study of bird navigation.

CONCEPTS OF NAVIGATION

The ability to home from great distances and from places well beyond the familiar area of the individuals involved is clearly documented among birds. The most extensive data come from homing pigeons, of course, but there are many cases from other taxa, both migratory and non-migratory. Such homing might be accomplished by means of one or more of the following mechanisms. (1) The animal might maintain direct or indirect sensory contact with the home area. (2) It might employ some random or patterned search strategy. (3) It might perform path integration by some method of "inertial navigation." (4) It might use a route reversal strategy based upon sensory information assimilated during the displacement journey. (5) It might refer to a learned, familiar-area map to localize its position. (6) It might possess a more extensive map that extends well beyond areas of familiarity, a so-called gradient or grid map. These mechanisms are not mutually exclusive; a bird might call upon any or all of them when confronted with a navigational problem. From homing pigeons there is good evidence that familiar landmarks are used when available and that outward journey information is consulted. There is also compelling evidence, most notably from studies by Wallraff (1980) (Fig. 2), that neither of these pieces of information is necessary and that pigeons can quickly determine the homeward direction from very distant, unfamiliar sites when they have been prevented access to all information except that at the release site. Thus, whereas it remains interesting to determine how pigeons and other birds use all of the various means available to them when solving a homing problem, at the limit we are left with the conclusion that there appears to exist a

very extensive, perhaps unlimited, map that is sufficient to enable true navigation. (Wallraff [1974, 1991] provides the theoretical basis for modern concepts of homing and navigation maps.) Much of the work on pigeon homing during the past four decades has been devoted to discovering the nature of this map.

It is intuitively appealing that the navigation of birds be based on a unitary system. Several have been proposed. Early on, Yeagley (1947) proposed a global map based on physical coordinates (Coriolis force and the vertical component of the magnetic field). Matthews (1953) proposed an astronomical bicoordinate navigational system based on various parameters of the sun's arc and Sauer (1957) described a nocturnal version based on hourly and seasonal changes in the positions of star patterns. Experimental work forced the rejection of each of these hypotheses (reviewed by Keeton 1974, Emlen 1975, Schmidt-Koenig 1979) and I see no prospect that, even in some modified form, they contain a nugget of the solution to the problem.

A hybrid or two-step navigational system was proposed by Kramer (1953) (Fig. 3). With his discovery of the sun compass in birds, Kramer (1950) considered how such a compass capability might be incorporated into a homing navigation system. Obviously, a compass alone will not be sufficient to enable an individual to navigate from an unfamiliar locale. If possessed of something analogous to a map that could reveal the direction home, however, the compass could then be employed to identify that direction. Thus Kramer put forth his "map and compass" model of homing navigation, assuming that the sun (the only known bird compass at that time) provided the compass component, and leaving the physical basis of the map unspecified.

Virtually all data from pigeon homing experiments are at least consistent with the map and compass hypothesis and some provide strong support. Perhaps the most robust experimental paradigm in homing pigeon research is the effect of clock shifts on initial orientation at the release site. These effects are strongly consistent with the use of a time-compensated sun azimuth compass and completely inconsistent with predictions of a one-step navigational system, regardless of its physical basis (see Keeton 1974, Wallraff 1991). Kramer's map and compass hypothesis has provided a productive framework in which to think about the problem and remains the best heuristic available.

COMPASS MECHANISMS

Some sort of compass sense is involved not only in homing navigation, but also in migratory orientation. The experimental analysis of avian compasses has depended primarily upon two systems: the initial orientation of homing pigeons released at sites distant from home and the spontaneous oriented hopping activity of birds in migratory condition (Zugunruhe). Studies of the latter were made possible by Kramer's (1949) discovery that such restless hopping was oriented when birds were placed in circular cages. Over the subsequent decades, various types of cage designs have been employed with greater or less success (see Helbig 1991a). The inexpensive, portable Emlen funnel design (Emlen and Emlen 1966) incorporates a

FIGURE 3.   Gustav Kramer (1910–1959), shown releasing homing pigeons, was the leading founder and pioneer of the study of bird orientation. He discovered the sun compass in birds, devised the orientation cage, and put forth the map and compass model of homing navigation that still guides research today. (Photo courtesy of J. Aschoff and E. Gwinner.)

number of desirable features that have made it the nearly universal standard in the field.

During the first twenty years or so of serious study of compass orientation in birds, there was a general assumption that we were searching for a single mechanism subserving a particular type of orientation. Kramer had demonstrated the time-compensated sun compass in several species, Hoffmann (1954) elucidated the role of the circadian clock in the time-compensation mechanism, and Schmidt-Koenig (1958, 1960) demonstrated the actual use of this time-compensated sun azimuth compass in pigeon homing (Fig 4). Kramer (1949) had also discovered that nocturnal migrants showed seasonally appropriate oriented hopping when placed outdoors in circular cages under the clear night sky. Following Kramer's untimely death, Franz and Eleanor Sauer took up the study of the mechanisms of nocturnal orientation. In a series of classic experiments under planetarium skies, they showed that night migrants use the stars as a compass (Sauer and Sauer 1955, 1960; Sauer 1956, 1957, 1961). These results gave rise to the reasonable conclusion, still found in some textbooks, that diurnal migrants and homing pigeons relied upon a sun compass and night migrants upon a star compass. Things turned out not to be nearly so simple.

Over the next twenty years, evidence accumulated that a number of migratory species as well as the homing pigeon possessed a magnetic compass (recent reviews, Able 1994, Beason and Semm 1994). The initial demonstrations of magnetic orientation in the laboratory of Friedrich Merkel (Fig. 5) and Wolfgang Wiltschko at the University of Frankfurt were met with considerable skepticism, and earlier claims about magnetic effects on pigeon homing (Yeagley 1947, 1951)

were not convincing and could not be replicated. The situation changed only slowly. Over the decade following Wiltschko's (1968) demonstration of magnetic orientation in the European Robin (*Erithacus rubecula*), the accumulation of data from the Wiltschko laboratory along with evidence from studies on gull chicks (Southern 1969), homing pigeons (Keeton 1969, 1971; Walcott and Green 1974) and the Indigo Bunting (*Passerina cyanea*) (Emlen et al. 1976) gradually convinced

FIGURE 4.   Klaus Schmidt-Koenig (about 1970) demonstrated that the time-compensated sun compass provides the compass of first choice in pigeon homing. In recent years, he has been an opponent of the olfactory navigation hypothesis. (Photo courtesy of K. Schmidt-Koenig.)

FIGURE 5. Friedrich Merkel (mid-1980s) obtained the first evidence for magnetic orientation in migratory birds in his laboratory at the University of Frankfurt, Germany. Using the orientation cage design that bears his name, he and his student Wolfgang Wiltschko launched a pioneering research program to elucidate the mechanism of the magnetic compass. (Photo courtesy of W. Wiltschko.)

most workers in the field that a magnetic compass was a component in the avian orientation system. Rigorous demonstrations of magnetic orientation are now available from eight species of migratory birds and the inclination compass mechanism first discovered in the European Robin (Wiltschko and Wiltschko 1972) (Fig. 6) has been documented in five other species (see Able 1994).

The drumbeat of evidence for magnetic orientation was joined by results from field studies with radar which showed that migrants were often well oriented when flying under solid overcast skies and that wind direction sometimes took precedence over all other orientation cues. Both field and experimental studies indicated that visual cues at sunset had a large influence on the orientation of obligate night migrants (review, Moore 1987). Exploration of sunset orientation later lead to the discovery that patterns of polarized skylight provide the primary directional information for nocturnal migrants at dusk, the most recent new orientation cue to be found (Able 1982; Helbig 1990a, 1991b). By the time Keeton (1974) (Fig. 7) and Emlen (1975) wrote their reviews of the field, it was apparent that we were no longer searching for *the* mechanism of orientation. The ideas of orientation systems based on multiple sources of directional information, redundant mechanisms and a hierarchical relationship among orientation mechanisms became the coda for research in this field over the next two decades.

The relationships among orientation cues in migratory birds have been explored using two main approaches (1) The ontogeny of orientation behavior in young birds has been studied by manipulating their experience during the first months of life, (2) The orientation of mature birds has been examined in cue-conflict experiments in which birds are presented simultaneously with two or more relevant orientation cues, one or more of the cues is manipulated, and the bird's orientation is monitored for any change. Both
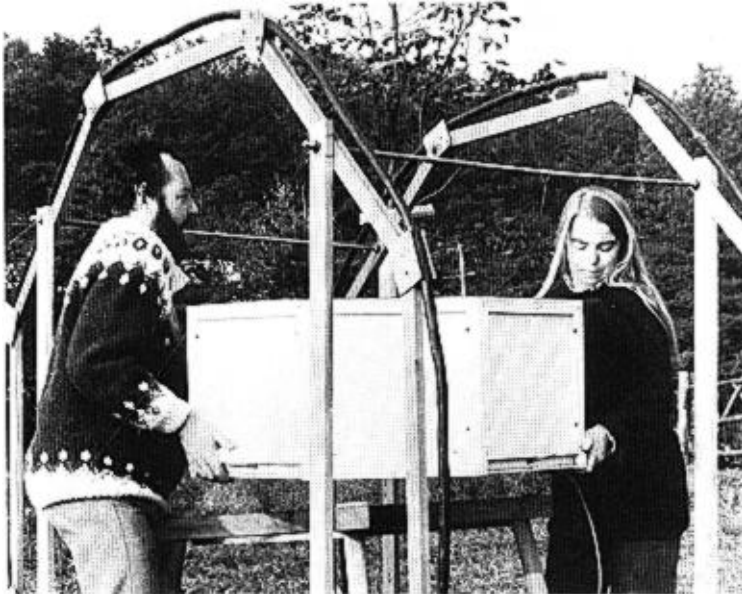

FIGURE 6. Wolfgang and Roswitha Wiltschko (mid-1970s) setting up a Merkel orientation cage within Helmholz coils. The Wiltschkos have studied many aspects of both migratory orientation and homing in pigeons, including the mechanisms and role of the magnetic compass and the development of orientation behavior in homing pigeons and migrants. (Photo by V. Dröscher, courtesy of W. Wiltschko.)

paradigms permit one to infer the relative weighting or importance of the different stimuli involved in orientation.

I recently reviewed the data from cue-conflict experiments relevant to the relationships among orientation cues (Able 1993). Arriving at any general picture from these studies requires ignoring a number of exceptions and putting much faith in a small set of results. The weight of evidence suggests that in *short-term* orientation decision-making magnetic cues take precedence over stars, that visual information at sunset overrides both of those stimuli, and that polarized skylight is the relevant cue in this dusk orientation. This view is dramatically different from that current twenty years ago. In the years since Emlen's elegant analysis of the star compass in the Indigo Bunting (Emlen 1967a, 1967b, 1970, 1972) (Fig. 8), remarkably little work has been done on stellar orientation. Today, it seems much less important in the pantheon of orientation mechanisms of migratory birds, but new comparative studies on stellar orientation in the absence of directional magnetic information are badly needed. In the initial orientation of homing pigeons it seems clear that the sun compass is the mechanism of first choice with the magnetic compass providing an overcast sky backup (Keeton 1971, Walcott and Green 1974).

Though I must admit a personal bias here, I believe that the developmental approach to problems of orientation in both migrants and homing pigeons has proven to be a powerful one. In the early years of the discovery of the basic components of the avian navigation system, it was assumed that the mechanisms were entirely innate. Sauer (1958:46), for example, proposed that birds possessed an inherited image of the starry sky that was not only employed as a compass, but was also coupled with a precise time sense to comprise a sophisticated bicoordinate navigation system. As general thinking about the development of behavior changed, so did the approach to the development of orientation mechanisms. Work by Emlen (1970) on the Indigo Bunting and by the Wiltschkos and Keeton (Wiltschko et al. 1976, Wiltschko and Wiltschko 1980) on homing pigeons showed that the development of the star and sun compasses, respectively, required substantial and specific experience with the relevant visual stimuli. Later work demonstrated that although a functional magnetic compass develops in isolation from visual orientation cues, magnetic orientation too may be modified by such experience (Bingman 1983). It now appears that the young migratory bird enters the world with a migratory direction coded with respect to two reference systems: the earth's magnetic field and celestial rotation, which reveals true compass directions. The development of its compass capabilities during the first few months of life results from a complex interplay of experience with specific stimuli and apparently innate learning rules. For example, if young Savannah Sparrows (*Passerculus sandwichensis*) are raised in a situation in which magnetic directions and true compass directions differ markedly, their preferred direction of magnetic orientation will be altered, calibrated by information about true compass directions derived from celestial rotation (for review, see Able 1991b). Celestial rotation is assessed by stars at night (Emlen 1970, Wiltschko 1982, Wiltschko et al. 1987a,

FIGURE 7. William T. Keeton (1933–1980) at a gathering of orientation workers at Cornell about 1973. Keeton's work touched all aspects of pigeon homing, from his documentation of magnetic influences on initial orientation to the ontogeny of the sun compass, the abilities of pigeons to perceive UV light, polarized light and ultrasound, the nature of release-site biases, and olfactory navigation. Ideas put forth in his 1974 review changed the course of research in the field. (Photo by N. J. Demong.)

Able and Able 1990) and by patterns of polarized skylight during the day (Able and Able 1993, in press).

Both the cue-conflict experiments and the ontogeny studies have thus far examined only a small number of species. Because experimental designs have often been dissimilar, it is not yet possible to say to what extent or even whether species may differ in the relative weighting of the various orientation capabilities (Helbig 1990b). Only the European Robin, Blackcap, and Savannah Sparrow are fairly well studied and even in these we do not have a complete picture of the relationships among the several orientation mechanisms. It has seemed apparent for some time that the hierarchical interaction of cues differs between adult birds making short-term decisions about orientation and young birds developing their initial navigational equipment. Most striking, during migration magnetic directions seem to take precedence over stars, and star patterns may even be recalibrated by the magnetic compass (Wiltschko and Wiltschko 1975a, 1975b, 1976), whereas during early life, rotation of stars (perhaps not functionally the same as star patterns, *per se*) can calibrate magnetic orientation.

Much more comparative work will be required to flesh out what is now only the most broad-brush outline of what is going on. Cue-conflict experiments performed on a diversity of species, but employing a carefully standardized experimental procedure are badly needed and necessary before we can draw any firm conclusions about similarities or differences in orientation mechanisms across species (see Helbig 1990b). In the case of ontogeny experiments wherein it is by definition necessary to control and manipulate the sensory experience of young birds, it is critical to interpret the results in light of the behavior and experience of

FIGURE 8.   Stephen T. Emlen (in 1970) setting up an orientation experiment in the research planetarium at Cornell University. Elegant experiments on indigo buntings revealed how the star compass operates and develops. He showed that young birds learn the relationships among star patterns and compass directions by observing the rotation of the celestial sphere around Polaris. His 1975 review codified the idea that avian orientation was based upon multiple cues. (Photo courtesy of Cornell University.)

wild birds. The experience of hand-raised birds will differ both quantitatively and qualitatively from their wild conspecifics; it would be all too easy to produce atypical responses or weightings of cues and thus spend time studying an artifact of our own creation.

THE NAVIGATIONAL MAP

The void created by the rejection, on empirical bases, of the several navigational map hypotheses current in the 1950s and 1960s was soon filled by the surprising hypothesis that odors formed the physical basis of the map (Papi et al. 1971, 1972) (Fig. 9). The hypothesis as proposed by Papi and his colleagues has from the beginning been that pigeons form a mosaic map of the surroundings of the loft based on a learned association between airborne odors and the directions from which winds carry them past the loft area. This map may be extended through exploration of the loft vicinity. Empirical results indicating that olfactory information is involved in homing by pigeons at distances of 500 km or more from the loft has led Wallraff (1989a, 1989b, review 1991) to propose that odors might form a much more extensive gradient map.

The olfactory navigation hypothesis has been controversial from the very beginning. One factor generating skepticism was certainly the general perception at the time that birds had a very poor sense of smell. As with perception of the magnetic field and polarized light, I wonder if our own sensory limitations did not introduce a bias in the consideration and acceptance of the roles of less familiar stimuli. Another may have been that the initial results emerged suddenly, published in an obscure journal, by a research group which was at the time not one of the established players in the study of pigeon homing. Whatever the reasons, the subject remains contentious after more than twenty years of work involving nearly all of the pigeon homing research groups in the world (for critiques and responses, see Papi 1982, 1991; Wallraff 1983, 1991; Schmidt-Koenig 1987; Schmidt-Koenig and Ganzhorn 1991; Waldvogel 1989).

It is beyond the scope of this commentary to review in detail the theoretical bases, empirical results and interpretations of data relevant to the olfactory navigation hypothesis. Scores of papers have been published. Summaries of the types of experiments per-

formed and their results may be found in Papi (1982, 1991). In the broadest sense, two main types of experiments have been involved. 1) Some involved the production of anosmia by either nostril plugs, olfactory nerve section, local anesthesia of the olfactory membrane, transport in sealed containers, or some combination of these. This approach has been used to eliminate access to environmental odors during transport to release sites (to eliminate outward journey or route-based information), at the release site, or both. 2) Others were designed to manipulate the odor environment experienced by the pigeons. This approach has been used to attempt to alter the development of the odor map by birds at the loft (various cage and enclosure designs, fan-produced winds, artificial odorants) and predictably to change the pigeons' perception of the displacement route (detour experiments of various types) or the release site (site-simulation experiments).

Criticisms have been leveled at all of the experiments. They fall mainly into four categories. 1) Attempts by other research groups to replicate some of the experiments have been unsuccessful. 2) Concerns have been raised about non-specific effects of olfactory nerve section and the application of local anesthetics, and about effects of these treatments on possible magnetoreceptors in the anterior part of the pigeon's head. 3) The physical substrate of an olfactory map remains unknown. 4) Whether the distribution and dynamics of these unknown substances in the atmosphere is sufficient for use as a map. A number of important issues about olfactory navigation remain unresolved. It is not clear whether odors constitute a mosaic map or a gradient map, nor what substances are providing the information. However, I find the behavioral data compelling that odors play a very substantial role in that part of the homing navigation process that tells pigeons where they are relative to the loft. To my mind, the experiments that have directly manipulated the odor environment either during the development of the map (e.g., Ioalé 1980; Ioalé et al. 1978, 1990; Foá et al. 1986) or during the homing process (e.g., Benvenuti and Wallraff 1985, Kiepenheuer 1985) provide the strongest evidence directly implicating odors in this process. Here the criticisms about detrimental effects of the experimental procedures do not apply and the specific directional effects produced (as opposed to random vanishing bearings) are difficult to explain by alternative hypotheses.

It is also clear that the dramatic results frequently seen in Italy have not always been obtained elsewhere (e.g., Wiltschko et al. 1987b). It appears to be the case that regardless of stock of origin, pigeons home very well in Italy. Whether this is due to something about the environment in Italy or to the handling and training regime employed by Papi and his colleagues is not clear. At some lofts elsewhere, especially in Germany, even control pigeons are often not homeward oriented, making it very difficult to draw any convincing conclusions. Papi and Wallraff have generally claimed that olfaction provides the necessary and sufficient map information for pigeon homing, although Papi (1991) grants that there might be an auxiliary mechanism that comes into play in certain situations. The data from Italy might be so interpreted, but I do not feel that the sum of data from all sources permits so rigid a con-

FIGURE 9.   Floriano Papi (left) and long-time colleague Silvano Benvenuti (right) at a symposium on animal navigation held in Tübingen, Germany, in 1977. With two colleagues, Papi and Benvenuti published the first paper on olfactory navigation in pigeons in 1971. Over the next twenty years the Pisa group published scores of experimental tests of the hypothesis. (Photo courtesy of F. Papi.)

clusion. Even in the case of some of the Italian experiments (e.g., Ioalé et al. 1978, Ioalé 1980), the greater scatter among experimentals versus controls and the ability to home by birds deprived of relevant olfactory information suggest that they were influenced by other information that was at variance with or substituted for odors.

The only currently viable hypothesis for what that other positional information might be is the magnetic field. There has been a tendency to think of the olfactory map and the magnetic map as mutually exclusive alternatives and various factions have advocated one or the other. The fate of unitary thinking concerning compass orientation mechanisms should warn us not to ignore Keeton's (in Larkin and Keeton 1978) suggestion that we think of the map in much the same way, as a redundant system based upon multiple stimuli that may be weighted differently depending upon circumstances (Ganzhorn 1990, Schmidt-Koenig and Ganzhorn 1991). The evidence supporting a magnetic map in pigeons comes almost entirely from studies of pigeons released at magnetic anomalies (Walcott 1991, Able 1994) and it is rather indirect and not nearly so voluminous or persuasive as that related to olfactory maps. Although Walcott's (1991) (Fig. 10) assessment of the likelihood that there is a magnetic component to the pigeon's map was decidedly negative, I think the situation remains unresolved. Pigeons from the lofts where the phenomenon was originally discovered are still disoriented when released at magnetic anomalies and Walcott (1992) has recently found a suggestive correlation between the magnetic environment around the loft and disorientation at anomalies. Birds living at a loft situated in a magnetic environment more likely to provide useful navigational information were disoriented when released at the anomaly whereas those from a loft situated in a magnetically very uniform

FIGURE 10.   Charles Walcott has performed many clever experiments designed to reveal the role of magnetic cues in pigeon homing. His experiments with tiny coils surrounding the heads of flying pigeons provide the strongest evidence for the role of the magnetic compass in pigeon homing. The discovery that pigeons released at magnetic anomalies were disoriented provided the empirical basis for magnetic map hypotheses. (Photo courtesy of C. Walcott.)

region were not affected. This sort of observation is consistent with the idea that pigeons, and perhaps other birds, possess a flexible navigation system in which the weighting of map cues might depend in part on the availability and reliability of several potential components. Support for this sort of flexibility also comes from experiments by the Wiltschkos which showed that pigeons raised exposed to winds and air flow were strongly affected by anosmia whereas those that grew up in a sheltered locale were not (Wiltschko et al. 1989, see Benvenuti et al. 1990).

The nature of the navigational map of the homing pigeon (whether a grid map or mosaic map), its physical bases, and precisely how it works remain, after more than thirty years of concentrated work, the single largest challenge in this field. Although I am convinced that olfaction plays a major, sometimes primary, and sometimes perhaps exclusive, role in the map component of homing, we still cannot explain in a rigorous, step-by-step, mechanistic way how the pigeon does what we known it does. In the case of migratory birds, we know that many species exhibit remarkable site fidelity to breeding and overwintering locations, but next to nothing about when and how this navigation takes place. We do not know, for example, whether most of migration is accomplished by compass orientation alone, the navigation to the goal occurring only in the final stages of the journey, or whether the birds are goal orienting throughout the trip. There is some evidence that anosmia produces similar effects in migratory birds as in pigeons (Fiaschi et al. 1974, Wallraff and Hund 1982, Wallraff et al. 1995) but we

know little else about the basis of navigation in these species.

THE PAST AND THE FUTURE

Inasmuch as it has been almost exactly thirty years since the publication of the seminal reviews of Keeton and Emlen, I thought it interesting to consider what they felt were the major open issues and promising directions at that time and see what progress we have made. Clearly, the result of three decades of work is a mixed bag with much advance in some areas and other questions no closer to answers.

One of the major themes of those reviews was an emphasis on multiple, redundant mechanisms in orientation and navigation. This inevitably led to a focus on the interrelationships among cues and here we have clearly learned a great deal through cue-conflict and developmental experiments. At the time of these reviews, the magnetic compass was viewed with skepticism, and the importance of sunset information for night migrants, predicted by Emlen and others, was yet to be demonstrated. Stars were thought to be the preeminent orientation tool of night migrants. Since then, of course, magnetic orientation has assumed a position of central importance in the suite of capabilities, and for night migrants the patterns of polarized light in the dusk sky seem to be paramount. Although significant progress has been made, we still do not know the mechanism of magnetoreception in any vertebrate.

Much less progress has been made in other areas. Remarkably little new work has been done on stellar orientation and questions about possible time compensation of the star compass or navigational responses based on stars have hardly been discussed in the intervening years [but see Rabøl 1985]. Some things have been learned concerning how the weighting of cues varies with age and experience, but many gaps and inconsistencies remain. We have learned very little that is definitive about possible species differences in orientation mechanisms, how the weighting of cues might vary under different environmental conditions, the relative advantages of reliance upon one cue over another, and whether simultaneous use of cues results in an increase in accuracy of orientation. Progress in these areas will be very difficult unless we produce a better means of assaying orientation directions than the currently used cages. Until a representative set of comparative studies is at hand, it will be impossible to develop an evolutionary ecological approach to orientation/navigation systems. At the moment, we can do little more than expound just-so stories in response to questions such as why migratory birds are equipped with such a richness of orientation and navigation capabilities that interact in such complex ways?

Virtually no advance has been made in understanding the navigational capabilities of migrants or even the circumstances under which they show navigational responses. Although long-distance radio tracking of migrants has provided some very rich information concerning orientation behavior enroute (e.g., Cochran and Kjos 1985), we will be hard-pressed to discover much about navigation processes until it is possible to track a bird with a precisely known goal during most or all of its migration. Recent advances in satellite tracking

have been impressive (Nowak and Berthold 1991), but the technology is still applicable to only the largest species.

The homing pigeon has long been the laboratory rat of bird navigation studies. Based on present knowledge, there is no reason to question its usefulness as a model system. It is important to remember, however, that the homing pigeon has undergone thousands of generations of intense artificial selection favoring the performance of this very specialized task. We might very well expect quantitative, if not qualitative, differences in orientation mechanisms to exist. Until we know a good deal more about the navigation behavior of other species, we will not be able to test the assumption that they do things in the same way.

From the beginning, major advances in this field have resulted from the development of new techniques (e.g., orientation cage) or the emergence of new and unexpected experimental results (magnetic orientation, olfactory effects on pigeon homing). New ways of looking at things have been forced by the weight of data, often after a considerable period of disagreement and controversy over the validity or meaning of the new results. Theory and hypotheses derived from first principles have played little effective role in the development of the field. The grand unified hypotheses of bird navigation derived from theoretical considerations (Coriolis force and the magnetic field, sun-arc hypothesis, star navigation, inertial navigation) were all rejected after substantial amounts of effort were devoted to testing them. Likewise, attempts to go from the discovery of potentially useful sensory capabilities to their behavioral relevance in orientation and navigation have not been especially productive (infrasound, ultraviolet light, barometric pressure). Advances have tended to be more rapid and with fewer dead ends when we have followed the leads presented to us by the spontaneous behavior of the birds and formed our hypotheses not in the vacuum of theory but in the empirically-driven milieu of our experimental results.

In 1984, Robin Baker wrote a thought-provoking book entitled *Bird navigation: the solution of a mystery.* He concluded that the mystery of bird navigation faded away, scarcely noticed, in the late 1970s and early 1980s, and that although the problem has been solved, those who work in the field will probably not believe it for some time. Based on his review of the data, he concluded that all the observations could be accounted for by assuming several compasses and a mosaic map based on a number of unspecified landmarks, including odors. Is the mystery really solved and are those of us working in the field simply in denial? By enumerating some of the many unanswered questions, I hope to have shown that we cannot yet explain in a mechanistic way the behavior that we observe birds perform. At its rather general level, Baker's solution to the mystery is a good null hypothesis. But it will be a very unsatisfying solution until we know exactly what information constitutes the maps and compasses, how it is perceived and employed in these processes, and what conceivable alternative hypotheses have been tested and rejected. My guess is that all the pieces of the puzzle are at hand, though we should remain ever alert for indications that they are not. However, no one has yet assembled those pieces into a picture that the majority of students of

the subject agrees adequately depicts the navigation behavior of any bird species.

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