Conceptual approaches to avian navigation systems

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Summary. The general basis of migratory orientation in birds is most probably an endogenous time-and-direction program. Directions are selected with respect to celestial and geomagnetic clues. Using these clues, a bird may reach a large population-specific area; however, it will hardly be able to find a particular location, for instance its previous breeding site. Homing to a familiar site over several hundred kilometres of unfamiliar terrain appears to be based on the smelling of atmospheric trace compounds. Conceptual approaches to the mechanism of olfactory navigation have as yet only reached an early state of speculation.

Key words. Birds; pigeons; migration; orientation; navigation; homing; sun compass; magnetic field; olfaction; airborne odours; atmospheric trace compounds.

Introduction

Young birds belonging to a particular population of a particular migrant species leave their birth region on a predictable date and fly a roughly predictable route to a predictable wintering area in a foreign continent. In the following spring they fly back to the area of their origin. Thereafter, the adult birds shuttle, once every year, between two precisely defined geographic locations, breeding site and wintering site, which may be 5000 km or more apart. Members of many species migrate predominantly at night.

It is immediately obvious that these briefly-outlined phenomena imply substantial problems of navigation. In search of solutions, it is necessary to inspect the birds' performances more closely, to formulate precise questions and where possible to find answers to them (which will often result in the finding of new phenomena and questions), and where this is not yet possible, to develop conceptual lines along which research may try to proceed. In the following survey, this last aspect will be emphasized; conclusions resulting from empirical investigations will be mentioned only as far as is necessary in order to keep alive the interplay between empirical observations and theoretical considerations, upon which scientific progress is based. For more detailed information, especially on empirical results leading to the conclusions mentioned, the reader is referred to the other reviews in this issue.

The specific problems of bird navigation can be reduced to some general guidelines controlling the orientation of an organism in space. They require three conditions to be met: 1) suitable spatial structures in the physical environment; 2) sensory equipment of the organism to perceive relevant signals from these structures and/or about its own motions; 3) suitable strategies to make adequate use of these signals. Which of these conditions will pose the most serious problems may vary under different circumstances.

The third condition requires that two kinds of biological causation[35] be distinguished: a) evolutionary ('ultimate') causation resulting in ecological adaptations of the population and b) immediate ('proximate') causation, as shown by physiological stimulus-response relations in the behavioural actions of the individual organism. In bird migration the two aspects are closely linked. The animals react to currently perceived external stimuli as if they could foresee future situations in different environments in other geographical regions.

The word 'navigation' is used in this essay, as in the literature, in both a broad and a narrow sense. On the one hand it may imply all kinds of orientation in space, preferably long-distance orientation. On the other hand, in its narrower form, the term is restricted to goal orientation (homing) from unfamiliar areas.

A paradigmatic experiment and resulting problems

Every autumn The Netherlands are crossed by huge numbers of starlings coming from northeastern Europe and subsequently wintering in northern France and southern England. What determines this migratory route? Two hypotheses are possible: the birds may arrive in their population-specific wintering area, because they are programmed either 1) to fly in a particular direction, or 2) to reach a particular geographic location. To resolve the issue, Perdeck[51] conducted an experiment which has meanwhile become a classic. More than 11,000 starlings, caught during migration in Holland, were transported to and released in Switzerland. Distributions of recovery sites in the subsequent winter months met both possible expectations, depending on the age of the birds (fig. 1):

1) Young starlings, migrating for the first time, when displaced perpendicularly to the compass direction normally taken by the population, continued to fly this normal compass course and hence arrived in an abnormal area dislocated by approximately the direction and distance of displacement.

2) Older starlings, which had spent a winter in the population-specific area at least once, flew an abnormal compass direction leading them toward the normal (already familiar) wintering area.

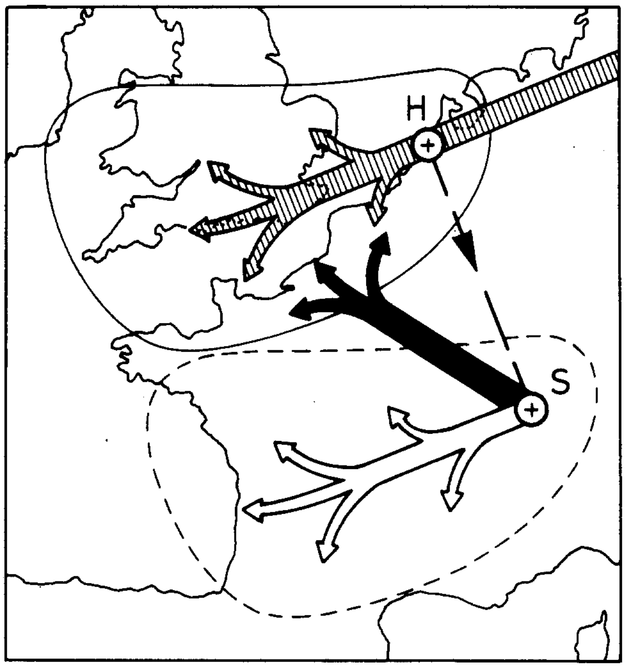

Figure 1. Starlings migrating in the autumn through Holland (H) arrive from breeding grounds in northeastern Europe and subsequently winter in southern Britain, northern France, Belgium and Holland, in an area approximately limited by the solid line surrounding the hatched arrows. Many such starlings were displaced from Holland to Switzerland (S) and released there. In the subsequent winter months, most of the juveniles (empty arrows) were found in an area displaced accordingly (as marked by the broken line). Adults, in contrast, were found in the original wintering area or on the way towards it (black arrows). (Schematized[70] after Perdeck[51])

These two outcomes induce two questions:

1) How do the young birds 'know' in which relation to which environmental reference they should fly? What causes them to stop in the appropriate area? As will be discussed below, more complex routes than those of the starlings in some species entail more complicated problems.

2) How can adult birds determine, in an unknown area, their position in relation to a distant familiar area or site?

Course control of migration in inexperienced birds

Bearing-and-distance migration

Compass orientation and 'intended direction'. The result obtained with the young starlings suggests two conclusions: a) Some environmental references were apparently available in Holland as well as in Switzerland according to which an identical compass course could have been chosen. b) The birds apparently followed some 'internal command' to select just one specific course angle – an intended direction – with regard to this reference(s).

Only a few environmental structures are known that can provide analogous directional reference within large latitudinal ranges. A suitable terrestrial (geophysical) parameter is the geomagnetic field. Extraterrestrial (astronomical) visual objects like the sun or the stars are also suitable. Both types of clues are utilized by bird migrants[2,96]. Both have their specific advantages and disadvantages.

The geomagnetic field immediately provides a direction of reference, viz. magnetic north (or south). This reference does not change with season and time of day and is fairly constant over the entire globe. It is permanently available during the daytime, at night, and in all kinds of weather. Hence the geomagnetic field fits the above requirement in an ideal way. Astronomical clues lack most of the advantages mentioned. Their evaluation for compass orientation requires additional knowledge; a stable ubiquitous reference direction is not immediately provided; temporal and geographical changes of celestial features have to be taken into account. Under overcast skies, these features are not available at all.

If the birds were able to utilize the spatio-temporal properties of the geomagnetic field in a comprehensive way, there would be no need to utilize other less convenient features in addition. Actually, however, the birds preferentially orient their courses with reference to the sun, to the sunset direction, or to the starry sky. Without visual clues, directedness tends to be weaker (in cages quite considerably[83,88]) or is inappropriately oriented downwind[1,3]. If magnetic and celestial clues are at angular variance to each other, the birds' immediate response usually fits the astronomical condition[41,58,83,92].

Most probably there are sensory limitations restricting the capacity for magnetic orientation, whereas it is the sensory aspect which is the least problematic one in celestial orientation based on visual inputs. Analysis of the physiology of magnetic perception has just begun[61], and the kind of spatial information the birds derive from the magnetic field is unknown (direction?; intensity, or merely change of intensity, depending on body alignment or direction of flight?[72]). It seems that the geomagnetic field is primarily used for adjustment of astronomical clues to the compass scale rather than as an immediate directional reference for a currently selected course angle[6,7,72,91,92]. Interaction of various clues in migratory compass orientation appears to be rather complex and seems to be different in different species[2,96].

Our second problem is the source of information telling the birds which angle to an environmental reference they have to adopt and maintain. Empirical research strongly suggests that intended migratory directions of juvenile birds are products of evolutionary processes during which the most appropriate course angles for the various populations have been selected and genetically fixed[11,20].

Termination of migration. Migrations usually end in a population-specific area, i.e., the birds must in some way be induced to stop their flight. Termination of travel could be induced by the birds' 1) reaching a certain geographic location, 2) reaching a certain habitat, 3) having covered a certain distance, 4) having spent a certain length of time flying, or by 5) a periodic time program determining phases with varying motivation to migrate. Empirical evidence supports the conclusion that a population-specific endogenous time program (item 5) roughly determines the spatial distance to be travelled[11]. Where the birds actually terminate their journey, however, depends on ecological properties of the habitat (item 2)[52]. Hence the final outcome seems to be a co-product of an endogenous circannual[11, 18] program and immediately acting exogenous influences[4].

Adaptation to static and dynamic geographical features

Population-specific intended direction plus time program plus flexible responses to actual ecological conditions are sufficient to explain broad-front migrations as observed in many species. There are other species, however, whose migratory routes do not simply follow a bearing-and-distance scheme. Routes of long-distance migrants, in particular, are often more complicated, include one or more directional shifts, and usually fit quite well the geomorphological configurations of the areas crossed[14, 16, 60, 98, 99]. Moreover, many of those routes probably reflect the history of the particular species, e.g., paths of ancient dispersal[14, 60, 63].

Some cases of curved routes appear to be a simple outcome of mechanical forces acting on the flying birds: transoceanic migrants, going out over the sea from North America in a southeasterly direction and keeping their headings constant, finally reach northern South America owing to the 'help' of the northeasterly trade winds which bend the resulting tracks more and more towards the south or even southwest[54, 87].

Another mechanism which might result in curved routes, while the internal command controlling flight direction is kept constant, has not yet been shown to be more than an appealing idea; the external signal used for orientation might change with latitude, and its unchanged evaluation would lead to a gradual directional shift. A certain magnetic parameter has been shown to fulfill this demand[28]. Actual migratory routes often appear too well-adapted to specific geographic constellations, however, to be explicable solely by a global mechanism.

As an example, let us consider the European-African migration system. A bird from central Europe, when flying the shortest route to tropical Africa, has to cross three kinds of ecologically unfavourable and thus dangerous areas in succession: high mountain ridges (the Alps), a large surface of water (the Mediterranean Sea), and an extended desert (the Sahara). Two lines of selection may have been 'at evolution's disposal' to cope with this problem: birds could either be equipped with physiological capabilities to surmount the threefold barrier or could be induced to avoid it by making an appropriate detour. Both lines have apparently been followed, and some balance seems to have been achieved. On the one hand, many birds do in fact cross the Alps, the Mediterranean Sea, and the Sahara[13, 38], but on the other hand, the majority of migrants leave Europe flying southwest or southeast, and at the flanks of the barrier re-orient their courses toward the African wintering grounds[60, 98, 100].

In a first attempt to explain the detours, one might assume that while they are actually migrating the birds immediately respond to a topographical barrier by following its edge with the smallest possible angular deflection, until they reach an end of the barrier[71]. At that point, the birds may either compensate for the deviation (which they must have recognized and quantified) by following a course now deviating to the other side from the intended direction, or they may continue their originally-intended flight course. In the latter case, the amount of detour should have been taken into account by the phylogenetic process by which an intended direction of the population has been selected.

Though immediate deflections by topographical features do occur, on a smaller spatial scale, they cannot explain the large-scale pattern of migration routes. The threefold barrier is probably the ultimate reason for the detours, but actually most of the bird populations steer directly to its western or eastern flank[60, 98, 100]. Thus, an invariable intended direction seems to be insufficient to explain the behaviour of all bird migrants.

In several species, an angular shift of the intended direction probably does occur during migration. It might be considered possible that control of this shift has been taken over by the endogenous time program mentioned above, which would then not only determine the onset and end of migration, but also the temporal course of directional changes. There is, in fact, experimental support for this idea[19, 21]. It seems doubtful, however, that the problem can be entirely solved on this basis. As it depends on varying weather conditions[4, 53, 54], the temporal progress of actual migration can hardly be precisely programmed on a day-by-day basis. In some cases, however, directional shifts occur, and even have to occur, within quite narrowly limited geographical areas[21, 22, 84] and thus at the exact time of arrival in this area.

Hence external signals might well be involved additionally or alternatively. For instance, some positional information as derived from the starry sky, the geomagnetic field, or something else may inform the birds that they have reached a critical site or line (e.g., latitude) at which they should change the direction of their compass course. (Experimental findings indicating dependence of the intended direction on magnetic intensity and/or inclination, and thus possibly on magnetic latitude, have in fact been reported[8, 96].) Alternatively, some peculiar features of the landscape may induce a directional shift. While it seems unlikely that birds are genetically programmed to respond to an individual but never experienced configuration (like a particular bay, mountain, cape, etc.), they might well be programmed to behave differently when flying over basically different types of landscape as, for instance, land and sea. In fact, it has been observed that night migrants, when flying over water at dawn, alter their courses in an appropriate manner to reach land[40].

Immediately deflecting influences of landscape features on migratory directions can often be observed on a smaller spatial scale[60]. In some cases it may be difficult to distinguish between 'barriers' and 'signals' which 'force' or 'induce' a directional change and hence act as deflection lines or leading lines. A mountain chain, for instance, can be overflown in principle, but if it is of limited length and the course angle need not be changed too much, the advantage for selection may be greater to fly parallel to the ridge and hence to deviate for a while from the endogenously intended direction[12, 84].

All these considerations are applicable to a juvenile bird migrating to its wintering grounds for the first time in its life without social contact to conspecifics. Thus, they are certainly applicable, for instance, to the many passerines migrating at night[101]. They are also applicable to all other species, but daytime migrants flying in flocks have additional opportunities from which they may profit. Social contact may not only be a general help to average diverging directional tendencies toward the presumably best-adapted mean of the population[73], but more specifically it also can help juveniles to profit from the experience of older birds[59, 60]. Particularly in larger species, as in ducks and geese, migratory routes are largely an outcome of tradition[10, 62]. They are well-adapted to environmental features and even quickly adaptable to changes of the environment.

In conclusion: actual migratory routes result from an interplay of phylogenetically developed endogenous programs and immediate responses to environmental features (including, in some species, conspecifics). Our understanding of the more complicated phenomena observed in nature (directional changes; species-specific, narrowly channelled routes[49]) is still quite limited. From a list of conceivable systems[71] only a few can be excluded by empirical evidence, and on the other hand, such a list may not include all the solutions which actually exist.

Goal-oriented homing to familiar sites

So far the considerations have been restricted to autumnal migrations of juvenile birds. From the first spring migration onward, at least potentially, a new orientational element can contribute to the system, namely greater or lesser familiarity with features of the areas the individual has already experienced. From this point on, the birds return to an earlier experienced goal.

In the experiment shown in figure 1, the adult starlings did not maintain their normal travel course but apparently created a new 'intended direction' pointing towards the normal wintering area which they had experienced during at least one winter before. Homing experiments like this, but with birds directly displaced from their home site to an unfamiliar site, have been conducted with many species, preferably, however, for practical reasons, with the homing pigeon. So far there is no indication that this domesticated form might use orientational mechanisms basically different from those used by wild birds.

Principles of goal orientation

Several methods are conceivable by which an animal might find its way home from a distant site: 1) the animal may have direct sensory contact with the goal or to stimuli emanating from there; 2) it may use some random-search strategy; 3) it may store a sequence of landmarks observed during the outward journey from home and then trace this chain backward; 4) it may record and integrate its angular and linear motions during the outward journey and then return by 'clearing its integrator'; 5) it may find the goal by the use of some 'topographical map' it had built up earlier by exploring site-specific features (landmarks) in a larger area around home; 6) it may find home by use of a 'navigational map' exceeding in extension the range of earlier sensory experience. The different methods are, of course, not mutually exclusive.

With respect to pigeon homing, neither direct sensory contact with the goal (method 1) nor random search (method 2) can be the sole solution. Pigeons return to their loft over hundreds of kilometres and fly towards it from the beginning[69, 75, 76]. Clock-shift experiments (see below) demonstrate that the birds do not refer directly to the goal even at shorter distances. Method (3) can be excluded, because pigeons displaced by car (mostly without a view of what is outside) do not follow their outward route while flying back home.

Path integration (method 4) may be more seriously considered. It is known for many animals (especially arthropods and mammals) that they do in fact record and integrate all their movements while going out and thereby are always informed of their direction and distance relative to home, so that they are able to return by the shortest route even if they had made long and winding detours[37, 39]. This homing system has the advantage of being independent of any site-bound environmental features, but the disadvantage of requiring a continuous input flow and updating during the animal's movements outward and back. Animals known to use path integration which were passively displaced on a route including several angular and linear shifts, under conditions of visual isolation from the environment, were unable to find the way back home[15]. In homing experiments with pigeons, however, the birds are usually transported under similarly adverse conditions. Moreover, even if all conceivably useful input channels are interrupted or disturbed during the outward journey, pigeons are still able to orient their courses homeward in a goal-directed manner[75]. These experiments do not exclude the possibility that pigeons and other birds might also use path integration when performing spontaneous flights away from home and back. While nothing is known about this we can conclude, on the other hand, that pigeons are able to home from unfamiliar areas without using a path-integration system[75,86].

Hence there remain the two kinds of 'map' mentioned above (items 5 and 6). The first one has been called a 'mosaic map'[70,77,93,94], 'familiar area map'[5], or 'topographical map'[78,82,85]. Like our maps, it duplicates individual features composing a landscape, including their spatial relationship to each other as well as to the home site (fig. 2, A and B). Landmarks and spatial relationships have to be learned by individual exploration. Hence the range of this map depends on the range of preceding experience. At sites outside a 'familiar area' the map is useless for homing. The borders of the familiar area are probably less distinct than figure 2B would indicate. Visual landmarks, for instance, can often be seen from quite long distances. It is another question, however, over what distance they are recognized and adequately utilized by birds. Certainly there are different grades of familiarity, usually increasing with decreasing distance from home. It can hardly be doubted that birds make use of such 'topographical maps'[85]. Probably they are based (at least primarily) on visual landscape features. This kind of home-finding by means of familiar landmarks is most adequately called 'pilotage'.

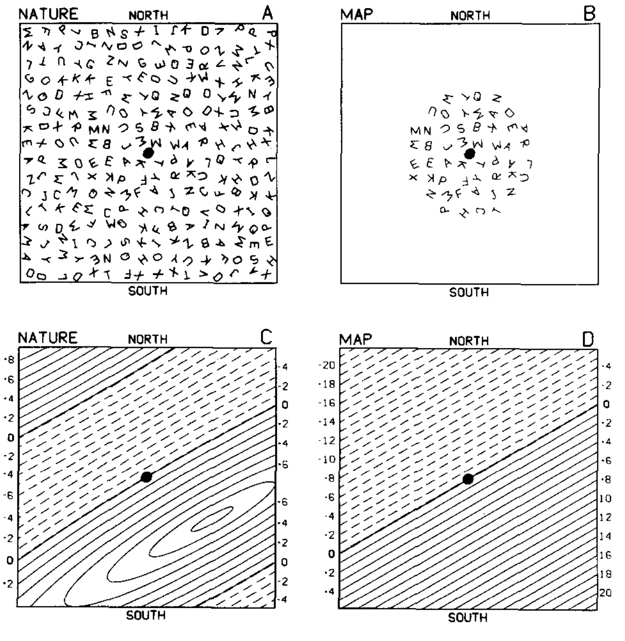

Figure 2. *A* Mosaic of landmarks, symbolized by letters, surrounding a bird's home site (central dot). *B* The corresponding mosaic map (topographical map), which is limited in extent by the bird's range of experience. *C* Iso-lines (arbitrary units) of a gradient field. The line running through the bird's home is designated as 0, higher values indicated by solid and lower values by broken lines. *D* The bird's corresponding gradient map as established by extrapolation of home-site conditions. Notice that in *C* and *D*, for the sake of simplicity, gradients of only one variable are shown. For complete site localization, at least two gradient fields are required intersecting at sufficiently large angles. The sections shown are thought to be of different size; sides of the square in *A,B* may be at most a few hundred km, those of *C,D* 1000 km or more. (From Wallraff[77])

For 'navigation' in its narrower sense, i.e., for goal-finding from unfamiliar distant areas, another sort of map is appropriate, a 'gradient map', which in principle is unlimited in extension (fig. 2, C and D)[70,77,82,93,94]. This type of map is thought to be based on at least two gradients of any physical substrate which extend over a sufficiently large area. Assuming that the gradients extend monotonically beyond the familiar area, scalar values of the respective physical parameters at the current position of an animal, as compared with those remembered from the home site, could provide information on the animal's position with respect to home. Although the range of a gradient map is basically unlimited, its range of useful applicability may factually be limited by the sizes of the gradient fields to which it refers. For a bird with a 'map' as given in figure 2D, the actual pattern of gradients shown in figure 2C would be misleading at some sites. If displaced to the northwestern or southeastern corner of figure 2C, for instance, the bird would fly away from home.

As pointed out elsewhere in detail[70], a 'map' linearly extrapolating gradient slopes from the home area to an unlimited extension, as illustratively assumed in figure 2D, need not be presupposed. The distance from home need not be encoded at all. If so, the metaphorical term 'map' may not be fully appropriate. As long as the system actually operating is unknown, it may nevertheless serve as a short-cut term indicating that birds refer, in an indirect manner, to spatial relationships between different sites. So far, a homing mechanism based on gradients, and thus a 'gradient map', is merely a hypothetical concept. Unless it can be shown, however, that either a mosaic map with some modifications (see below), or a completely different system, not yet considered, could also be capable of explaining long-distance homing of birds from unfamiliar areas, I see no alternative to basing navigation hypotheses on this general concept.

Gradient map and compass

Localization of a point in a plane requires two coordinates or, in physical terms, a grid of at least two gradients, e.g., of substrates x and y (fig. 3). If an animal is displaced from its home H to a distant point P, and if it is able to recognize the differences Δx and Δy, or at least their signs, it is able to orient more or less precisely homeward, provided that it is also informed about the directions of the gradients, i.e., the directions in which variables x and y increase and decrease. There are three possible ways by which this information might be obtained. The animal can a) immediately perceive not only the scalar values of Δx and Δy (or at least their signs), but also the directions of the gradients (as indicated by arrows at the grid lines in fig. 3; as an example, the geomagnetic vector would, for one gradient, provide both kinds of information). The animal can b) immediately perceive scalar values only but has some additional knowledge or assumption about the compass alignment

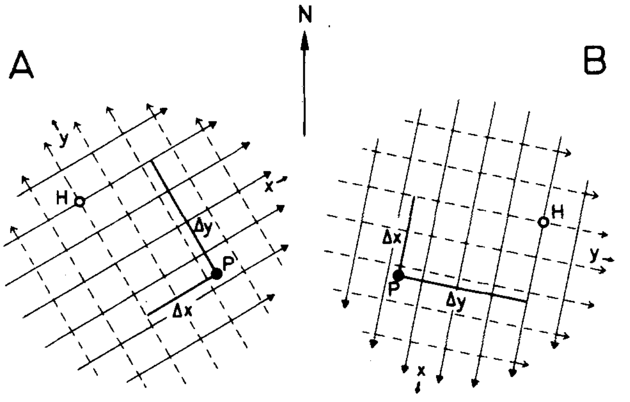

Figure 3. Grid of coordinates (gradients) x and y with home site H and a bird's current position P. The grids themselves are identical in *A* and *B*, but geographically they are differently oriented. (From Wallraff[70].)

of the gradients (for instance, whether A or B in fig. 3 is correct). If the animal c) perceives only the scalar values without having any idea of the gradient direction, it may less directly find home by scanning the field on a trial-and-error basis (whereby a compass could also be helpful)[70]. To reach some minimum level of efficiency, this last method would require that the quantification of x and y should not be too crude (a condition that might be problematic).

Empirical findings strongly suggest that in pigeons homing alternative (b) is realized. An experimental shift of the pigeons' circadian clock causes deviations of initial bearings upon release that correspond to the angular difference between the sun's azimuth at real local time and shifted circadian time[41,55,58]. This correspondence can reasonably be interpreted only by assuming that in a first step, by 'map reading', an intended compass direction is established, and in a second step this direction is determined by means of a sun-azimuth compass[23,58,70] (G. Kramer's map-and-compass concept[29,30]). A result like this could not be expected if either one of the above alternatives (a) or (c) were realized, since in both these cases the birds would directly refer to the gradients themselves, whose recognition would not be affected by the clock-shift (more detailed discussion elsewhere[70]).

The appropriate linkage between map and compass, including knowledge of or assumptions about the compass bearings, in which the values of relevant physical variables increase and decrease (e.g. decision that in fig. 3 alignment A is correct and not B or any other one), must either have been created phylogenetically or by a learning process during a long-term stay in the home area. Empirical findings suggest that in pigeons the latter alternative is realized[45,70] (see below).

Physical nature of gradient fields

Since pigeons are able to home over hundreds of kilometres, grids of suitable gradients must cover correspondingly large areas. A search for possible candidates reveals only a few physical variables that are known to meet this requirement. The first candidates are (again, as in compass orientation) the geomagnetic field and celestial bodies. Geomagnetic inclination as well as total intensity, for instance, has a north-south gradient; the same is true for sun altitude at a given time. Both kinds of clues have, therefore, been in the focus of research during four decades. From the fifties to the early seventies, many investigations dealt primarily with Matthews' sun-navigation hypothesis[23,30,33,34,50,56,66,70], and those before and after this period with a potential 'magnetic map'[17,65,95,97]. Since all these efforts were finally unsuccessful, it is unnecessary to discuss theoretical details of possible navigation systems using astronomical or magnetic parameters.

It is difficult to assess the role of magnetism in pigeon homing and other areas of bird orientation. Disoriented behaviour at magnetic anomalies has been described[27,64], correlations with temporal geomagnetic fluctuations were reported[25,31], and a number of effects of artificial magnetic fields on initial orientation of pigeons have been observed[26,48,90,95]. Piecing together all these findings, however, does not substantiate a 'magnetic map' concept. So far, no clear evidence has been found that site-specific magnetic signals contribute to the process of site localization[76].

Such evidence, however, has unexpectedly been found for quite another sensory modality which had never been considered as a potentially useful navigational aid. A single experiment, conducted by F. Papi and his co-workers in 1971, initiated a long series of investigations which eventually showed that olfaction appears to be a necessary sensory input for homing from distant, unfamiliar areas. It could also be shown that substrates obviously containing site-specific information are atmospheric trace gases[44-46,78,81,82].

Other sources of information, used in addition or alternatively, have repeatedly been proposed. Olfactory clues were assumed to be one kind among several others that were thought to be used for site localization[17,24,56,57,68,89]. From a conceptual point of view, a system implying a multiplicity of more or less redundant inputs is, of course, quite conceivable. It might have advantages, since it could react flexibly to the variable availability or reliability of different types of environmental features. However, a double or multiple system, functioning outside a familiar area and using still unidentified navigational clues, has not yet been shown to exist. So far there is no evidence that non-olfactory avian navigation (in the narrower sense, excluding pilotage) ever occurs[78,82,85].

The empirical findings created an entirely new situation. Instead of proceeding from well-known spatial configurations of the environment and searching for animal behaviour patterns reflecting adequate use of them, the direction of search has to be reversed. Now we start with biological responses and have to search for unknown physical configurations which make such responses possible.

Olfactory navigation: problems and speculations

The most problematic part of olfactory navigation is not the biological machinery but the physical environment of which it makes use. The reason for not considering odours as potentially useful for long-distance homing in birds certainly had to do with a particular expectation which was automatically connected with such an idea. This was the expectation that a bird would have to smell odorant molecules emanating from the familiar home site or area (like a salmon migrating upstream to the source of its home odour). It can hardly be considered possible that specific home-site odours could be detected and identified at a site 300 km distant from home, especially with winds blowing from the current position towards home.

To consider possible mechanisms of olfactory navigation, it is important to know that development of a functioning navigation system requires long-term exposure of the pigeons to natural wind conditions at the home site. Apparently the birds build up some kind of 'olfactory map' by associating varying olfactory conditions with synchronously varying wind conditions[44,45,81,82].

Papi proposed an olfactory map that may be visualized as a modified and spatially extended topographical or mosaic map whose landmarks consist of qualitatively different odours[42,43,47]. At the home site, presence or absence of specific odours is assumed to depend on wind direction. Odour A, for instance, may always be correlated with wind from the north. If a bird is displaced to a site where it smells odour A, it concludes that it is north of home and flies southward.

A system exclusively based on qualities of airborne compounds, however, is hardly capable of explaining the pigeons' homing abilities. Even along only one directional axis, a chain of huge numbers of sources of different chemical compounds would be required, since one cannot expect that each home site lies just between two large source areas of distinct compounds, A in the north and B in the south. Pigeons would home over short as well as long distances from north as well as from south to each of twenty lofts built along one meridian at distances of 20 km. A transfer from the one-dimensional axis to the two-dimensional plane would multiply the number of necessary compounds to an extent beyond any conceivable feasibility. What seems simple at first glance leads to completely unrealistic consequences (of which not all have been mentioned).

Possibly the mosaic idea should not be narrowed that way, as it is not quite clear what the word 'odour' in Papi's concept actually means. Odour A should perhaps not be presumed to be a single chemical compound but a particular mixture of a number of compounds. Even if each of the mixtures A, B, C, etc. were unique, however, the compounds composing them cannot all be unique as well (otherwise the above problem would be multiplied once more). Yet if the same compounds are included in many mixtures, it must be the quantitative relations between compounds which characterize the air at any given time and place. Thus, we end up with varying spectra of odorants, and these might be suited to providing a continuum of site-dependent variations without requiring very large numbers of different substances. Different sites would not be distinguishable by simple observations like 'odour A or B present or absent', but by gradual differences between proportions of compounds composing a spectrum of relevant odorants. Although differing from each other by quantitative relations between compounds, different spectra might induce different 'qualitative' sensations; compounds need not be distinguished individually (as a banana smell, for example, can be recognized without any knowledge about the cocktail of odorants causing it).

On this basis of proportions between odorants, a spatial olfactory pattern might be suitable for the construction of an olfactory mosaic map within a familiar area known to a bird from exploration flights. Odours coming with winds from beyond this area might help to extend the range of the map for some distance outside the area. But up to 300 or 500 km and more? Extrapolations to such long distances would require atmospheric structures that so far have not yet been shown to exist. In order to find out whether they do exist, we need some idea of their possible nature.

Let us forget, for a moment, that the atmosphere is a very dynamic medium. It may be considered to be static, but diffusion should still be permitted. Assume that a long-lived odorant emanates from the ground, in different areas at different rates depending on the distribution and productivity of its sources. Over thousands of years, concentrations of this compound may form extended gradient fields like the one shown in figure 2C. Other compounds, a dozen or so, may form similar fields, but with gradients extending in a variety of different directions. Everywhere, a spectrum of all these compounds is available. It varies in a site-specific manner, with a unique pattern of proportions between the compounds at each site. By scanning a restricted area around home, a bird can recognize the trends of spectrum changes in various directions and thereby extrapolate to distant areas, where it has never been (as shown, for one component, in fig. 2D).

A first step toward reality is the introduction of winds. A slight breeze affecting the whole area in question and changing direction in a regular manner would make active scanning unnecessary, because now the air mass would be moved across the home site. The bird only needs to associate varying compositions of the spectrum with contemporaneous wind direction. (This assumption would fit the experimental data which show that flights around home are not necessary for developing a navigational map[69,70], whereas exposure to winds is necessary[44,45,74].)

The real dynamic atmosphere, however, does not provide a regularly changing breeze but strong semi-chaotic turbulences, which can hardly be considered primarily 'helpful'. They whirl our fictitious pattern of almost static gradient fields around to such an extent that one may doubt whether any remainder might have survived in the real world. Due to this turbulence, long-lived substances are homogenously distributed over the entire globe, whereas short-lived compounds have hardly any chance to build up fairly stable gradient fields over a larger area. However, there are compounds between the two extremes. Large-scale gradients of hemispheric dimensions from lower to higher latitudes have in fact been found for several substances[32]. Since very few of the hundreds of atmospheric trace compounds have been studied from this point of view, little is known about potential gradient fields extending over an area some hundreds or thousands of kilometres in diameter. If they exist at all, they most probably change their shapes depending on large-scale wind patterns. Consequently, an assumed olfactory gradient map would have to be dynamic too, in that it takes large-scale weather conditions into account, either also on an olfactory basis or otherwise[80]. (If certain assumptions are made, it might be concluded that dependence on meteorological conditions would be only slight[80, 81]; yet these assumptions may be considered unrealistic, at least as long as there are no empirical data supporting them.)

Sufficiently large gradient fields of airborne odorants, if they do exist, must be expected to include considerable irregularities in space and time. They may hardly be suited to provide reliable coordinates for precise site localization (even if current weather conditions are taken into account). Precision, however, need not be an unavoidable prerequisite. Instead of a minimum of two fairly stable and monotonic gradients, a larger number of variable and noisy gradients could be used, leading to a similar level of performance. A system using quite noisy inputs and evaluating them on a basis of statistical averaging may well be able to reach the efficiency of pigeon navigation, which is usually much worse than the theoretical optimum of homing on a straight course[79].

At the present stage, any conceptual approach to the mechanism underlying olfactory navigation is necessarily speculative; its heuristic value cannot be assessed yet. However, without attempts like those outlined here in short, and elsewhere more extensively[79, 80], there is hardly any chance at all to advance in the search for a solution to the problem. It is certainly not constructive simply to dismiss olfactory navigation as 'unfeasible', because at first glance the meteorological environment appears unsuitable to provide adequate spatial information[9, 57, 67, 68]. This avoids one problem but creates two others, whose solution cannot be expected to be easier. First, the many experimental results indicating that site localization is based on atmospheric odours would have to be explained in a different, no less plausible way. Second, an alternative physical basis of bird navigation would have to be found.

Integration of orientation mechanisms

It seems reasonable to assume that the navigational portion of bird migration comprises a system integrating a number of different mechanisms, which themselves include different sub-systems (see, e.g., compass orientation). The primary framework is most likely to be a circannual time-and-direction program which leaves the birds responsive to various environmental features in a way that ultimately makes good sense, i.e., results in a well-adapted teleonomic[36] process. This system would be capable of guiding the birds over very long distances to their winter quarters and back to their breeding grounds. Due to interfering influences, such as variable weather conditions, particularly wind drift, birds relying on this system alone can hardly be assumed to find a specific breeding site. A bird returning from Africa, for instance, may find its way back to Central Europe on this bearing-and-distance basis. Once it is there, the next mechanism may come into action, olfactory navigation, which operates over several hundred kilometres. Finally, in order to pinpoint the last year's breeding site, visual landmark recognition (pilotage) would certainly be helpful.

The three assumed components of the system – time-direction program, olfactory navigation and visual pilotage – have different ranges of operation, but large zones of overlap within which two mechanisms are capable of operating jointly. The integrated system as a whole makes it possible to cover very long distances, up to several thousands of kilometres, and still to find a distinct geographic location at the end of the journey.

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Experimental studies of the development of migratory orientation mechanisms

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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.