The Navigational System of Birds

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Abstract

The avian navigational system is based on an external reference, giving the home direction as a compass course. When young, inexperienced birds begin to fly, their only available orientation mechanism is a magnetic compass provided by their ability to perceive the geomagnetic field. They navigate by using this compass to record the direction of the outward journey and, by reversing this direction, obtain the home course. At the same time, the magnetic compass provides a directional reference system for learning processes establishing the sun compass and the complex navigational mechanisms of experienced birds: a 'mosaic map' and a navigational 'map'. These 'maps' are formed by combining information on the route travelled with site-specific information, leading to directionally oriented mental representations of the distribution of landmarks and of environmental gradients, respectively, in the home region of birds. These 'maps' enable birds to derive they homeward course from local site-specific information; once established, they are preferentially used as they allow correction of errors.

Pigeons are famous for their ability to return home after displacement over hundreds of kilometers. The question how they navigate, how they determine their home direction at distant, totally unfamiliar sites has always fascinated man, and so it is not surprising that it has for a long time been a topic of intense scientific research. Today, essential aspects of avian navigation are fairly well understood, even if many questions are still open. In the present paper, we want to describe the avian navigational system as it is indicated by experimental evidence, focusing on the structure of the system and how the relevant information is represented and processed.

1. Orientation Based on an External Reference

Some general consideration may outline the problem. An most important characteristic of bird orientation is the long distances involved. Birds rarely have direct contact with their destination, which means that in most cases, they must establish contact to the goal indirectly. When a bird wants to fly from a site A to a distant goal B, the position of site B with respect to A must be represented in a way that the bird can derive the required information. The most economic way to define the position of a goal is in terms of its directional relationship to the starting point, using an external reference system based on cues that are accessible from the starting point A as well as from the goal B. This leads to specifications that are equivalent to our human use of compass directions, when we say: 'Site B lies east of site A'.

Because of the large home areas of birds with their numerous potential goals, it is advantageous to use cues that are independent of any specific location, being accessible from everywhere within the home area and beyond. Two types of factors possess the required characteristics: the *geomagnetic field* and *celestial cues*. Homing pigeons make use of both, thus having two compass mechanisms at their disposal, a magnetic compass (see R. Wiltschko and Wiltschko 1995 for details) and a sun compass that compensates the changes in sun azimuth with the help of an internal clock (see Schmidt-Koenig 1958, R. Wiltschko 1980 for details). Both mechanisms provide birds with essentially the same type of information. The sun compass, a learned

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mechanism, is preferentially used as long as the sun is visible, but can be replaced by the magnetic compass without apparent loss under overcast skies (e.g. Keeton 1969).

2. The 'Map and Compass'-Model

G. Kramer, a pioneer of orientation research, was the first to realize that birds might base navigation on an external reference provided by a compass. Therefore, he described avian navigation as a two-step process: In the first step, the bird determines the compass course leading to the goal, then, in the second step, it uses a compass to locate this course (e.g. Kramer 1959). For example, a pigeon east of its loft determines its home direction in terms equivalent to "*west*", then it uses a compass to find out where west lies, obtaining a specification like *"go there"* or "*this way*", thus transforming the compass course into an actual direction of flying.

Kramer's 'map and compass'-model represents the basic theoretical concept in animal navigation. It can be easily tested by making use of two facts: (1) Pigeons prefer the sun compass over the magnetic compass, and (2) the sun compass involves the birds' internal clock. In the now classic clock-shift experiments, introduced by Schmidt-Koenig (1958), the internal clock of pigeons is reset by subjecting them for a few days to an artificial light regime, with the light/dark period corresponding in length to the natural day, but with the beginning and end of the light period shifted, usually by 6 hours (see Schmidt-Koenig 1958 for details). This causes the birds to misjudge the time of the day, and as a result, the azimuth of the sun. When such pigeons are released away from their home, they show a characteristic deviation from the direction of untreated controls (Fig. 1). By thus indicating the use of the sun compass, clock-shift experiments offer an easy means to demonstrate a general involvement of compass orientation. This, in turn, allows us to decide whether or not the orientation strategy in a given case follows the 'map and compass'-model proposed by Kramer (1959).

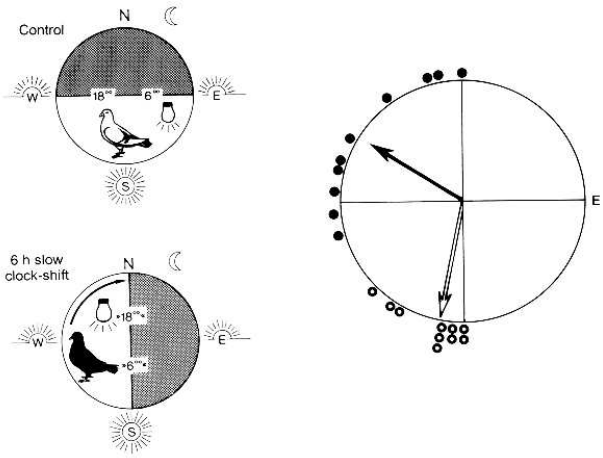

Fig. 1:
The effect of shifting the internal clock on pigeon navigation. Left: Photoperiod of the controls and for pigeons, whose internal clock is shifted 6 h backward. Right: Orientation behavior at a site north of the loft; the control birds (open symbols) head homeward, the 6 h slow shifted pigeons (solid symbols) show a typical deflection that roughly corresponds to the difference in sun azimuth between the time of the day and the time indicated by their internal clock. - Symbols at the periphery of the circle indicate vanishing bearings of individual birds, the arrows represent the mean vectors proportional to the radius of the circle. The home direction coincides with the control vector

Clock-shift experiments with homing pigeons have produced the typical deflection in all directions from the loft (Fig. 2) and at distances ranging from less than 1.5 km (e.g. Graue 1963; Keeton 1974) to 167 km (Schmidt-Koenig 1965). Thus avian navigation follows the 'map and compass'-model within the entire range studied so far, and we may conclude that the relation to home is generally established via an external reference.

The positive results of clock-shift experiments have another important implication: They exclude all navigational strategies *not* based on an external reference. This applies, for instance, to inertial navigation, i.e. dead-reckoning based exclusively on internal representations of the route, as suggested by Barlow (1964) and demonstrated for small mammals moving within the limited area of an arena (Etienne et al. 1985). Likewise, a response to clock-shifting excludes 'piloting' in the sense of orientation based solely on familiar landmarks, as proposed by Griffin (1955) and recently reconsidered as a strategy at familiar sites (e.g. Papi 1986). The available data clearly argue against such an exclusive use of landmarks. Pigeons respond to clock-shifting also at sites in the vicinity of their loft where familiarity with the terrain and the landmarks might be inferred (e.g. Keeton 1974; Schmidt-Koenig 1979), and at sites that are extremely familiar to them from more than 60 previous homing flights (Füller et al. 1983; R. Wiltschko 1991). There do not seem to be any differences in this

respect between near and distant sites, nor between familiar and unfamiliar sites: Pigeons always seem to establish their home direction first as a compass course.

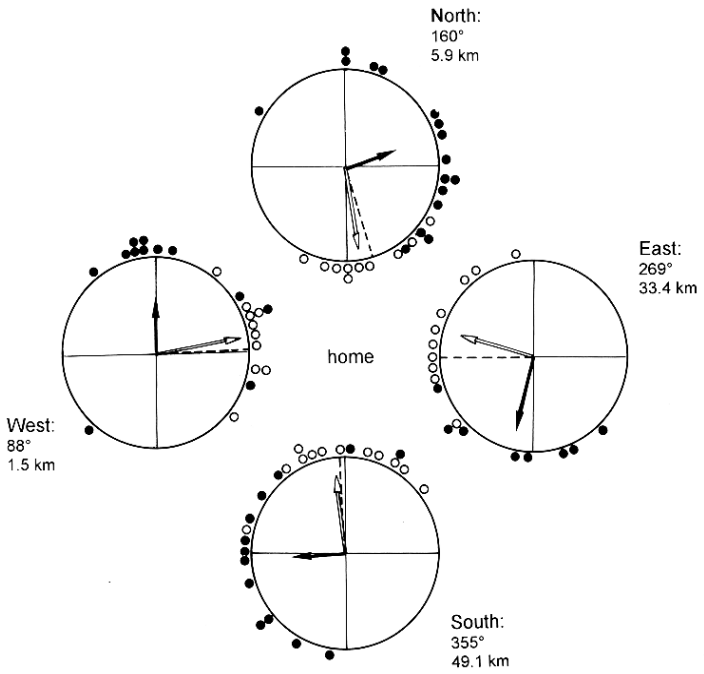

Fig. 2:
The result of shifting the pigeons' internal clock 6 h forward at sites at varying directions and distances between 1.5 km and 49.1 km from the loft, indicating that the sun compass is used. Symbols as in Fig. 1 (data from Keeton 1974).

3. Navigational Strategies

This leaves two types of navigational strategies, namely (1) the use of route-specific information in the sense that birds record the direction of the outward journey with a compass, integrating detours, if necessary, and obtain the home course by reversing this direction, and (2) the use of site-specific information whose directional relationship to the goal is known to the birds (W. Wiltschko and Wiltschko 1982). Birds have been found to use both types of strategy.

3.1. Navigation Based on Information Obtained During the Outward Journey

The use of navigational information obtained *en route* during the outward journey is suggested by a series of experiments with young pigeons that were displaced whilst in a distorted magnetic field. Birds treated this way were no longer oriented and departed in all directions (Fig. 3). The observation that the same magnetic treatment had no effect after arrival at the release site clearly shows that the treatment itself did not affect orientation, but only its application during displacement (R. Wiltschko and Wiltschko 1978). This indicates a crucial role of route-specific information from the magnetic field. Young pigeons seem to obtain their homeward course by reversing the net direction of the outward journey. This strategy has been characterized as *route reversal* (Schmidt-Koenig 1975; W. Wiltschko and Wiltschko 1982). It appears a simple, straightforward strategy; all that is needed is a functioning compass and the ability to record and process directional information, including the integration of detours. The basic computations may be complex, but the birds may be prepared to carry them out; i.e. the respective computations might represent an innate ability, thus being performed automatically.

The effect shown in Fig. 3 is restricted to very young, untrained pigeons, however. Untrained pigeons older than about 12 weeks were found to be no longer affected by depriving them of magnetic outward journey information, and neither are trained pigeons (R. Wiltschko and Wiltschko 1985). Other manipulations that interfered with the pigeons' access to navigational information during the outward journey likewise failed to affect adult pigeons (e.g. Walcott and Schmidt-Koenig 1973; Keeton 1974). This indicates a change in navigational strategy with increasing age and/or experience, which takes place in about the pigeons' third

month of life. The birds no longer rely exclusively on route-specific information, but turn to site-specific information.

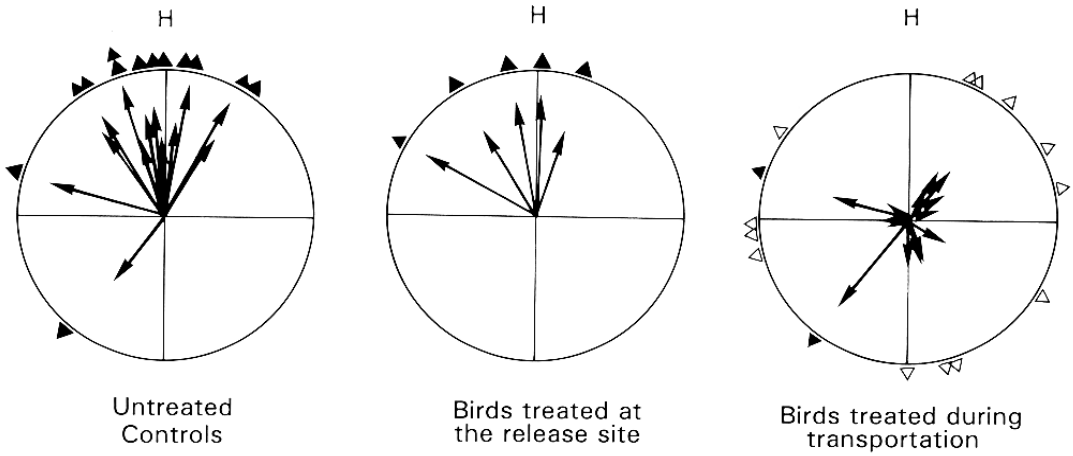

Fig. 3: Displacement in a distorted magnetic field results in disorientation in very young, untrained pigeons, indicating that these birds rely on information collected en route during the outward journey. The arrows represent the mean vectors of groups of 10 to 12 pigeons with respect to home, H; the symbols at the periphery mark the respective mean directions, solid symbol: significant directional preference; open symbol: no significant preference (data from R. Wiltschko and Wiltschko 1978).

3.2. Navigation Based on Information Obtained at the Release Site

The fact that the 'map and compass'-model regards an external reference provided by a compass as an integrated component of avian navigation implies that spatial information used for navigation is generally organized in a directionally oriented way. As a consequence, the present models of the avian navigation system assume that the birds base their navigational decision on *directionally oriented* mental representations of the spatial distribution of navigational factors, so-called 'maps' (see Wallraff 1974, 1991; W. Wiltschko and Wiltschko 1982, 1987 for details).

3.2.1. The Navigational 'Map' or 'Grid Map'

The concept of a navigational 'map' was inspired by the commonly used maps with their world-wide grid of coordinates. The idea, dating back to the last century (Viguier 1882) assumes that birds make use of at least two factors with the nature of *gradients*, i.e. with values that vary continuously in space. These factors should form some kind of a grid (Fig. 4) and must not intersect at extremely acute angles. Birds know in what directions the gradients increase and decrease and can thus derive their home course by comparing the local scalar values at their present location with the ones remembered from home. In the example in Fig. 4, the birds know that one gradient increases to the east and another to the south. If they find themselves at a location where the local values of both are lower than the home values (P_1 in Fig. 4), they know that they are in the northwest of home and have to head towards southeast.

Comparing the models of the 'grid map' with the actual findings on pigeon navigation, it becomes evident that it provides convincing explanations for some commonly observed phenomena. Pigeons are able to head more or less directly home from distant sites where all local features are unfamiliar to them, and they can do this even when they have been deprived of all known navigational information during the outward journey - this can be attributed to the gradient nature of the navigational factors. Gradients may be extrapolated beyond the range of direct experience. However, the birds have to base this extrapolation on their knowledge of the gradient directions within the familiar area. If the distribution of navigational factors is not completely regular, this might cause birds to misjudge their position and, as a consequence, depart in directions deviating from the true home course (see Fig. 4, sites P_2, P_3 and P_4).

Such deviations from home are commonly observed. Usually, they are not very large, seldom exceeding 60°. From their being attributed to unexpected irregularities in the distribution of navigational factors (see Keeton 1973; W. Wiltschko and Wiltschko 1982), it follows that they should be similar in all releases from a given location. This is confirmed by numerous sets of data. The deviations are indeed typical for each site: At some sites, the deviations are almost all to the right, at others to the left (e.g. Wallraff 1959;

Schmidt-Koenig 1963; Keeton 1973, R. Wiltschko 1993). The phenomenon is therefore referred to as 'release site bias' (Keeton 1973). Release site biases are not restricted to pigeons, but are observed in other species of birds as well (Keeton 1973, 1974). This points out that the factors causing these deviations act on the various bird species in a similar way. Apparently, at many locations, the navigational factors do not indicate the true home direction, but a direction deviating from it.

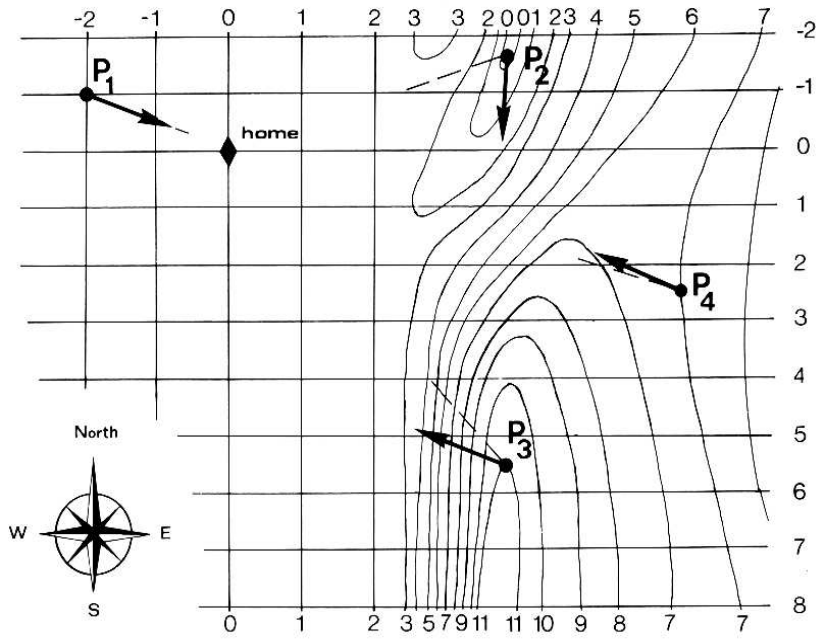

Fig. 4:
Model of the navigational 'map' or 'grid map' which is assumed to be a *directionally oriented* mental representation of the spatial distribution of environmental gradients. The isolines of two such gradients are given in relative units. Left side: at site P_1, where the gradients show a regular distribution, the birds determine their home course correctly; right side: irregularities in the distribution of gradients at P_2, P_3 and P_4 lead to initial errors, *release site biases*, which are later corrected (after W. Wiltschko and Wiltschko 1982).

Another phenomenon is the pigeons' ability to head immediately, i.e. in less than 20 seconds (e.g. Pratt and Thouless 1955) into the direction in which they will finally depart. This means that the navigational process does not require extended searching flights, and thus excludes the possibility that pigeons need to scan local gradients to learn gradient directions. Pigeons appear to have at least a rough idea about their home direction even before they start flying. When they were released from a cage with several openings, they tended to choose the ones pointing towards the direction in which they will later vanish from sight (e.g. Chelazzi and Pardi 1972; Kowalski 1994). The model of the navigational 'map' explains these findings by assuming that birds know in which direction the gradient values increase and decrease, have this information incorporated in their 'map' and thus can immediately interpret the local factors.

The model described so far refers to the type of factors and the way they are represented. The specific nature of the factors involved is still largely open. Theoretical considerations (Wallraff 1974) indicate that celestial cues, once favored (e.g. Matthews 1953), are not suitable as components of the navigational 'map', because they would require highly complex compensation mechanisms due to the rotation of the earth and the movements of the earth around the sun. Furthermore, the results of clock-shift experiments clearly show that the sun is used as a compass only (see Fig. 1,2; Kramer 1959; Keeton 1974). This leaves geophysical factors originating in the earth itself. They need not necessarily form a world-wide grid as originally proposed (Viguier 1882). As most birds move around within a limited area, regional factors might also be enlisted for navigation, provided they are available within an area of sufficient range. Presently, several factors are in discussion, among them magnetic and gravitational cues, odors, infrasound, the view of distant landscape feature etc.

3.2.2. The 'Mosaic Map' of the Home Area

In the immediate vicinity of home, the birds will be unable to distinguish the local gradient values from the home values, because the differences are below threshold. Here, the 'grid map' based on gradients is supplemented by a 'mosaic map' of landmarks, which is assumed to be a directionally oriented representation of the lay of the land with the positions of prominent local features (Fig. 5). The model of the 'mosaic map' corresponds to that of the 'grid map', with the only difference that instead of a few continuous gradients, the 'mosaic map' involves numerous separate entities whose directional relationship is familiar to the birds (e.g.

Graue 1963; Wallraff 1974, 1991; Baker 1982; W. Wiltschko and Wiltschko 1982, 1987). The features involved are believed to be mainly visual landmarks, but may include marks of other sensory qualities (see Kreithen 1978), like local sources of infrasound, magnetic anomalies etc., as well.

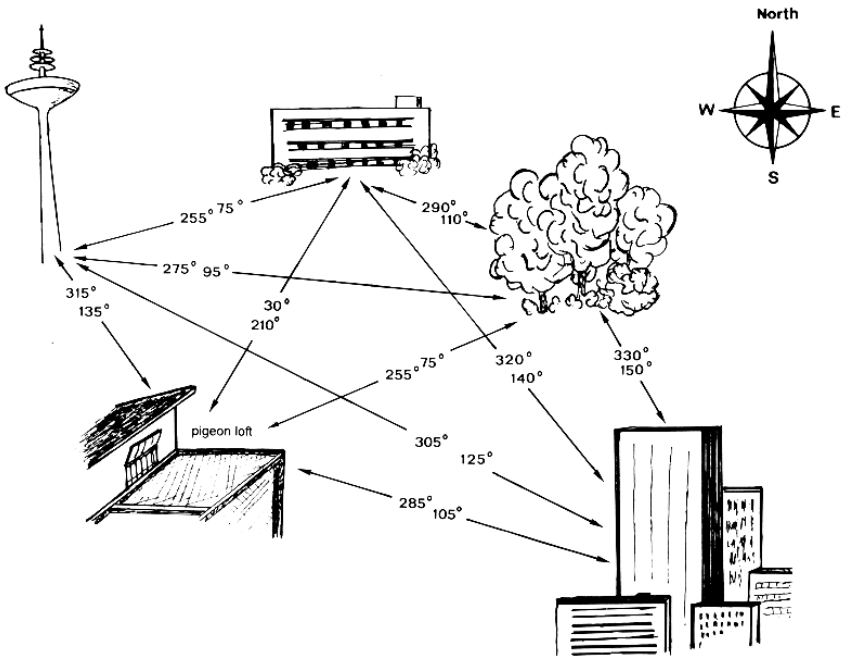

Fig. 5:
Model of the 'mosaic map' which is assumed to be a *directionally oriented* mental representation of the distribution of prominent feautures in the vicinity of home (after W. Wiltschko and Wiltschko 1982).

The use of the 'mosaic map' is assumed to be analogous to the 'grid map'; landmarks indicate *locations*, not routes. The directional relationship of these locations to the goal is known, so that the navigational system here, too, gives the direction to the goal as a compass course (see Graue 1963; Wallraff 1974; W. Wiltschko and Wiltschko 1982). However, as a consequence of being based on local features, the 'mosaic map' cannot be extrapolated. It thus includes only terrain that birds know from direct experience and, maybe, a small area beyond, as Baker (1982) suggested in his concept of the 'familiar area map'.

4. The Development of the Navigational System

This leads to the question how birds obtain the necessarily knowledge on the distribution of navigational factors in their home area and beyond. In the case of the 'mosaic map', it is obvious that the positions of landmarks and their relationship to each other and to the home site have to be learned. The same is true for the navigational 'map'. None of the known environmental gradients is completely regular; so birds have to familiarize themselves with the distribution of these factors within their home region. Learning processes, on the other hand, allow birds to include all suitable factors into the 'map' and guarantee that the navigational 'map' is perfectly adapted to the situation in the birds' home region.

4.1. Establishing the 'Mosaic Map' and the 'Grid Map'

Very little is known about the respective learning processes. The spontaneous change in navigational strategy observed in young pigeons about three months old suggests that most learning takes place during free flights at the loft. These free flights escape experimental analysis; however, some details may be inferred from the orientation behavior of pigeons of varying age and experience.

The magnetic compass is the only innate orientation mechanism of birds. The ability to perceive the course of the field lines provides young pigeons with a first means of detecting direction, which is their only available orientation mechanism when they begin to fly around at their loft and undertake their first spontaneous flights. Thus they have only one option: They must rely on directional information obtained during

the outward journey (cf. section 3.1). This allow them to determine the home course (see Fig. 3) and appears sufficient for the first short flights. Such a strategy based entirely on route-specific information has one crucial disadvantage, however: there is no possibility to correct for errors. The accuracy of navigation depends strongly on how accurately birds can measure and process directional information. Errors may balance each other to some extent, but absolute accuracy cannot be expected. Yet any mistake bears the danger that the birds might miss their home by a certain distance - this may become of crucial importance when the young pigeons extend their flights. Hence any system that allows course corrections appears advantageous. The 'mosaic map' and at greater distances the 'grid map' allow determining the home course from any given site; birds can redetermine their home course as often as they feel necessary, which increases the safety of getting home.

The use of the 'maps', on the other hand, requires detailed knowledge on the spatial distribution of the factors involved - knowledge, that is not immediately available, but must be obtained through learning processes which require a certain amount of time. We may assume that pigeons begin to establish their 'maps' as soon as they have reached a certain level of flying skill. As the young birds venture farther and farther away, they gradually become familiar with vicinity of their home. During these flights, they probably begin to establish a 'mosaic map' by storing in memory the position of prominent features of the terrain and their directional relationship to home. Later, on more extended flights, young pigeons explore an increasing area of their home region, thus enlarging their 'mosaic map' and familiarizing themselves with the local distributions of gradients as they experience increases or decreases in gradient values.

Specifically, establishing the 'maps' means that information on the route travelled is combined with site-specific information to store the site-specific information in its directional relationship to home. We assume that for the 'mosaic map', young pigeons during exploratory flights are continuously aware of the direction to home with the help of their compass mechanisms and possibly also of the distance to home; at the same time, they are alert for prominent features which they might encounter. These pieces of information are associated and stored together in memory, forming the directionally oriented mental representation of the distribution of landmarks the 'mosaic map' is assumed to be. For establishing the navigational or 'grid map', birds are assumed to proceed in an analogous way: Birds, aware of their direction of flight, register changes in gradient values encountered *en route*. This information is are incorporated in the navigational 'map' by combining changes in gradients with the current direction of flight. The observation that initial orientation of displaced pigeons is equally good in all directions suggests that the birds interpret larger differences to the home values as greater distances from home and consider the respective distances when determining their home course. It implies that not only the direction, but also the steepness of gradients is included into the 'grid map'. This gradually leads to a mental representation of the navigational factors which reflects the distribution of gradients within the home region in a realistic way.

The learning processes begin as soon as young birds fly well enough to venture away from their loft, and are promoted by experience obtained on these flights. The decreasing effect of transportation in a distorted magnetic field (R. Wiltschko and Wiltschko 1985) indicates that pigeons if left to gather their own experience, are ready to use the navigational 'map' when they are about 12 weeks old. These experiments, however, indicated considerable variability, which must be attributed to differences in how fast the 'map' develops. This is typical for all spontaneous developments. The willingness to undertake exploratory flights differs enormously between groups as well as between individuals, and this is reflected in their responses to the deprivation of magnetic outward journey information. For a more detailed discussion of the processes leading to the 'map', see W. Wiltschko and Wiltschko (1987) and R. Wiltschko (1991).

4.2. Updating the 'Map'

However, the learning processes establishing the navigational 'map' are not restricted to spontaneous flights where the birds actively control the outward journey. Apparently, pigeons can also include information obtained after passive transport, i.e. when they are released after displacement. It is a regular routine at most lofts to subject young pigeons to a training program consisting of flock releases up to certain distances in all directions, in order to substitute the extended foraging flights of wild pigeons. This gives birds direct experience with the true distribution of the navigational factors within a more extended area of their home region, and, as a consequence, leads to generally improved orientation at distant sites (R. Wiltschko 1991).

The development of the navigational 'map' must be assumed to be a continuous process that is never completed. The experience during the first months of life seems to set up a general set of rules for the 'grid map', specifying how navigational factors are to be extrapolated. But the system remains flexible, and later experiences are continuously included. This is demonstrated by a series of experiments with experienced

pigeons more than one or two years old at distant sites 120 - 200 km from the loft. The results document a continuous improvement of orientation with increasing familiarity (Grüter and Wiltschko 1990). Pigeons familiar with the distant sites from a previous release were much better oriented than birds that had the same flying experience in a different region (Fig. 6). The most interesting point, however, is that even birds that had covered 60 to 80% of the route from the test site on a previous homing flight were better oriented than the birds that had their entire experience in a different region. Knowing parts of the terrain between home and the distant site apparently helped the orientation at the distant site. This suggests that knowing the true distribution of navigational factors in the region halfway to the distant release site allowed the birds to extrapolate the local factors at the distant site more accurately than birds that did not have this knowledge (Grüter and Wiltschko 1990).

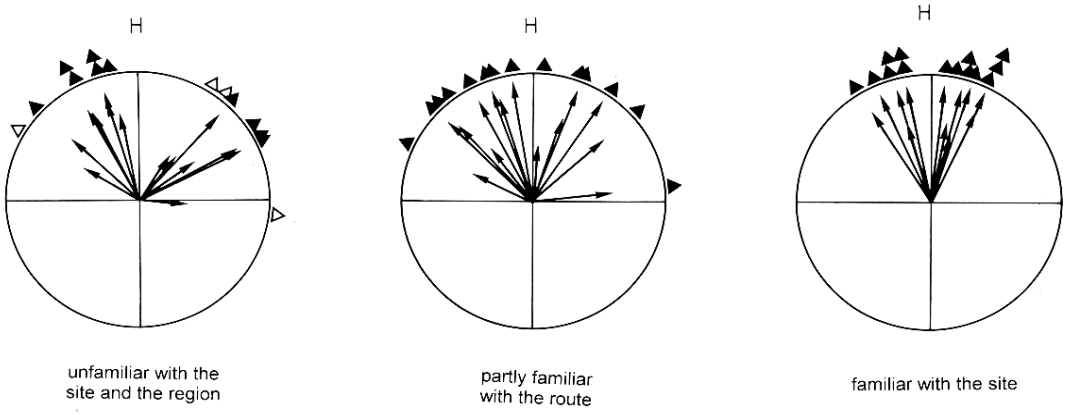

Fig. 6: Behavior at sites more than 100 km from the loft of adult pigeons with varying experience in the region of the test site. The continuous improvement of orientation with increasing familiarity indicates that old pigeons continue to incorporate new experiences into their map. Symbols as in Fig. 3 (data from Grüter and Wiltschko 1990).

Thus even pigeons several years old extended their 'map' and included new information when they found themselves in a region where they had never been before. Details on the processes updating the navigational 'map' are not known; one would tend to assume that they are similar to the ones establishing the 'map' during the birds' first year. However, the processes updating the 'map' appear to modify the 'map' only locally in the region where the pigeons have had the new experience (see W. Wiltschko et al. 1984). This guarantees a highly efficient 'map' for an extended area, taking regional and perhaps even local irregularities in the distribution of the navigational factors into account.

4.3. Allocentric 'Maps' Allowing Free Movements

The learning processes establishing the 'maps' center around the bird's home, in the case of pigeons, the loft. Yet the resulting 'maps' are not assumed to be 'home-centric' in the sense that movements are restricted to returning to the loft. Rather, they represent allocentrically organized representation of environmental features (Thinus-Blanc 1988) that allow direct movements between arbitrary sites. 'Home' may represent a very prominent site, but functionally, it should be just one site among others. Birds should be able to determine the course from any site to any other site, provided the coordinates of the goal are known.

Within the home area, such free movements between multiple goal sites are usually implied, even if they escape experimental testing. With respect to the navigational 'map', an interesting experiment by Baldaccini et al. (1976) suggests that birds can indeed head for more than just one goal. Old, experienced pigeons were moved into a new loft about 90 km from the old one and kept there in an aviary. When these birds were afterwards released from sites between their old and new home, they departed heading towards, and returned to, the loft that was *closer*, irrespective of whether it was the old or the new loft. This indicates that the pigeons were able to determine the course toward two goals and choose between them. At the same time, this experiment has another important implication. As the birds were able to compare the distances from the release site to the respective goals, they must have had quantitative information on distance available. This implies that the navigational 'map' represents the distribution of gradients roughly true to scale.

5. A Flexible, Efficient System

There is a fascinating variety and flexibility in the ways birds utilize potential navigational cues. Starting out with the ability to distinguish directions, pigeons develop a highly efficient navigational system that allows them to navigate within the range of several hundred kilometers. Some seabirds can navigate even within a range of more than thousand kilometers (see R. Wiltschko 1992 for summary). The navigation system makes use of a variety of factors whose existence is reliable, but whose specific manifestation cannot be anticipated. For example, it is absolutely certain that birds will encounter suitable features and factors to be incorporated into the 'mosaic map' and the 'grid map'; however, neither the specific nature and the position of landmarks, nor the regional distribution of gradients can be predicted. Hence, to make use of these factors, animals have to obtain the information on their distribution by individual experience.

A very efficient way to do this is pre-programmed learning during the birds' early youth. Nature supports such learning processes by a sensitive period, during which the young animals pay increased attention to the relevant factors and search actively for the relevant information. Also, specific brain areas are prepared to store that particular information. Although there is no direct evidence, it is assumed that the processes establishing the 'maps' show similar features. During their first few months of life, young pigeons show a much greater readiness to undertake extended flights than later in life. These spontaneous trips may be exploratory and thus form the basis for establishing the navigational system (see also Baker 1982 for discussion). The respective learning processes may be similar to those establishing human speech, where young children at a certain age are eager to learn to speak and will pick up any language they hear.

Since the learning processes guarantee that the resulting mechanisms are perfectly tuned to the situations in the bird's home region, regional differences in the navigational 'map' may be expected. These may involve the nature of the gradients used as well as how the various navigational factors are rated and ranked. Differences in response to identical experimental treatments of pigeons in different countries (e.g. W. Wiltschko et al. 1987) and different behavior of pigeons from different lofts at certain sites (e.g. Walcott and Brown 1989) have been documented. These differences can be attributed to differences in experience and thus may reflect differences in the way the 'map' developed (see W. Wiltschko et al. 1991 for a detailed discussion).

In all navigational mechanisms, compass orientation plays a fundamental role, as the 'maps' are directionally oriented representations of the environment, indicating directions as compass courses. Compass orientation thus forms the backbone of the birds' representation of space. This might not only be true for homing over long distances, but also for small-scale orientation tasks. Recent experiments suggest that the same principles apply to locating specific places within the limited space of an aviary (e.g. W. Wiltschko and Balda 1989; Sherry and Duff 1996). For birds, spatial information seems to be generally represented in a directionally oriented way over the entire range of distances, from several hundred kilometers to a few meters within the home area - this may be the general way how birds code space.

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