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1

Orientation and Navigation Cues

Abstract For proper orientation and navigation, animals use a variety of reference cues. These cues may be of different types, such as visual objects, smells, or even the geomagnetic field, and may require different senses to perceive these navigational markers. The importance or choice of a particular cue or cues may depend on the navigational task in question, starting from short-range navigation that may apply for an area of just a few meters to long-distance navigation during, say, bird migration. The conditions under which animals navigate are also diverse, so that a navigating subterranean mammal underground is expected to employ other senses than a bird looking for a hidden food cache, and birds migrating at night probably rely on a navigation strategy slightly different to that employed by those migrating during the daytime. This chapter describes what cues animals use for orientation and navigation, and what senses they employ in any particular case. Among the conventional senses described in any animal physiology book, the nature of the enigmatic hypothetical magnetic sense and its applications in animal navigation are discussed.

1.1 Magnetoreception

1.1.1 *Earth's Magnetic Field*

Earth's magnetic field, also called the geomagnetic field, has been shown to constitute a significant orientation and navigation cue for many migrating animals. It is generated deep in the Earth's core, and consists of two major components – dipole and non-dipole. The dipole component, as can be inferred from its name, creates two poles at the surface of the Earth that are geographically close to the rotational poles, also known as geographic poles of the planet, so that the vector of the field equal intensity lines at the South Pole (or the Antarctic Pole) is directed upwards, making the lines leave the surface of the Earth. Then the lines curve

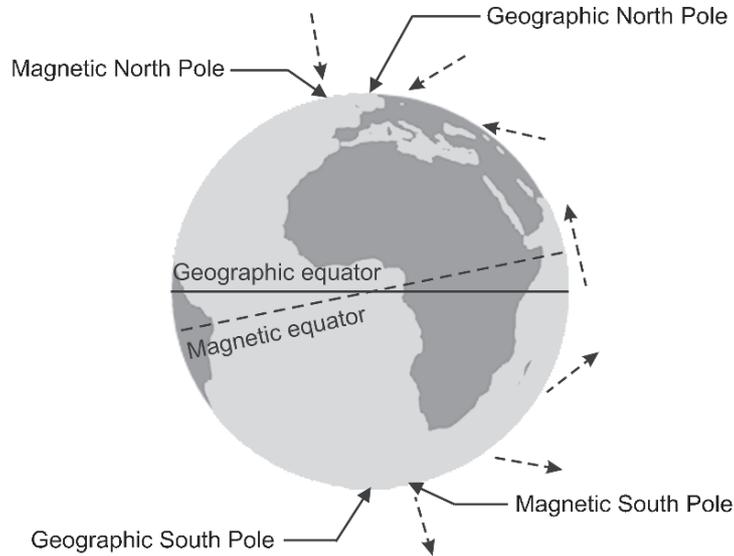


Fig. 1.1 Schematic view of the geomagnetic field. *Dashed arrows* indicate the geomagnetic field lines with different angles of inclination across the surface of the Earth. The inclination distribution of the western hemisphere (not shown) is symmetrical (adapted from Wiltchko and Wiltchko 1996)

around the planet and re-enter the ground at the Arctic Pole, being parallel to the Earth's surface at the magnetic equator. So, at different latitudes, the magnetic vector is characterized by different inclination, or dip, of the magnetic lines as shown on Fig. 1.1.

What is this vector? At the Earth's surface, the geomagnetic field vector (usually denoted by F) can be decomposed into three constituent vectors. Taking the point of origin as the origin of a Cartesian coordinate system we can decompose F into the x -axis that coincides with the meridian towards the north, the y -axis directed along the geographic parallel towards the east, and the z -axis that is vertical at the point of origin and positive downwards. The three components of the geomagnetic field vector, thus, will be X , Y , and Z directed along these axes. In that way the geomagnetic field vector will be

$$\sqrt{X^2 + Y^2 + Z^2} = F \quad (1.1)$$

The horizontal component (H), respectively, will be defined as

$$\sqrt{X^2 + Y^2} = H \quad (1.2)$$

Thus, inclination of the geomagnetic field lines is the angle between the magnetic vector and the horizon. Roughly, lines of equal latitude are parallel and have the same inclination; although in reality equal inclination contours on the Earth's surface are somewhat curved and do not coincide precisely with any given latitude.

Corresponding magnetic and geographic poles don't coincide geographically, and make some angle between meridians (true geographic northward course) and the line towards the magnetic North. This angle, or declination (actually, the angle between H and the x -axis), is negligible at low latitudes and increases to become substantial at the poles (for more details see Lanza and Meloni 2006). The intensity of the Earth's magnetic field ranges from about 60,000–65,000 nT at the poles to near 25,000–30,000 nT at the magnetic equator (Wiltchko and Wiltchko 1996; Fischer et al. 2001). It should be noted that some authors use Gauss (G) as units referring to the magnetic field intensity, while others utilize the conventional SI system and operate with Tesla (T). So, when different works are analyzed, it is useful to know that $1\text{ T} = 10,000\text{ G}$. Total intensity of the geomagnetic field gradually changes across the surface of the Earth by approximately $3\text{--}5\text{ nT km}^{-1}$ from the magnetic equator to the magnetic poles. Its inclination shift makes about 0.01°km^{-1} ranging from 90° at the magnetic poles to 0° at the magnetic equator (Fischer et al. 2001).

Overall, Earth's magnetic field is fed from two main sources: Earth's core deep inside the planet, and the crust forming the planet's surface. The molten core produces a bicomponent field consisting of the dipole and non-dipole constituents.

The dipole part dominates, comprising near 90% of the total geomagnetic field. It is important to notice that these characteristics are rather a planet-scale generalization, and the real pattern of the geomagnetic field involves various deviations in time and space.

Daily variations in Earth's magnetic field intensity may range from 30 to 100 nT. Local magnetic anomalies caused by specific rock compositions may produce differences from the normal intensity expected for a given geographical location, in some rare cases reaching up to 1,000 nT (though in most cases they are significantly smaller). Furthermore, the so-called magnetic storms, which are irregular fluctuations of the geomagnetic field caused by the solar wind and flares, are common as well (Wiltchko and Wiltchko 1996).

Electric processes in the ionosphere, such as strokes of lightning, are also known to interfere with Earth's magnetic field, and represent yet another source of deviations. In addition to these short-term alterations, the geomagnetic field is also known to be dynamic on longer time-scales. For instance, it is subject to gradual secular variations. On a significantly longer timetable stretching from 100,000 to 1,000,000 years, the field may even reverse its polarity to the opposite. During such reversals, the dipole component gradually fades away during some 1,000 to 10,000 year period (up to 100 nT per year; Skiles 1985) until it completely disappears, and reappears later with switched poles. In contrast, the non-dipole component changes over time but doesn't ever vanish (for more detailed characteristics of the geomagnetic field and its relevance to living organisms see Skiles 1985; Walker et al. 2002; for a thorough description of the geomagnetic field see Lanza and Meloni 2006).

1.1.2 Models of Magnetoreception

The first ideas that birds might use Earth's magnetic field for orientation were expressed in the middle of the nineteenth century, when von Middendorf (1859) proposed what we now call the "animal magnetic compass." Later, in 1882, Viguier suggested that displaced homing pigeons, *Columba livia*, use local intensity and inclination of the geomagnetic field to determine their home direction. Nevertheless, experimental evidence supporting the hypothesis didn't appear until the mid-twentieth century, when Wiltschko and Merkel (1966) demonstrated in laboratory conditions, in the absence of any other cues, that European robins, *Erithacus rubecula*, placed in an artificial magnetic field changed their orientation according to shifts in the direction of the external magnetic field. Subsequent studies have supported the results of these experiments, and revealed Earth's magnetic field to be a common and reliable source of navigational information for migrating birds as well as many other animals.

Among the modern models proposed to explain the process of magnetoreception in animals, the chemical mechanism (based on radical-pair reactions) and the use of magnetite particles located in animal bodies seem to be the most substantiated and accepted ones. So here we will devote our major attention to the description of the phenomenon based on these two hypotheses, as more and more experimental evidence supporting them both continues to emerge. Earlier researchers considered the models as incompatible and "competing" ones, but now much evidence has been obtained suggesting (or rather predicting) that vertebrates might use both mechanisms simultaneously, or as alternate ones.

However, in addition to these two, it has been suggested that some groups of fishes employ yet another mechanism based on the electromagnetic induction phenomenon; but no conclusive evidence supporting this hypothesis has been presented so far (Lohmann and Johnsen 2000).

Unfortunately, despite the huge amount of experimental data contributing to our understanding of the animal primary magnetoreceptor structure, location, and function, so far we do not have any definite picture of the design of this sense in any animal.

Before discussing different models of the magnetic sense, it should also be figured out what types of orientational information an animal could derive from the magnetic cues. Migrating animals, in principle, need primarily two types of information: they need to know (1) their relative location, and (2) the direction to follow towards their selected destination. These two types of senses based on the geomagnetic field are hypothesized to function respectively as the "magnetic map" sense – identification of present position within an area in question – and the "magnetic compass" – establishing the proper direction towards a destination (Lohmann and Johnsen 2000; Gould 1982). Some features, such as inclination and intensity of the geomagnetic field, vary throughout Earth's surface with some regular pattern, and could possibly be used by animals to obtain some navigational information. So, let us look in more detail at how it could possibly function.

Radical Pairs Mechanism: A Chemical Compass

Actually, there are several widely discussed hypotheses for the function and structure of the putative chemical mechanism of magnetoreception. According to Leask (1977), magnetoreception probably involves a radio-frequency resonance process, in which the geomagnetic field lines alignment influences a hypothetical triplet state of the electron spins of the visual pigment rhodopsin. The proportion of triplet-state products in the underlying reaction, and thus the effect of a magnetic field, is determined by the characteristics of differently polarized light resulting from the radiative decay of the suggested triplets to the ground state (see also Deutschlander et al. 1999a). This so-called “optical pumping” mechanism, however, has some serious limitations. Among other constraints is the fact that it requires internal energy in the radio-frequency range, which has not been found to occur in biological systems (Edmonds 1994).

Hong (1977, 1995) suggested a magneto-orientation effect of rhodopsins, which has been found to occur at magnetic field strengths of 1,000 times the Earth’s magnetic field.

Edmonds (1996) has developed still another hypothesis, which theoretically resolves some discrepancies between the adherents of magnetite-based and chemical models. In his model, single-domain magnetite particles able to rotate freely in a photoreceptor’s internal liquid-crystal medium can modulate the intensity of light that reaches the photopigment-containing component of the receptor. According to the author, the single-domain needle-shaped particles of magnetite align corresponding to the alignment of the lines of an external magnetic field, and by doing so they change the angle of photopigment molecules. Indeed, it has been shown, for example, that absorption efficiency of some elongated light-absorbing molecules is dependent on the angle at which light descends upon them (Fein and Szuts 1982). In birds, as well as in some other vertebrates, photoreceptors contain oil droplets with carotenoid pigments, which might possibly serve for Edmonds’s model (Bowmaker et al. 1997; Goldsmith et al. 1984).

However, one of the most experimentally supported hypotheses has arisen based on the early studies of, and subsequently introduced by Schulten et al. (1976), Schulten and Weller (1978), Schulten (1982), Schulten and Windemuth (1986), Werner et al. (1978), and Ritz et al. (2000). This hypothesis suggests that magnetic compass orientation is based on a radical-pair reaction, including the influence of magnetic fields on the singlet-triplet recombination rates. The conjecture was proposed in view of the dependence of the product ratio of some red-ox reactions on the alignment of weak magnetic fields applied.

Therefore, the suggested radical-pair mechanism, according to the authors mentioned, is based on a red-ox reaction that takes place in the photoreceptors of the animal eye and is stimulated by photon-induced excitation of the molecules involved. The simplest principle of the mechanism encompasses a three-step process (Ritz et al. 2000). Figure 1.2 shows a simplified scheme of the reaction. During the first step, a donor molecule excited by light (D^*) transfers an electron to an acceptor molecule (A). This leads to formation of a pair of radicals $D^+ + A^-$. Under,

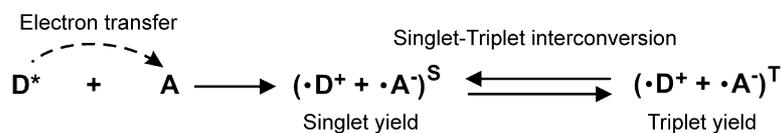


Fig. 1.2 Reaction scheme of interconversion of a radical pair with resulting magnetic field-dependent products (adapted from Ritz et al. 2000)

but not limited to, photon-induced electron transfer conditions, the radical pair will transform into the so-called spin-correlated singlet or triplet states (which are two distinct states of the electron spins able to inter-convert depending on the presence and characteristics of a magnetic field). Excitation of the molecules in this case is hypothesized to result either from direct interaction of the donor with a photon, or by photon-induced generation of an excited state in the photoreceptor and subsequent transition of excitation to the donor molecule. Normally, the components of the red-ox reaction (the donor and the acceptor molecules) will be in singlet states before electron transfer, forming an overall singlet population. So, at this first step, we have a mostly singlet population of pairs of radicals $^{\text{S}}(\text{D}^+ + \text{A}^-)$.

In the presence of a weak magnetic field, interconversion between singlet and triplet states of the radical pair will take place: $^{\text{S}}(\text{D}^+ + \text{A}^-) \leftrightarrow ^{\text{T}}(\text{D}^+ + \text{A}^-)$. This process constitutes the second step, and is highly dependent on the characteristics (intensity and direction) of the lines of a surrounding magnetic field.

To clarify the terms “singlet” and “triplet”, they can be simply understood as representations of the nuclear magnetic resonance (NMR) spectrometry readings pattern, and relate to corresponding energetic states of the electron and nuclear spins. The effect of multiple splitting of spin spectrum lines was first observed by Pieter Zeeman on hydrogen electron spins, and is now called the Zeeman effect. An external magnetic field causes precession of the nuclear spin due to partial spin polarization. The nuclear spin polarizes a nearby electron spin by means of the so-called hyperfine interaction, and this polarization is transferred to electrons of other atoms, which in turn polarize their nuclei. This process is known as “indirect nuclear spin-nuclear spin coupling” (Wasylishen 2002). Splitting of the spin spectrum lines takes place during this process.

According to the hypothesis under discussion, this point (singlet-triplet interconversion) is crucial for the putative chemical magnetic compass, because the parameters of an external magnetic field at this stage of the reaction influence the singlet–triplet ratio among the final products.

In the final step, singlet and triple pairs will react and a back transfer of electrons from the acceptor to the donor radicals will occur, giving distinct products – pairs of molecules in either triplet or singlet state. The ratio of these molecules will correspond to the ratio of singlet and triplet radicals on the previous stage. This reaction decreases the population of radical pairs at respective rate constants k_{S} and k_{T} (for singlets and triplets respectively).

The triplet yield, as a result of the third stage of the basic reaction, has been hypothesized to be crucial for detection of the geomagnetic field lines direction, inclination, and intensity by animals.

The singlet–triplet ratio resulting from the final stage of the reaction has been found to have several properties that are in accordance with the hypothesis. Experiments show that the final triplet yield is proportional to the value of k (see above). Also, the triplet yield increases with the increase of a weak magnetic field intensity applied in the range from 0 to 50,000 nT (the geomagnetic field ranges from 25,000–30,000 to 60,000–65,000 nT), and this yield increase is higher and steeper at higher k -values (Ritz et al. 2000). Further, the triplet yield has been shown to be dependent on the angle between the magnetic field lines applied and the z -axis (normal) of the radical pair (for explanation see below). As presented in Schulten (1982), the maximal triplet yield is observed when the z -axis of the radical pair is parallel or antiparallel to the direction of the magnetic field lines applied. This suggests that some animals may be able to derive the direction of the geomagnetic field lines on the north–south axis but unable to distinguish between the northward and the southward directions, which has obtained plentiful experimental proof, at least with regard to birds (e.g., Wiltschko and Wiltschko 2001b; Wiltschko et al. 2004). And finally, the triplet yield has been demonstrated to depend on the inclination of an external magnetic field (Ritz et al. 2000), suggesting that animals may be able to detect the local inclination, which appears to give them latitudinal as well as directional information. This last property is suggested to provide animals with the ability to distinguish between “poleward” and “equatorward” directions (requires detection of local magnetic inclination) but not between “north” and “south” (requires determination of local polarity of the geomagnetic lines). This idea was broached by several investigators (Light et al. 1993; Wiltschko and Wiltschko 1996; Ritz et al. 2000) and has been supported by experimental evidence.

But regardless of the propitious properties of such reactions, the red-ox system has to meet at least one basic condition if it is to provide orientational information for animals. This condition is that the molecular system involved must have a fixed position in relation to the sensory organs employed. In addition, the system obviously has to influence the sensory signal transduction pathways of the organ.

The visual rod and cone receptors located in the eye’s retina, which contain light-sensitive pigments on its membranes oriented tangentially to the retina, are supposed to host the reaction. The recently discovered photopigments called cryptochromes, which appear to have some necessary features, are also assumed to participate. Positional fixation of the pigments hosting the reaction is expected to result in that any change of the head position of an animal alters the direction of the reaction components’ z -axis (which is a fixed axis tangential to the retina) in relation to the geomagnetic field lines.

It should be mentioned, however, that vision is not necessarily the only perception system that could be responsible for magnetoreception. Ritz et al. (2000) suggest, and stress it, that other systems, such as olfactory or tactile senses, could qualify as well. This suggestion is particularly interesting in view of the fact that

some vertebrates (namely loggerhead, *Caretta caretta*, and leatherback, *Dermochelys coriacea*, sea turtles, blind mole rats, *Spalax ehrenbergi*, the mole-rats of the genus *Cryptomys spp*, etc) have been shown to use the geomagnetic field in their orientation even if light is not available (Light et al. 1993; Lohmann and Lohmann 1993; Marhold et al. 1997; Kimchi and Terkel 2001; Thalau et al. 2006).

Nevertheless, the best-developed concept of orientation with the help of a chemical compass suggests that the underlying red-ox reaction takes place in the eye (Ritz et al. 2000). The eye is convenient as a model, since so far a great deal of experimental evidence has been collected on light-dependent magnetoreception, and it is easy to test compatibility of the results of these experiments with the hypothesis.

To illustrate the concept, the bird eye is taken as an ideal sphere, with a pinhole opening on the front side and the retina scattered uniformly through the hind inside wall of the eye as shown on Fig. 1.3. The photoreceptors in the retina are assumed to be normally oriented to the center of the eye. It is not exactly the case in nature, but still close to this, and this ideal model can serve for purposes of illustration. Further, if we use some speculative eye placed in the center of the head (and in front of it), we will have the line connecting the infinitesimal opening of the eye and its center as an axis reflecting the orientation of the head. Ritz et al. (2000) depict the bird's zone of vision, for purposes of simplification, as if it looked as a totally gray even pattern with an increased color density within a black circle in the center of the vision zone. Figure 1.4 shows a schematic illustration to the concept. If we

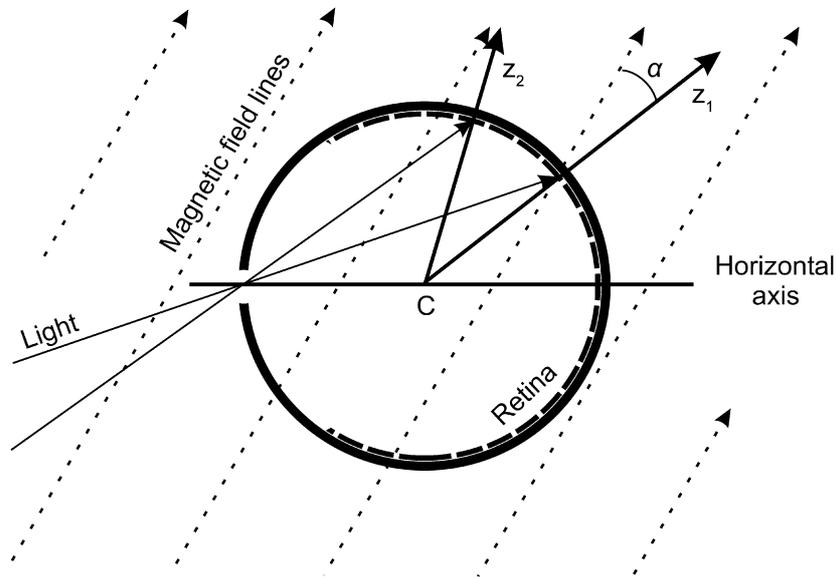


Fig. 1.3 A model of the avian eye used for describing the principle of visual pattern modulation based on the radical pair mechanism. C means the geometric center of the sphere; z_1 and z_2 arrows are axes oriented normally to the retina (adapted from Ritz et al. 2000)

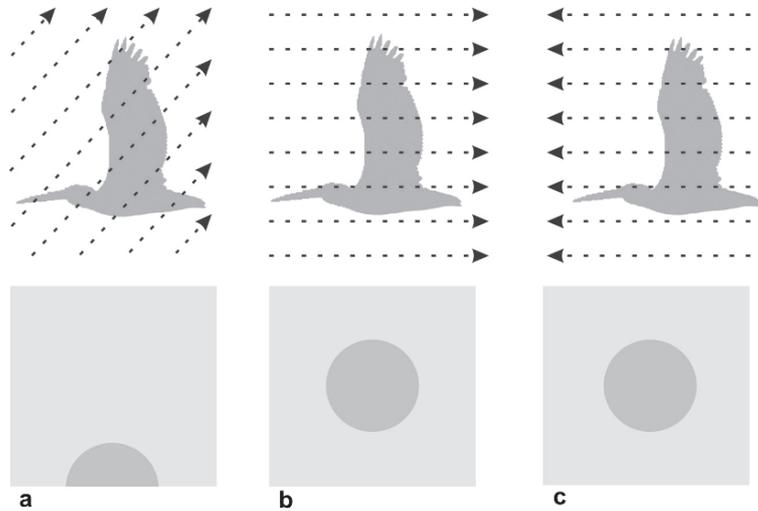


Fig. 1.4 The principle of visual pattern modulation on the avian retina (*light gray rectangles*) by the geomagnetic field (*dashed arrows*). The position of the modulated pattern (*dark gray circles* on the retina) depends on the inclination (compare **a** and **b**) but does not depend on the polarity (compare **b** and **c**) of the geomagnetic field lines (adapted from Ritz et al. 2000)

assume the total vision zone to fit to the area of the retina, then the dark circle will relate to the part of the retina which is oriented as much as possible normally (parallel or antiparallel, see below) to the direction of the magnetic lines. The bigger the angle between magnetic lines and the z -axis of the receptor, the paler the corresponding region is. Higher intensity of the color of certain regions, in view of the radical-pair reaction mechanism, corresponds to higher triplet yield in receptors belonging to this region compared to “pale” areas. The idea is that the proportion of triplets resulting from the radical-pair reaction is a factor that modulates visual signals perceived by the bird’s eye. Therefore, it has been hypothesized that due to the influence of a magnetic field in the way just described, different regions of the retina will perceive light signals differentially depending on the position of the head in relation to magnetic field lines. The representation in monochromatic gray is just made for the sake of simplification, as the real pattern might be much more complex. Therefore, by reasoning from the illustration it is possible to assume that if a bird is flying parallel to the horizon the dark circle will be located on the retina up from its center, and the bird will see it down from the center (due to upside-down turning in the visual analyzer). The degree of this displacement downwards will depend on the inclination of the local geomagnetic lines.

However, this is just how we represent it, because in real life the pattern might be quite different. But still, modulation of visual signals by the products of the radical-pair reaction seems possible, though so far we don’t know exactly how it works or, literally, how it makes a bird or any other animal feel.

Assuming the aforementioned, we can figure out a hypothetical representation of the inclination compass, which is in accord with the tentative evidence obtained on representatives of some groups of animals.

One more illustration closer to the real pattern can be produced provided that most of the time (especially the period related to flight) birds try to keep their heads horizontally (see Fig. 1.5). Heading in different directions in the horizontal plane, a bird gets, again, similar differences in triplet yield, which, in its turn, will also produce visual patterns of differing intensities moving horizontally across the retina from one side to the other in accordance with the turns of the bird's head, thus providing the bird with compass directions.

In addition to inclination, there is another parameter of the geomagnetic field animals are found to be sensitive to – intensity. As has been shown experimentally (Wiltschko and Wiltschko 1972; Wiltschko 1978), birds' magnetoreception is well tuned to the ambient geomagnetic field (30,000–60,000 nT). It has been revealed that birds are well oriented only in the range close to $\pm 30\%$ of the local geomagnetic field intensity of the territory they reside on, and fail to orient when the parameter reaches far beyond these values. However, some adaptation mechanism has also been revealed. After 3 days of acclimatization, the birds gained the ability

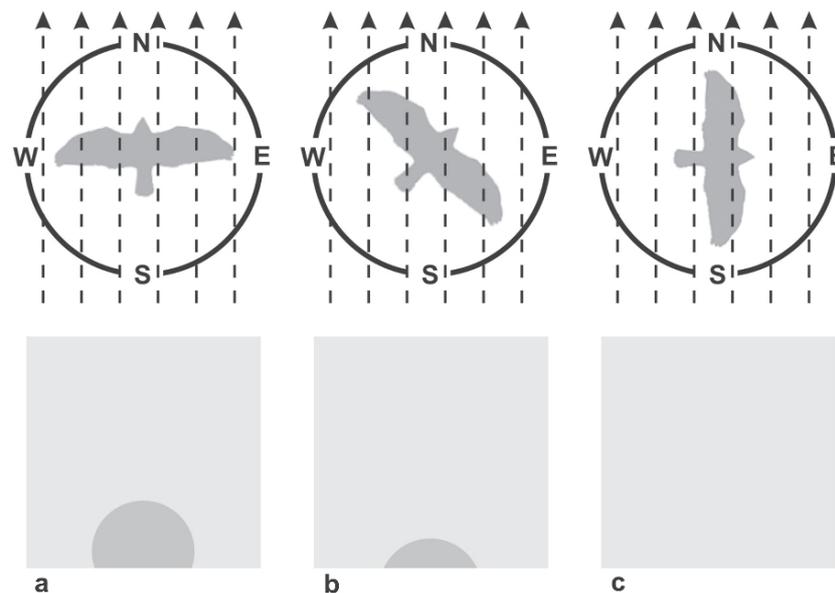


Fig. 1.5 Hypothesized visual pattern modulation in a bird flying parallel to the horizon and looking in different directions. The maximal visibility of the modulated pattern (*dark gray circles*) will be achieved by flying northwards (**a**) or southwards (reversed: **a**). The total area of the circle will depend on local magnetic inclination. Once a bird turns in other directions (**b** and **c**), visibility of the visible modulated area will decrease in size depending (compare **a**, **b**, and **c**) on the compass course (adapted from Ritz et al. 2000)

to orient in field intensities far outside the normal range of the local ambient field, e.g., 16,000 up to 150,000 nT, though they remained unable to orient at an intermediate value of 81,000 nT (Wiltschko 1978). Ritz et al. (2000) suggested a possible explanation of this phenomenon by assuming that different field intensities could produce differing modulated vision patterns in the bird eye. They presumed that the visual circle patterns generated by magnetic fields would possibly be different at varying field intensities, and would differ not only in color intensity but in structure as well, e.g., appearance of additional rings and so on, as shown on Fig. 1.6. Certainly, from this point of view, the intermediate values of the field strength that disoriented the birds might have produced some pattern that was quite “unfamiliar” to the birds. Placing birds back in the previous normal (or “familiar”) intensity conditions afterwards didn’t prevent their orientation.

Another point of consideration is location of the process in the body of vertebrates and the nature of the receptors involved. Several possible candidate receptors have been proposed. Ritz et al. (2000) suggest that virtually any sensory system could be involved, implying that the radical-pair mechanism and the excitation of the reaction components engaged must not necessarily have light-induced origin. Other types of signals subject to nervous transmission could possibly qualify as well. Leask (1977) and Hong (1977, 1995) suggested that rhodopsin participates in magnetoreception. In addition, it has recently been discovered that cryptochromes, a novel class of photoreceptors, are present in mammalian and bird eyes, and they can also be considered as candidate host receptors for the reaction.

To qualify for possible magnetoreceptive function, a receptor must meet several basic requirements. According to Ritz et al. (2000), these would include the following: (1) the magnetoreceptor should contain a pair of molecules that are able to react with the resulting pair of radicals, and the output of this reaction must be dependent on weak magnetic fields, (2) the magnetoreceptor should be linked to a photoreceptor (in case the visual system is involved), starting a radical-pair reaction after excitation by light, and it also should be connected to a signal transduction pathway in the nervous system, and (3) the receptors should be arranged in an ordered way, with a wide angle of orientations of different receptor units for proper spatial (compass) representation.

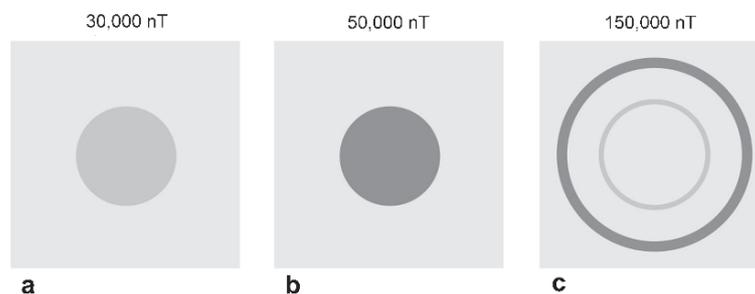


Fig. 1.6 Putative visual modulation patterns (*circles*) in the avian retina (*light gray rectangles*) depending on the ambient magnetic field intensity (adapted from Ritz et al. 2000)

Cryptochromes present in the mammalian (for review see Cashmore et al. 1999) and avian (Möller et al. 2004) eyes have several features suggesting their possible role in magnetoreception through the radical-pair mechanism. It has been shown that cryptochromes are involved in regulation of animal circadian rhythms, and that circadian rhythms are affected by magnetic fields (see Phillips et al. 2001; Moore-Ede et al. 1992). Cryptochromes appear to have evolved from the photolyases (Cashmore et al. 1999) – a type of DNA repair protein removing Pyr–Pyr dimers. They contain two cofactors – the flavin FADH⁻ and a chromophore. 300–500 nm light excites the chromophore, and this excitation transfers to FADH⁻ which, once excited, transfers an electron to a Pyr–Pyr dimer, resulting in the formation of two radicals – neutral FADH and negative Pyr–Pyr. Pyr–Pyr is an unstable radical, and splits with a back electron transfer event (Sancar 1994; Ritz et al. 2000). So it is suggested that cryptochromes, being highly homologous to photolyases, may also participate in some radical-pair reactions (Ritz et al. 2000). It has been shown on different groups of vertebrates that cryptochromes are expressed in the inner nuclear layer of the retina, where they are in the close vicinity of the large ganglion cells projecting (by their axons) into the nucleus of the basal optic root (nBOR) known to respond to magnetic field stimuli (Miyamoto and Sancar 1998; Semm and Demaine 1986). Moreover, in a recent study of cryptochromes in the eyes of garden warblers, *Sylvia borin*, at least two types of cryptochromes (CRY1 and CRY2) were detected in the ganglion cells which show high level of neuronal activity at night (the time when the warblers perform their migration). In addition, the study revealed a striking difference between migratory and non-migratory birds in expression of CRY1 in the large displaced ganglion cells known to project in the area of the brain where magnetically sensitive neurons have been detected (Mouritsen et al. 2004a).

In the context of the putative magnetosensitive role of cryptochromes, an interesting brain area has been found in birds. This area demonstrates activity during night vision in migratory birds, and is called Cluster N (Mouritsen et al. 2005). This cluster of neurons is located at the dorsal surface of the brain, in close proximity to a visual pathway. If bird eyes are capped, the structure stops demonstrating activity. Moreover, so far it has not been found in non-migratory species. A further study (Heyers et al. 2007) employing simultaneous tracing of retinal projections to the brain and connections innervating Cluster N has revealed colocalization of the neuronal tracers in the visual thalamus. This study has detected that Cluster N receives inputs through the thalamofugal visual pathway, and thus demonstrates the connection between the retina and Cluster N through the thalamus, suggesting that Cluster N is at least partially located in the visual wulst – the telencephalic termination area of the thalamofugal pathway which transfers visual signals from the retina to the forebrain. Therefore, there may be a system of magnetic signal transfer and processing based on the scheme just described, and cryptochromes (based on the whole body of research) are good candidates for the primary magnetoreceptors within it.

Birds have several classes of single cones and one class of double-cones in their retina. The role of the double cones has not yet been clearly established. Therefore,

there is an assumption that these structures might possibly be involved in magnetoreception (Beason and Swali 2001). Nowadays, there is evidence that chemical and/or possibly other types of magnetoreception are connected with the pineal gland in birds, e.g., pied flycatchers, *Ficedula hypoleuca* (Schneider et al. 1994), and amphibians, e.g., eastern red-spotted newts, *Notophthalmus viridescens* (Phillips et al. 2001).

Schneider et al. (1994) divided pied flycatchers into three groups. The first group served as an untreated control, while the other two had undergone pineal ectomy. Then, one of the pineal-removed groups was regularly injected melatonin – the main hormone of the pineal gland. Later, during the following autumn migration, the ability of the birds to orient in a weak magnetic field was tested. The results showed that the control group and the pineal-ectomy group that had been injected melatonin were well oriented in their normal autumn migration direction, and the groups didn't differ in their behavior, while the last group of pineal-removed birds that lacked melatonin was disoriented. The findings indicated the crucial role of the pineal gland and melatonin in the normal migratory orientation of pied flycatchers and, consequently, implied that this function of the gland during magnetic navigation process might be similar in other vertebrates as well. However, in this particular case the results should not be interpreted as evidence of direct involvement of melatonin in the process of magnetoreception, since the results might have been caused by some still not clearly understood disorders in day–night rhythm perception by the treated birds, which, for example, might have affected their motivation, as the authors report a little less vigorous migratory restlessness in melatonin-deficient birds.

Later, Phillips et al. (2001) studying eastern red-spotted newts developed the approach further. In the newts, the shoreward migratory orientation had previously been shown to operate with the use of celestial and magnetic cues and to be dependent on the wavelength of incident light (Phillips and Borland 1994). It had been shown that the newts appeared to have two alternative mechanisms operating at short-wave and long-wave light respectively. The mechanisms were found to have opposite effects, with the short-wave one preferentially used during natural daylight orientation (this will be discussed in more detail later). Based on these previous studies, the researchers tested the engagement of the newt pineal gland during this behavior, and revealed that capping (blocking) the region of the head close to the pineal gland with different (short-wave or long-wave) spectrum filters significantly influenced the newts' magnetic orientation behavior, suggesting, thus, the involvement of some extraocular photoreceptors (common for a variety of vertebrates including newts) in the newts' magnetoreception. In this case, direct involvement of the pineal gland in photoreceptor-based (chemical) magnetoreception is more evident.

Evidence for Chemical Models

At the present time, the radical-pair mechanism is just one of the most substantiated variations of chemical models proposed. As has already been mentioned above, there exist several other similar chemical explanations of the phenomenon of magnetic

sensitivity in animals, most of them rather having the character of assumptions. In contrast, the radical-pair mechanism has obtained some amount of indirect, though seemingly consistent, experimental evidence both on chemical and behavioral levels. One of the most convincing arguments for this type of magnetoreception derives from the fact of the light-dependence of magnetic field perception well established for many animals (though not for all of those for which navigation with the help of magnetic cues has been documented). Most of this evidence is obtained with regard to birds (Wiltschko and Wiltschko 2001b; Wiltschko et al. 2004) and amphibians (Phillips and Borland 1992a; Deutschlander et al. 1999b; Freake and Phillips 2005).

As stated above, retinal ganglion cells project into the nBOR, and some neurons in the nucleus of the basal optic root, as well as in the optic tectum, of the homing pigeons have been shown to respond to the directional changes of the magnetic field applied (Semm and Demaine 1986), which suggests possible involvement of these cells in the putative magnetic compass of pigeons. Cutting the optic nerves eliminated this effect.

Interesting evidence supporting the involvement of the eyes in magnetoreception was obtained while studying lateralization of magnetoreception in birds (Wiltschko et al. 2002a). Lateralization of functions and information processing in the brain (differences between the left and the right hemispheres) has long been thought to be an attribute of the human brain only. Now it has been found in many vertebrates, including birds. In this study, European robins, *Erithacus rubecula*, were tested under conditions where the magnetic field was the only available reference for orientation. The birds were shown to orient in their proper migratory direction when using the right eye only, with the left capped. By contrast, when they used only the left eye, they were disoriented. These results imply that the right eye may be important in magnetic orientation by birds, and, therefore, the left hemisphere may be primarily responsible for processing magnetic stimuli perceived through the eye.

These and many other results suggest that the magnetic compass sense is at least partially connected with the visual system and, obviously, with its photopigments. Experiments with different incident light wavelengths and intensities conducted on pigeons, European robins, and newts have revealed various orientation disorders in these animals under some wavelengths. Shifts by 90° from the proper migratory direction in newts (Phillips and Borland 1994) and scattered random orientation patterns in European robins (Wiltschko and Wiltschko 2001b; Muheim et al. 2002; Wiltschko et al. 2004) were among the most common abnormalities. Moreover, the pigeon nBOR was shown to respond to magnetic field stimuli at different rates when the eyes were exposed to light of varying wavelengths (Semm and Demaine 1986).

Recently, Ritz et al. (2004) have provided some convincing additional evidence for the functioning of the chemical compass. In addition to the ambient magnetic field, European robins in the state of their spring migratory restlessness were placed in oscillating magnetic fields that were in the range of frequencies close to the frequency of the spin splitting already mentioned (0.1–10 and 7 MHz). The oscillating fields were aligned at different angles with respect to the geomagnetic field vector,

including 24°, 48°, and parallel alignments. Such fields had previously been shown to cause a magnetic resonance effect on the spin and to directly drive the singlet-triplet transition. The control birds (subjected to the geomagnetic field only), and those treated with an oscillating field aligned parallel to the geomagnetic vector, were oriented towards their normal northward direction. But the other two groups (under the fields applied at the aforementioned angles) were completely disoriented. Here, it should be noted that according to Kirschvink et al. (1992), weak oscillating fields with frequencies higher than 100 kHz produce no effect on magnetic alignment of magnetite particles. Thus, the experiment provides some proof of the chemical compass (at least in birds), and largely excludes the possibility that the experimental birds responded using a magnetite-based mechanism.

The involvement of the pineal gland in some birds seems to be in accord with the chemical model as well, which constitutes additional evidence in support of this hypothesis. When the gland was cut off from the nervous system, the orientation response became reduced but not eliminated (Demaine and Semm 1985), suggesting a possible partial role of the gland.

Photoreceptors possess yet another feature that supports their involvement in magnetoreception. Photoreceptors are, as a rule, assembled in ordered structures, with arrays of receptors arranged to be oriented in different directions. For example, the receptors of the retina form a kind of spherical arrangement. This attribute makes them qualify for the chemical light-dependent mechanisms of magnetoreception shown to represent rather compass perception (in contrast to the “map” sense).

To summarize, at present we have obtained sufficient evidence to suggest that at least part of the putative vertebrate magnetoreception system is associated with photoreceptors. In birds the retinal receptors would possibly qualify, whereas in newts photoreceptors in or near the pineal gland seem to be engaged as well, though some experiments indicate (Demain and Semm 1985; Schneider et al. 1994) an important role of the gland in magnetic orientation in birds, too.

Nevertheless, the exact location and structure of light-dependent magnetoreceptors is still unknown, let alone their diversity among different groups of vertebrates. A great deal of this gap in knowledge is due to the fact that most of the experimental evidence obtained so far has been elicited from behavioral experiments, which makes this evidence indirect. But a thorough study of any animal sense has never been just a behavioral study, and while at present we have a set of anatomical and physiological works on this issue, certainly much more are still needed.

Magnetite-Based Mechanisms

The idea that ferromagnetic material could possibly serve as a transducer of magnetic information in animals was initially formulated by Gustaf Ising in 1945 (for reference see in Kirschvink 1982), as he tried to detect magnetic material in the head of migratory swallows. Unfortunately, Ising was unable to discover some experimental corroboration of his ideas, as he didn't have equipment of sufficient

sensitivity. The first experimental corroboration came when Lowenstam (1962) detected magnetite in the radular teeth of chitons, and suggested its possible use in magnetoreception. Later, in the 1970s, magnetic material was experimentally detected in animal tissues (Gould et al. 1978; Walcott et al. 1979).

The magnetite-based model of magnetoreception in animals proposes a mechanism that has obtained almost as much experimental support as the radical-pair based model. And nowadays the two models seem to have evoked tough dispute between the advocates of each of them. Many researchers have come to an agreement that the mechanisms might coexist in animals, with varying predominance and function depending on the group of animals and its lifestyle.

However, some adherents of the magnetite-based model posit it as the only mechanism possible (Kirschvink et al. 2001; Walker et al. 2002). The hypothesis is based on the suggestion that there are magnetite particles present in animal bodies which are responsible for magnetic-field detection. In fact, among the variety of magnetite-based magnetoreception models presented so far, there are two main hypotheses most intensively discussed nowadays: one grounded on single-domain particles (Kirschvink et al. 2001; Walker et al. 2002) and the other suggesting the presence of superparamagnetite particles in animals (Kirschvink and Gould 1981; Kirschvink et al. 1998; Hanzlik et al. 2000; Fleissner et al. 2003).

The hypothesis based on single-domain magnetite particles is centered around the suggestion that single-domain magnetite found in some animals (particularly in rainbow trout, *Oncorhynchus mykiss*; Walker et al. 1997; Diebel et al. 2000) could possibly be a component of animal magnetoreceptors. There are several structurally similar candidate schemes for such receptors, but generally the mechanism comprises a chain of single-domain magnetite crystals having a single common magnetic moment (Kirschvink and Gould 1981; Kirschvink et al. 2001).

According to the “ferromagnetic transduction model” proposed by Kirschvink (1992), the base of the chain is connected to several molecules with the help of special filaments. These molecules serve for plugging ion channels in the cell membrane and are, in turn, tethered to the membrane by some cellular filaments as demonstrated on Fig. 1.7. Thus the magnetite is free to move in any direction, but the filaments connected to the particle restrict its movement. When an external magnetic field interferes with the magnetic moment of the magnetite, the chain changes its position relative to the membrane, and physically opens some of the channels by “pulling” the corresponding filaments linked to the ion channel plugging molecules. Once the channel is open, it causes a discharge of the membrane potential, signaling, thus, the instant change of the magnetite position.

But in natural conditions, a magnetite particle is not likely to move so freely inside a living cell, and is subject to a randomizing effect caused by the background thermal energy in the cell. The energy of interaction between such a chain and an external magnetic field will be equal to μB , where μ is the magnetic moment of the chain and B is the intensity of the field applied; the background thermal energy is calculated as kT , where k is the Boltzman constant and T is the absolute temperature of the cellular inside (for more details, see Walker et al. 2002). Therefore, according to the Langevin function describing the alignment of extremely small magnetic

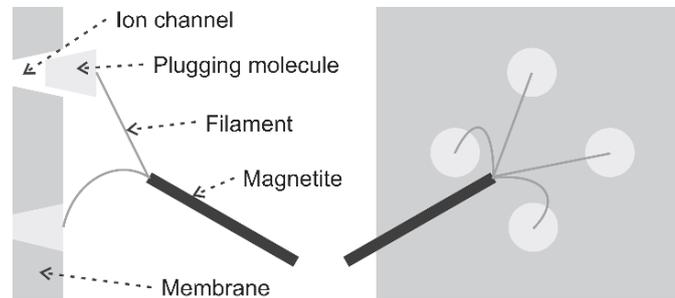


Fig. 1.7 A scheme of the “ferromagnetic transduction” model of the putative single-domain magnetite-based magnetoreceptors (adapted from Walker et al. 2002)

particles, the ratio of magnetic energy of a magnetite interfering with an external magnetic field to the background thermal energy inside a cell ($\mu B/kT$) will determine the behavior of a magnetite particle in the cellular matrix under the external magnetic field.

The mean alignment direction of a freely rotating particle will correspond to the direction of the magnetic field vector. The greater the magnitude of the applied field, the smaller the dispersion of the particle movements from the mean direction.

Consequently, we have a system that is potentially sensitive to both the magnetic field vector direction and intensity. Kirschvink and Walker (1985) reason that for direction identification the optimal magnetic-to-thermal energy ratio is 2, and for intensity determination it is 6. Walker et al. (2002) interpret such a “split” in the optimal ratios as a hint of the existence of two types of magnetoreceptors: separate ones for direction and for intensity.

In the model they present, the magnetite chain responsible for direction determination will rotate around a pivot at its base in response to an external magnetic field direction, being positioned at different angles between the axis of the chain and a fixed plane of the animal body. The more ion channels of the membrane are coupled with the chain, the more precise is direction measurement. The minimal simple model, thus, would include as few as six such cells corresponding to the six principal directions of the three-dimensional space: up, down, left, right, anterior, and posterior. The receptors supposed to measure field intensity, in contrast, are hypothesized not to be fixed to the membrane but to move freely in any direction limited by the length of the microtubule-like filaments they are coupled with. The principle is supposed to rely on the vibration the chain is expected to experience under an external magnetic field. This vibration would result from the competing forces of the magnetic field and the intracellular thermal agitation. If the external field vector, the axis of the chain, and the center of the range the chain moves across are closely aligned, then the corresponding ion channels will be plugged, preventing membrane discharge. Any movement out of such arrangement will be detected by the opening of one or more channels. Thus, provided that the thermal agitation impact

takes place, the variance in opening and closing of the channels will, in fact, be inversely proportional to the strength of an external magnetic field. The stronger the field, the less is the variance. And vice versa – if the intensity is low, the variance will be high. In this case, therefore, the resolution of such an intensity measuring system will increase with the increase of the number of ion channels connected to the chain, generally similar to the case of directional receptors.

The structures hypothesized represent just an inference from what is known about the magnetite crystals arrangement in the candidate cells of rainbow trout (Walker et al. 1997, 2002; Diebel et al. 2000), and there are several other similar schemes as well. And certainly, such structures (both directional and those for intensity) will not per se give very high orientation precision unless the signal is synthesized from many cells oriented in various directions, probably the more cells the better (Kirschvink and Gould 1981; Kirschvink and Walker 1985).

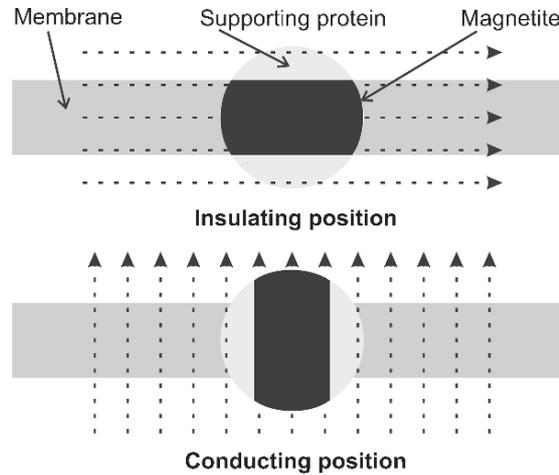
The sensitivity of this system will constitute the inverse square root of the duration of signal integration times the number of the receptive cells involved. The accuracy of determination of magnetic field direction seems to require, depending on the signal integration time, much less than 1,000 cells. But to measure the magnetic field intensities with the sensitivity shown by many animals the system would require considerably more receptor cells – up to 10,000–100,000. The amount of magnetite particles found in trout generally appears to match this requirement and to permit the discernment of field intensity changes as small as a few nT. An alternative mechanism by which single-domain magnetite particles might transmit signals to the central nervous system is by causing mechanical pressure on some other (secondary) receptors, such as stretch receptors, mechanoreceptors, or hair cells, as a result of movement of magnetite particles placed in an external magnetic field (Presti and Pettigrew 1980; Kirschvink and Gould 1981; Lohmann and Johnsen 2000).

The “ferromagnetic transduction” model still needs much testing, though some experimental evidence has been obtained which supports the interaction between weak magnetic fields and channel opening (Dobson and Pierre 1996).

In the “membrane-short model” developed by Kirschvink and Gould (1981), a single-domain magnetite crystal is supposed to form an organelle held across the membrane of a sensory neuron ending by hydrophobic proteins (see Fig. 1.8). Magnetite is known to be a good electrical conductor. So, in this model, a magnetite particle in such an organelle switches from insulating position to conduction position by rotating around its axis depending on and corresponding to the direction of magnetic field lines applied. When the organelle is set in the conduction position, it causes depolarization of the host membrane, which results in a neural signal. The authors of the hypothesis propose at least three such organelles, positioned orthogonally to track the direction of magnetic field lines in all the primary dimensions. In this case, host neuron firing frequencies are assumed to reflect the intensity of the field.

Along with its seeming plausibility, the model has several inconsistencies. First of all, it is not yet clear whether the field strength of the geomagnetic field is sufficient to overcome the electrical forces taking place in biological membranes.

Fig. 1.8 The “membrane-short” model of magnetite-based magnetoreceptors (adapted from Winklhofer 1999)



Further, depolarization of the neural cell membrane involves ion transport through ion channels in the membrane, due to the ionic nature of the membrane charges and currents (Winklhofer 1999; see also Muheim 2001), and a magnetite particle would form a barrier to the ion flow. These nuances are not taken into account in the model.

In spite of all the evidence and theoretically logical speculations, the role of single-domain particles found in the bodies of many animals in magnetoreception, and their involvement in the primary magnetoreceptor structure, remain debatable. Biogenic SD (single-domain) magnetites have primarily been obtained from tissue extracts, and so far no histological studies have been carried out to support the hypothesis (Fleissner et al. 2003). In contrast, a few detailed ultra-fine histological and theoretical modeling studies, with various methods employed, provide some evidence suggesting that the primary magnetoreceptor structure may be based on superparamagnetic crystals of magnetite (Fleissner et al. 2003; Shcherbakov and Winklhofer 1999; Davila et al. 2003; Winklhofer et al. 2001; Hanzlik et al. 2000).

Some animals have been shown to contain other than the SD type of magnetite particles. The biogenic crystals of this type are much smaller (2–5 nm) than SD (50 nm and larger). In contrast to single-domain magnetite, the magnetic axis of such a particle is not fixed, but instead is able to move in agreement with the direction of external magnetic field lines (Kirschvink and Gould 1981). The particles are called superparamagnetite (SPM) particles, and are supposed to be placed stationary in the putative SPM-based magnetoreceptors. Depending on the direction of the magnetic field they generate, they are able to attract or repel the adjacent particles as shown on Fig. 1.9. Some researchers state that the efficiency of such small particles is considerably lower than that of greater ones such as single-domain magnetites, and evolutionary constraints should have led to the preference of bigger particles (Kirschvink et al. 2001). But this speculation still remains an open question, and recent studies have brought some evidence in support of the SPM hypothesis.

Fig. 1.9 A schematic design of the behavior of a superparamagnetite chain (gray rectangles) in an external magnetic field (dashed arrows). Firm bold arrows inside gray rectangles represent the magnetic moments of superparamagnetic particles, and firm arrows outside the rectangles show the resulting attractive (a) and repulsive (b) forces (adapted from Kirschvink and Gould 1981)

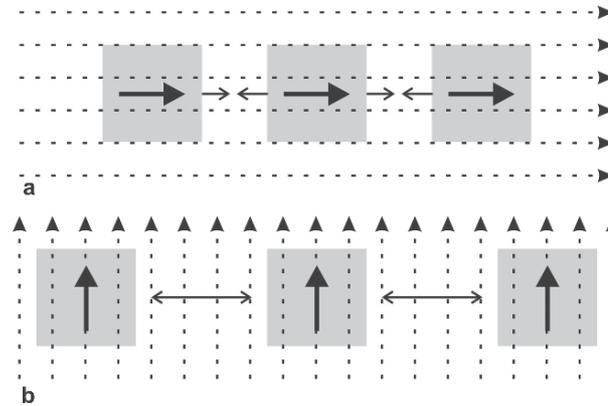
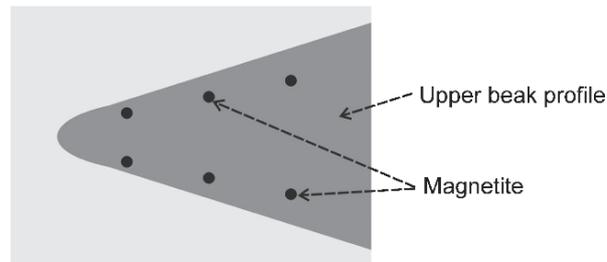


Fig. 1.10 A sketch of the pigeon upper beak profile with symmetrically arranged nerve endings (black dots) hosting SPM clusters (adapted from Fleissner et al. 2003)



The most comprehensive analysis of SPM structures supposed to constitute the putative magnetoreceptor system has been carried out on homing pigeons (Hanzlik et al. 2000; Winklhofer et al. 2001; Fleissner et al. 2003), although similar structures have also been detected in several other bird species (Stahl et al. 2007). Using light and electron microscopy it was revealed that the upper beak skin of homing pigeons contains several sites of Fe^{3+} enrichments. The six enrichment sites detected were located symmetrically in both left and right beak rim skin as shown on Fig. 1.10. The structures were found to be present always in the same skin layer – the *stratum laxum* of the subcutis – surrounded by connective tissue strands among fat cells. Since there is no direct method to detect magnetites histochemically, its presence is usually determined by using the Prussian blue (PB) reaction, the result of which is intensely blue staining of Fe^{3+} inclusions, and by low temperature magnetic measurements. Under a microscope of high resolution, the structures revealed in pigeons by PB-staining turned out to be agglomerations of dark blue spherical granules between 1 and 3 μm in diameter. Ultrastructural analysis of the granules showed that they contained magnetite nanocrystals encapsulated in a membrane. The crystals were as small as 2–5 nm in diameter, which suggested their superparamagnetic properties. The regular (symmetric) occurrence of the granules, their fixed histological location, and the region (upper beak skin) in which they had been found to occur, together led to a suggestion of their possible role as magnetoreceptors.

The point is that the tissue discussed is one of the sites of the sensory terminals connected to the ventral premaxillary ramus of the median ophthalmic nerve, which is a branch of the trigeminal nerve. Electrophysiological recordings from this nerve have shown that a magnetic field of changing intensities modulates the frequency of the nerve impulses (Semm and Beason 1990; Beason and Semm 1996). This suggests possible involvement of the nerve in the process of magnetic stimuli transduction. The transduction pathway was abolished by anesthesia of the ophthalmic nerve (Beason and Semm 1996). Similarly, several studies on fishes have suggested the involvement of the rostral V (*ramus ophthalmicus superficialis*) in magnetosensory pathways (Diebel et al. 2000; Walker et al. 1997).

Using immunohistological methods and electron microscopy Fleissner et al. (2003) demonstrated that the granules of SPM particles found in pigeons were located inside neuronal terminals, where they were associated with the inner membrane and formed elongated agglomerations along the inner sides of the nervous cells. No granules outside neurons were found.

Further studies have shown that the described intraneural structures consist of two minerals – magnetite accumulations connected with strands of rectangular platelets of maghemite (a ferromagnetic). A vesicle with incrustated iron nanoparticles is attached to these complex structures, and the complexes as a whole are arranged so that their long axes are parallel to the three primary planes of the three-dimensional space, so that one plane prevails in each of the three paired upper beak locations (Fleissner et al. 2007).

Based on these and other findings, two closely related models for primary magnetoreceptors in pigeons were proposed. Shcherbakov and Winklhofer (1999) and Winklhofer et al. (2001) propose the “ferrovesicle magnetometer” model based on the structure of a single granule containing superparamagnetic nanoparticles. Such a granule is supposed to be surrounded by a membrane that encloses nanoparticles dispersed in a liquid inner medium. Such a structure is in itself a ferrofluid. In the absence of a magnetic field, the granule assumes a spherical shape according to thermodynamic and mechanical equilibrium of such structures. The superparamagnetic particles, having no magnetic moment in the absence of an external magnetic field, are dispersed and form a homogenous colloid inside. Once a magnetic field is applied, agglomeration of the particles starts. It occurs because in the presence of an external magnetic field SPMs acquire a magnetic moment parallel to the reference field. Each particle becomes bipolar along the axis of the reference field lines. This results in the appearance of an attractive force between them along this axis. In this situation, the particles assume the energetically most favorable position and press the granule to form a prolate ellipsoid with its long axis parallel to the external magnetic field vector, as demonstrated on Fig. 1.11. It has been shown experimentally on artificial models and via theoretical calculations that such behavior of granules of ferrofluids is proportional to the magnetic field strength and granule size. The latter two factors have also been shown to increase the precision of the system, so that bigger granules and stronger fields cause better tuning of the granule shape to the direction of the magnetic field lines. One problem is that the system must be subject to thermodynamic, magnetic, and mechanic equilibrium

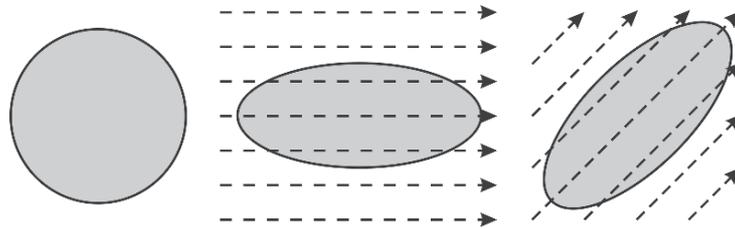


Fig. 1.11 Ferrovessicle deformation in an external magnetic field (adapted from Shcherbakov and Winklhofer 1999)

constraints, as well as osmotic forces. Nevertheless, superparamagnetite assemblages are characterized by a very short relaxation time ($\ll 1$ s) during which they come into a thermodynamic equilibrium if an external magnetic field changes. This property is very important for the model (for details on the properties of ferrovessicles see also Bacri et al. 1982, 1996).

The change in the ferrovessicle shape in response to a change in an external magnetic field is hypothesized to be the possible mechanism underlying magnetoreception in animals. The evidence that many animals (pigeons included) are not sensitive to the polarity of magnetic field lines is in agreement with the model, since the long axis of a ferrovessicle is able to provide information on direction of magnetic field lines, but hardly on their polarity.

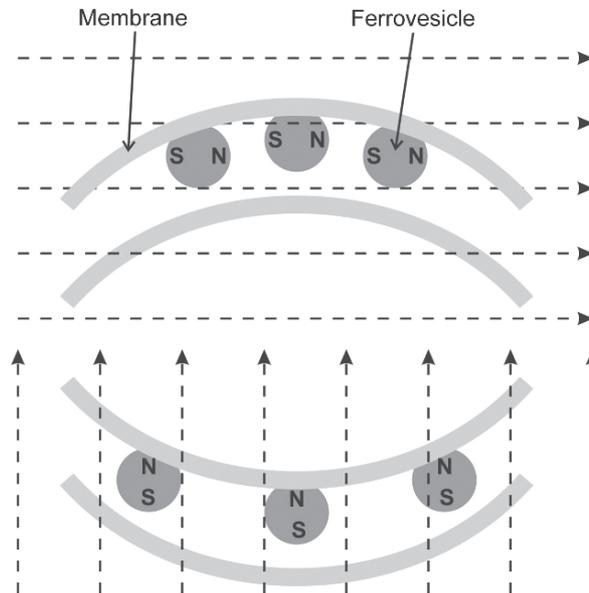
Several hypothetical mechanisms have been put forward to explain how changes in the shape of ferrovessicles could transform into a neural signal. Measuring magnetic field intensity may be based on the change in the ratio between the osmotic pressures outside and inside a granule as a result of a change of its shape. Another possible mechanism proposed for compass sense is that based on a granule surrounded by different neuron terminals reaching the surface of the granule from all the principal directions in the three-dimensional space. In this case, the direction of field lines is derived from vesicle elongation depending on the direction of its long axis. During elongation it touches (or excites) only certain terminals, namely those located on the path of the extension of its long axis (for details on these hypotheses and theoretical analysis, see Shcherbakov and Winklhofer 1999), and this selective neuron firing results in a signal giving information on the parameters of an external magnetic field.

In practically all natural animal systems of sensing, after the primary signal reception has occurred, a process of signal amplification starts. Such neural processing of a primary signal greatly increases the sensitivity of a system, making it able to perceive a signal change with much smaller increments. Similar amplification of the primary signal is predicted to be the case in magnetoreception as well. Shcherbakov and Winklhofer (1999) hypothesize that single-domain magnetite particles might possibly serve as a ferrovessicle granule core, being located in the center of a granule. Such a magnetic “pith” would turn around, having a permanent magnetic moment and tracking the external magnetic direction of the field lines. A SD

grain of magnetite, in this system, will not leave the center of a vesicle (granule), due to the so-called magnetic levitation phenomenon that will cause repulsion of the granule from the inner boundaries of the ferrofluid vesicle (for details see Rosensweig 1985). Theoretically, the dipole magnetic field created by such an SD particle superimposed on the external field would produce greater magnetic pressure on the membrane of a granule, thus amplifying the resulting signal (for details on this model see Shcherbakov and Winklhofer 1999; Winklhofer et al. 2001). Nevertheless, in reality this hypothesis is not devoid of drawbacks, in view of the recent discoveries on the location of SPM clusters. SPM clusters have never been found outside the neural cell terminals, and each cluster agglomeration has been found to interact only with one host neuron (Fleissner et al. 2003).

In view of these recent findings on granule location, Davila et al. (2003) conducted several modeling experiments, and proposed another possible explanation on how the cluster assemblages might function as magnetoreceptors. In contrast to the single-cluster model just described, they propose a mechanism based on multiple cluster interaction. By the time their study was initiated, extraction of ferromagnetic granules from pigeons' tissues, or direct in-tissue study of their response to magnetic fields, had never been carried out. So, they constructed artificial SPM ferrofluid droplets similar in size (and to some extent in structure) to those found in pigeons. This was done based on the assumption that the SPM crystals in the natural granules are embedded in a liquid matrix (in contrast to the elastic matrix also taken into consideration theoretically by some authors; see Winklhofer et al. 2001) to imitate the putative natural counterparts. They employed a colloidal suspension of magnetite nanoparticles in benzene. When the colloid was dissolved in an aqueous medium it formed macrodroplets of varying sizes, which were then broken into microdroplets by treating them with ultrasonic. Taking into account the study of Fleissner et al. (2003), which showed that the granules are not scattered randomly but seem to be aligned along the inner membrane of nervous terminals, the researchers placed their ferrofluid granules into artificial microgrooves, thus simulating neurons, where granules are supposed to move only along one axis – the long axis of a groove (axon). Predictably, when exposed to an external magnetic field the clusters (granules) will be polarized, and dipole interactions between them are expected. Indeed, the interaction has been shown experimentally. When the applied external magnetic field was parallel to the long axis of such a granule-filled groove, the granules (polarized according to the reference field so that the “north” end of one granule faced the “south” end of one of the two adjacent granules and vice versa) were driven towards each other by the attracting force that appeared between their opposite poles. In contrast, when an external field was applied perpendicularly to the long axis of the groove, the granules polarized so that the same poles turned in a common direction. In this situation, each granule neighbored next-door granules “south-to-south” and “north-to-north” (with the resulting repulsive force) and moved away from each other. Therefore, a chain of such clusters will shrink when a parallel external field is applied, and stretch when the reference field is perpendicular. Further, if each link (granule) in a chain is attached to the

Fig. 1.12 A model of a magnetoreceptor based on the behavior of SPM ferrofluid droplets in microtubules (presumably neurons) placed in an external magnetic (*dashed arrows*) field (adapted from Davila et al. 2003)



membrane of an elongated cell, shrinking and stretching of the chain will produce a corresponding deformation of the cell membrane they are attached to, as shown in Fig. 1.12. A signal could be produced in the presence of mechanosensitive ion channels that would change the membrane potential depending on the character of deformation.

The putative mechanism suggested by this model is not sensitive to the polarity of magnetic field lines, but hints at a plausible explanation for the inclination compass, which is in accordance with behavioral findings on birds and sea turtles. The inclination of the reference field lines is expected to influence the degree of deformation in such a system. Inclination changes between 0° and 90° , and the degree of membrane deformation will change gradually within this range depending on the particular angle the magnetic lines are applied (for details and calculations on this hypothesis see Davila et al. 2003, 2005).

Such an organized structure and location of the putative magnetoreceptor structures found by Fleissner et al. (2007) and described above together with recent discoveries of mechanosensitive ion channels with their specific lipids that close and open these channels under the pressure of mechanical intracellular forces (reviewed in Kung 2005), have led to yet another explanation. The putative magnetoreceptor is supposed to function based on a structure consisting of three main parts already described – a vesicle with incrustated iron nanoparticles, maghemite strands, and magnetite agglomerations attached along the strands.

The function of the vesicle is still unclear. It may serve as a relaxing system to the whole structure, or it may attune the whole system to the local geomagnetic conditions (Fleissner et al. 2007). Strands of maghemite platelets are supposed to enforce and concentrate external magnetic stimuli and direct their action to the magnetite agglomerations, which are supposed to exert a mechanical pulling force on the molecules that gate mechanosensitive ion channels. Theoretical physical possibility of such a mechanism has been analyzed (Solov'yov and Greiner 2007) and proved plausible. The three-dimensional orientation of these candidate structures theoretically predicts sensitivity to all magnetic field components in question – namely, vertical, horizontal, and total intensities. This, in its turn, may explain sensitivity to the magnetic field inclination.

In view of the evidence that the magnetic sense is light-dependent in many animals, Edmonds (1996) proposed yet another model based on ferromagnetic crystals assumed to be present in the special oil droplets found in the double cones of the retina of some groups of vertebrates, including birds and reptiles. These droplets are supposed to serve roughly like the immersion oil for microscopes, and provide better color vision. Edmonds supposed that these droplets present in the cone receptor cells of the retina might contain elongated magnetite particles that arrange parallel to an external magnetic field direction. When field lines are parallel or antiparallel to the long axis of the receptor cell, the crystals associated with large molecules (like, say, β -carotene) are also arranged parallel to the axis, thus allowing light to come through the droplet and reach photopigments. In contrast, if the direction of the field lines is not parallel or antiparallel to the cell's long axis, the arrangement of magnetite–molecule complexes doesn't allow light to get through. Thus, given the multifarious spherical orientation of the receptor cells, the model gives a bird (or any other animal possessing the system) a compass potentially able to detect not only the direction of magnetic field lines, but similarly to measure inclination, just as in the case of the chemical compass hypothesized by Ritz et al. (2000). The hypothesis is especially interesting in view of the fact that mammals studied for magnetic orientation are supposed to employ other mechanisms than those which birds and reptiles seem to use. Mammals seem to be sensitive to the polarity of the magnetic field lines. What is interesting about this difference is that most mammals do not have these oil droplets (as well as double cones) in their photoreceptors. And although there are some exceptions, such as some monotremes and marsupials which retain features of the avian and reptilian eye with the double cones and oil droplets, the hypothesis of oil-droplet involvement in magnetoreception is still not undermined by this fact, since these exception groups have not been studied for magnetic orientation. Studies on these groups would probably not only provide an additional test for Edmonds's model but also bring some novel data on the phenomenon of magnetoreception in vertebrates overall.

It is still unclear where magnetite-based mechanisms could be located in the animal body, and whether the same body parts are responsible for it in different animals. In fact, there is much less known than unknown here. Nevertheless, a certain amount of data has been collected. Just as in the case of all other magnetoreception models, it is assumed that the putative magnetite-based magnetoreceptors

are connected to the nervous system in order to transmit the signal to the analyzing centers in the brain. Direct anatomical evidence is, to date, scarce and mostly involves studies on bobolinks, *Dolichonyx oryzivorus*, and rainbow trout (Walker et al. 1997; Beason and Brennan 1986; Beason and Nichols 1984); and most of the evidence supporting this group of models has been obtained indirectly from behavioral studies.

Analyses of trout olfactory lamellae carried out with the help of confocal microscopy methods have revealed cells that appear to contain magnetite particles (Walker et al. 1997). This region is innervated by the ros V nerve, a branch of the trigeminal nerve. Electrophysiological studies have shown that this nerve contains units responding to abrupt changes in magnetic field intensities applied. The units, however, do not respond to a reversal of the direction of the magnetic field lines, which suggests that they could rather qualify for intensity detection. After the presence of magnetite particles was established, several nerve-tracing studies were carried out (Walker et al. 1997; Diebel et al. 2000). Walker and coworkers used Di-I labeling applied on the cut ends of the superficial ophthalmic (SO) nerve of the rainbow trout in the region where magnetic response activity had been found. Di-I moved in both anterograde and retrograde directions. The labeling has shown that SO is connected through the anterior ganglion of the trigeminal nerve to the *medulla oblongata*. Anterior to the orbit, the SO nerve splits into branches that innervate the skin and also surround and enter the olfactory capsules. Tiny rami also penetrate the olfactory lamellae from the base and the top. Some finer processes penetrate the lamellae from the distal end (see also Kirschvink et al. 2001).

Later (Diebel et al. 2000), the confocal laser-scanning microscope allowed imaging of the particles contained in the lamellae. They were identified as magnetite by using atomic and magnetic force microscopy. The magnetic-to-thermal energy ratio of the particles was shown to be 4, which met the magnetoreception requirements previously mentioned.

Studies on bobolinks (a migratory bird species) have led to similar results (Beason and Nichols 1984; Beason and Brennan 1986; Beason et al. 1995). In this case, magnetite material was revealed in the upper beak, where the region containing the putative magnetite receptors was found to be connected to the ophthalmic nerve as well.

Thus, most of the studies presented so far have suggested the involvement of the trigeminal nerve in magnetite-based magnetoreception signal transduction. Blocking this nerve in bobolinks abolished the effect of a strong magnetic field pulse (Beason and Semm 1996).

Evidence for Magnetite-Based Models

Biogenic magnetic material (Fe_3O_4) was first discovered in chitons (Lowenstam 1962) and magnetotactic bacteria (Blakemore 1975; Blakemore and Frankel 1981). This fact encouraged researchers to search further, and later, magnetite was found in honeybees, birds, sea turtles, and a number of other animals (for review see

Lohmann and Johnsen 2000). The magnetite material found in animals is in two forms: single-domain crystals that respond to an external magnetic field by rotating according to the direction of the magnetic field lines, and superparamagnetic crystals that are considerably smaller and (in the absence of an external field) possess no magnetic moment.

Direct anatomical studies that support the magnetite-based mechanism have been discussed above. Besides, there is a set of experiments that provide some indirect (behavioral) evidence. This type of study is based on the ferromagnetic properties of the single-domain particles. Ferromagnetic materials (including magnetite), unlike non-magnetic and paramagnetic substances, possess permanent magnetic moment and can retain particles in the alignment they form under strong external magnetic fields.

Beason et al. (1995) treated bobolinks with short strong magnetic pulses. They divided the studied group into three subgroups: controls (untreated) and two groups treated with different polarities. The results showed that after the treatment all three groups had different orientation relative to each other. A second treatment with fields having polarities opposite to the first treatment caused random orientation in both treated groups. Such results are in agreement with the magnetite-based magnetoreceptor models, since an opposite polarity pulse obviously causes demagnetization of previously magnetized particles, although the researchers assume that the treatment doesn't exclude the presence of any chemical mechanism, since the treatment was effective only in the absence of other orientation cues. The presence of at least a partially magnetite-based system is supported by the fact that measurements were conducted from several hours to several days after the treatment, and no other mechanism could be inferred, except for magnetite, because photopigments are not ferromagnetic.

However, disorientation after treatment with an external magnetic field may not be observed in some cases, which may be explained by the phenomenon called coercivity. In the simplest explanation, coercivity is the property of magnetizable materials that defines the minimal intensity of an external oppositely directed magnetic field needed to overcome the magnetic moment of the material. If the intensity of an external magnetic field is not sufficient to overcome coercivity, the material doesn't demagnetize. The maximum coercivity for the oval-shaped particles found in biological systems constitutes about 0.1–0.2 T. If the field applied is not so strong, magnetite particles probably will rotate in the ambient field, and after the field is removed they will return to their previous position, producing no effect on the birds' orientation. In contrast, a magnetic field that is strong enough to overcome coercivity is able to reorient the magnetic moment of a ferromagnetic particle with a long-lasting effect. Such effects were also obtained on Australian silvereyes, *Zosterops lateralis* (Wiltschko et al. 1994b, 1998a, 2002b), pigeons (Beason et al. 1997), mole-rats *Fukomys anselli* and hatchling loggerhead sea-turtles (for reference, see Wiltschko et al. 2007).

It is interesting that this long-lasting effect disappears after several days. If the single-domain magnetite was involved, it should have been permanently magnetized and would not have diminished in several days. This fact, although not clearly

explained so far, is suggested by some authors (Wiltschko et al. 2002b) to account for the superparamagnetite-based magnetoreception, as this model theoretically allows magnetoreceptor restoration to the original state after the damage caused by a strong magnetic pulse.

Brassart et al. (1999) presented another study indicating the use of both light-dependent and light-independent mechanisms and strongly supporting the presence of magnetite particles in the animal bodies. Newts previously used in a study on the influence of strong magnetic fields were tested for remanent magnetization, compared to the natural remanent magnetization (NMR) characteristic of the group. The remanent magnetization of these newts was two orders of magnitude higher than NMR, unambiguously suggesting the presence of magnetite in their bodies.

An additional argument in support of the model is its theoretical high sensitivity to the intensity of the magnetic field. The sensitivity demonstrated by many animals is not supposed to be possible with the help of the putative light-dependent magnetoreceptors (see Schulten 1982).

Moreover, several animals that have been shown to orient in the geomagnetic field (e.g., blind mole rats; Kimchi and Terkel 2001) have no access to light throughout their whole life, though this fact doesn't directly support magnetite-based magnetoreception in view of the possibility of light-independent chemical magnetoreception.

Electromagnetic Induction Model

The well-known phenomenon of electromagnetic induction, e.g., induction of electric current when a conductor moves through a magnetic field, is hypothesized to constitute a possible mechanism of magnetoreception in some elasmobranch fishes (some sharks, rays, skates, etc; Kalmijn 1984; Paulin 1995). In fact, the current is driven by the force that arises when an electron is moving through a magnetic field. This force is perpendicular to both the direction of the electron movement and the direction of the magnetic field vector, and is calculated as the product of the charge, velocity and the sine of the angle between the magnetic vector and the direction of motion.

In elasmobranch fishes, according to this model, ampullae of Lorenzini, small jelly-filled skin-hosted pockets containing electroreceptive cells, are assumed to function as the conductor bars, and the ambient water is supposed to be the conduction medium. When a fish moves (hence, moves in the geomagnetic field), its electroreceptors located in the ampullae detect the voltage of the current induced by the movement of the fish in the geomagnetic field (Kalmijn 1984; Paulin 1995). Therefore, these fishes are supposed to derive local geomagnetic field features based on the parameters of the current induced. Although the electric sensors are highly sensitive in elasmobranch fish, this mechanism may be complicated by the fact that sea and ocean currents create electricity themselves, and a fish is exposed to the need to distinguish between the currents produced by its motion and by the water movement. Another limitation for this mechanism is its obvious tie-in with

aquatic media because of the good conductivity of water. Terrestrial animals do not have such a possibility, and hence the mechanism cannot be universal in vertebrates.

Evidence for an Electromagnetic Induction Mechanism

There is no direct evidence for the use of a mechanism of this type by animals. However, it is well established that rays and sharks have a highly sensitive electric sense capable of detecting the weak electric fields produced in the tissues of their prey (Kalmijn 1971) and appearing to be sufficient for detection of the geomagnetic field (Kalmijn 1988). Still, a huge field for future investigations remains here, as this putative mechanism has not yet been proved experimentally, or supported by at least indirect behavioral or neurophysiological evidence.

1.1.3 Differences Between Models

Each of the hypothetical mechanisms presented above is potentially able to provide an animal with navigational information derived from the geomagnetic cues, though there are some differences between the models, which infer somewhat different information to be deduced from magnetic fields depending on the mechanism employed. Generally, induction- and magnetite-based models often imply that animals are able to distinguish between the magnetic “north” and “south” (Kalmijn 1988; Kirschvink and Gould 1981), whereas chemical models are not supposed to allow this (Schulten 1982; Ritz et al. 2000).

Many birds and sea turtles have been shown to use the so-called inclination compass, which is generally attributed to chemical mechanisms and is not sensitive to the polarity of the geomagnetic field lines (Wiltschko and Wiltschko 1996; Light et al. 1993). Instead, it gives an animal the information about the “poleward” and “equatorward” directions derived from magnetic inclination by sensing in which direction the lines go up or down and depending on the hemisphere, as previously described. Salmon (Quinn et al. 1981) and blind mole rats (Marhold et al. 1997; Thalau et al. 2006; Wegner et al. 2006), on the contrary, seem to be able to distinguish between the magnetic “north” and “south,” i.e., they are sensitive to the polarity of the horizontal component of the geomagnetic field lines. So it is suggested that these animals primarily use the magnetite-based mechanism. Nevertheless, this difference is normally placed between the chemical and single-domain magnetite-based mechanisms. In contrast, the superparamagnetite-based model doesn't exclude sensitivity to inclination (Davila et al. 2003; Fleissner et al. 2007).

In addition, one of the most curious situations concerning the mechanisms of magnetic orientation is that found in some newts. It has been suggested that Eastern red-spotted newts use both mechanisms: an inclination compass when migrating towards the shore, and a polar compass while homing (this will be discussed later;

see Phillips 1986a; Phillips and Borland 1994). Nevertheless, it should be noted that behavioral studies on newt orientation have brought much confusing evidence, and the system is not clear yet, which promises a potentially fruitful field for further investigation.

An additional obvious discrepancy between the mechanisms is their sensitivity to different features of magnetic fields. As has already been mentioned above, the magnetite-based mechanism is supposed to allow detection of very small changes in magnetic field intensities, theoretically up to a few nT as suggested by Walker et al. (2002), which is generally not a prerequisite of chemical or induction mechanisms (Lohmann and Johnsen 2000; Rosenblum et al. 1985; Ritz et al. 2000). In the induction model, the coexistence of electrical current produced by the fish body and the ambient current resulting from water movement can potentially constitute a major sensitivity limitation factor (Kalmijn 1984; Paulin 1995). In chemical models, sensitivity is reduced because the impact of magnetic fields on the underlying reaction is not very strong. So there is a point of view that the putative sense of “map” based on sensitivity to magnetic field intensity is not likely to rely upon light-dependent or electromagnetic induction mechanisms, and is probably controlled by a magnetite-based mechanism (Lohmann and Johnsen 2000). The suggestion seems to be quite logical, but in the absence of firm evidence is a rather hypothetical one.

Sensitivity to inclination of the geomagnetic field lines probably engages integration of the gravity and magnetic sensory systems. Although sensitivity to magnetic field inclination is generally attributed to light-dependent (chemical) magnetoreceptors, there are no theoretical barriers obstructing inclination sensitivity created by any of the three main groups of mechanisms proposed so far (Lohmann and Johnsen 2000).

1.1.4 Magnetoreception in Different Groups of Vertebrates

Despite the fact that a huge amount of work has been done on magnetoreception in vertebrates, the field still seems to stay at the beginning of its development. Significant discrepancies in results for different vertebrate groups impede formation of some general theory of magnetoreception for the group, not to mention the evolution of the sense. Therefore nowadays, thorough investigation of different vertebrates is of great importance, and is expected to contribute to bringing the “scattered” data together into a general conclusive theory. Certainly, during chordate evolution different ways of perception of the geomagnetic field in different groups might evolve, but since the phenomenon seems to be much older than chordate animals (many older groups are known to perceive magnetic fields), the common origin of chordates suggests that their magnetoreception is likely to have some basic features common for the whole group.

More or less detailed studies have been carried out on only a few vertebrates, but still involve most of their major classes. The most studied species include salmon

(bony fishes), eastern red-spotted newts (amphibians), sea turtles (reptiles), several bird species, and blind mole rats (mammals). Several other species, though, have also been addressed.

Fishes

There is a set of behavioral experiments and neuroanatomical evidence that support magnetoreception in fishes, though the primary magnetoreceptor and the magnetoreception system properties have not been identified in this group. Fishes differ from other vertebrates for which magnetic orientation has been established in that they almost exclusively inhabit water environments. Therefore, as has already been mentioned, an additional complication in studying the nature of fish magnetic orientation is that in addition to the two hypotheses of the primary magnetoreceptor structure discussed for terrestrial vertebrates, fishes have been proposed to employ yet another mechanism known as electromagnetic induction-based magnetoreception. The existence of an electromagnetic induction-based mechanism possible only in aqueous media is disputed by some authors; nevertheless, researchers have not yet come to a definite conclusion on it, because there is no experimental evidence supporting or disproving the model unambiguously.

In contrast, magnetite enrichments in the ethmoid region of the sockeye salmon, *Oncorhynchus nerka*, have been detected in large quantities (Walker et al. 1988; Diebel et al. 2000), and found to increase in an orderly fashion as fish mature from larvae to adults. These and other studies have given the magnetite-based hypothesis most recognition for the case of a magnetoreceptor in fishes.

The behavioral data available to date prove the presence of a magnetic sense in both bony and cartilaginous fishes. Thus, sandbar, *Carcharhinus plumbeus*, and scalloped hammerhead, *Sphyrna lewini*, sharks held in a big round tank surrounded by a coil system producing an Earth-strength magnetic field were conditioned (trained) to enter a feeding box for food once the ambient artificial magnetic field changed (Meyer et al. 2005). During testing, a shift in the magnetic field evoked a statistically significant rapid convergence of sharks at the feeding box instead of usual slow circling around the tank. The results seem to suggest possible detection of magnetic fields by sharks; however, the interpretation is not clearly evident. The problem is that changes in external magnetic fields simultaneously create electric fields. Which field was used by the sharks to orient remains a question.

Stronger evidence comes from another series of experiments with stingrays, *Urolophus halleri* (Kalmijn 1977, 1978). Kalmijn reasoned that altering external magnetic fields would produce simultaneous transient electric fields, and this would make it impossible to distinguish which fields would guide the experimental animals. Therefore, he constructed a circular tank surrounded by an external stationary field in which, in the absence of any other cues, rays had to move and were conditioned to enter one of two enclosures. After entering the one at the magnetic east side of the tanks the rays were given food, and they were punished once inside the other one on the western side. In these experiments, rays were

shown to be able to learn the location of the eastern enclosure even if its absolute position was reversed by altering the external magnetic field to the opposite, providing thus additional corroboration of the hypothesis of magnetic orientation in elasmobranchs.

It is difficult to speculate on the nature of the putative magnetoreceptors or magnetoreceptive system in elasmobranchs. Kalmijn's hypothesis of an electromagnetic induction-based magnetoreception system in elasmobranchs seems plausible. Nevertheless, some authors (Kirschvink et al. 2001) report that rays with tiny magnets inserted into their nasal cavities fail to demonstrate previously conditioned responses to magnetic stimuli, which is not consistent with the induction hypothesis. Nevertheless, the possibility of the presence and interaction of more than one mechanism should also not be rejected.

Magnetic orientation in bony fishes is supported by more ample evidence obtained primarily on salmon and eels, but also reported for a number of other migratory and non-migratory species. Salmon have always been a classical group of orientation study objects because of the migratory and homing aspects of their biology. In a set of early experiments, salmon were shown to possess a magnetic compass during all the postembryonic development stages (i.e., the fry, smolt, and adult). Thus, two fry populations of the sockeye salmon (one migrating in the western direction, and the other to the south) were tested in a circular tank surrounded by a magnetic coil system producing a field turned by 90° counterclockwise in respect to the ambient geomagnetic field. Both groups demonstrated their normal orientation direction under the coil switch-off position. Once the coil system was turned on, all the fry turned their orientation by shifting 90° counterclockwise according to the correspondent shift of the surrounding field produced by the coil system (Quinn 1980; Quinn et al. 1981), although such a response was produced only when magnetic field was the only orientation cue. When the tank was uncovered and the fry could see the sky, they oriented in their seasonally appropriate direction even in a shifted field, which implies that celestial cues may play a significant role in salmon orientation as well (Quinn 1980). The sky exposure, however, took place during the day. In view of the fact that migration of the sockeye fry mostly occurs during the nighttime, magnetic cues can be assumed to play a significant role in their migratory orientation (see also Scholz et al. 1992).

Similar results with employment of, in principle, the same testing procedures were obtained on smolts of the sockeye and chinook salmon, *Oncorhynchus tshawytscha* (Quinn and Brannon 1982; Taylor 1986, 1987).

An inference indirectly suggesting the use of magnetic information while orienting can be drawn also from another study. Sockeye salmon smolts migrating to their home creek tributaries of Babin Lake in British Columbia (Canada) encounter a very patchy and diverse pattern of currents on their way. They migrate at considerable depths and their route is very complicated, including many turns. All these circumstances led Johnson and Groot (Johnson and Groot 1963; Groot 1965) to an assumption that visual and olfactory cues might play a minor role in their orientation along this way. Groot (1965) carried out a series of experiments in which smolts placed in round tanks were tested for their orientation. As a result, salmon

were shown to change their orientation headings with timing closely resembling the average timing and directions of migrating smolts in their natural environment, which implies that the smolts may have some internal program that drives them to orient differently at different times of their migration, and possibly with the use of magnetic cues.

Application of electrocardiography methods and behavioral conditioning has shown sensitivity to magnetic fields in the fry and larvae of brook trout, *Salmo trutta* (Formicki et al. 2004), and the adult and glass eel (the newly metamorphosed juveniles) stages of Japanese eels, *Anguilla japonica* (Nishi et al. 2004; Nishi and Kawamura 2005). Interestingly, anosmic Japanese eels were not able to detect magnetic field (Nishi et al. 2005), which rather suggests a magnetite-based magnetoreceptor located in the nasal cavity or near it, and is in accord with the previous histological findings yet mentioned.

In addition to the indicated species, magnetic sensitivity has also been reported for a number of other fishes, like chum salmon, *Oncorhynchus keta* (Quinn and Groot 1983; Yano et al. 1997), Atlantic salmon, *Salmo salar* (Rommel and McCleave 1973), European and American eels, *Anguilla anguilla* and *A. rostrata* (Tesch et al. 1992; Rommel and McCleave 1973), yellowfin tuna, *Thunnus albacares* (Walker 1984), tilapia, *Oreochromis mossambicus* (Shcherbakov et al. 2005), and even non-migratory zebrafish, *Danio rerio* (Shcherbakov et al. 2005). In the last case, zebrafish were conditioned in a two-part tank installation where they were punished by weak electric discharges if they failed to swim to the other part of the tank after the ambient magnetic field altered. The authors suppose that magnetosensation in non-migratory short-range species may supplement other orientation cues. In the case of zebrafish, the sense may substitute for orientation with the help of landmarks which are impaired during the night.

Therefore, it seems that the ability to perceive magnetic fields in fishes is acquired at the early stages of postembryonic development, and most evidence suggests that it is of a magnetite-based nature.

In addition to standard and widespread laboratory methods with testing tanks, some other approaches, like field observations, have turned out to be helpful. A field study carried out directly in the littoral zone of a lake (Formicki et al. 2002) employed fyke nets of three types: two of them were equipped with permanent magnets directed South or North towards the entrance, and the third contained magnet dummies and served as control. After emptying, nets located along the littoral zone were placed at other sites for random yields. It was shown that magnet-equipped nets yielded near 70–90% more fish of different species than those with dummies, which seemed to suggest that the magnets stimulated fish to enter.

At the very least, the statistically significant difference between those equipped by magnets and those with dummies suggests that magnetic field had influenced orientation of the caught fish.

Studies of magnetic field effects on fish embryos seem to be a very promising approach as well. In particular, it is expected to greatly contribute to our understanding of the nature of fish magnetoreception, because it has recently been shown (Winnicki et al. 2004; Tanski et al. 2005) that magnetic fields influence fish

embryos well in advance of their eye development, and thus may indicate that magnetoreception in fishes is more consistent with the magnetite-based hypothesis.

Nevertheless, the authors refrain from suggesting any involvement of magnetite, at least until the nervous system is formed. The question is open. The fact is that at the end of gastrulation, planes of symmetry of the embryos of several fish species seem to be significantly oriented along the North–South axis of the ambient magnetic field, and stronger fields cause strengthening of the significance of the effect (Tanski et al. 2005).

Amphibians

As yet, magnetoreception in amphibians has mostly been studied on eastern red-spotted newts. The Eastern red-spotted newt is a small salamander common in the eastern United States. At the larval stages of their development, the newts inhabit aquatic environments. Adults are primarily aquatic as well, although representatives of some populations leave the water seasonally when water temperature reaches extreme values. The intermediate juvenile stage, however, is absolutely terrestrial, leaving its water habitats at the end of the larval stage and residing on the forest floor for up to 8 years. After this, it returns to the water as an adult (Phillips 1986b).

These two migrations are usually described in navigation literature as the shoreward migration (migration of juveniles towards shore in order to complete their terrestrial stage of development) and the homing migration (return of adults to their native ponds), respectively. Such a lifecycle of the species makes it a convenient object for orientation and navigation study. The seasonal shoreward migration, as well as homing behavior during late maturation stages and after displacement from the home pond, have been shown to employ geomagnetic cues for orientation and navigation.

Initially, Phillips (1986b) kept newts in special outdoor water tanks simulating ponds with an artificial “shore” on one side. The tanks served as training ponds where newts learned the direction towards the shore. Then, by artificially raising the water temperature he was able to elicit shoreward migration of the newts. Using indoor circular and visually symmetrical testing arena designed to detect newts’ orientation, it was revealed that newts were sensitive to weak magnetic fields and this was used as an orientation reference.

Further, Phillips (1986a), using similar methods, discovered some discrepancy in the newts’ magnetic compass orientation. Under laboratory conditions, the vertical component of the magnetic field was reversed (reversing, thus, the inclination angle of the lines to the opposite) and the horizontal component (polarity of the lines) was left unchanged as shown in Fig. 1.13.

As a result, newts migrating shorewards underwent a 180° reversal in their orientation, while those homing (a distinct type of migratory behavior) remained unaffected by the treatment. The results suggested two different magnetic orientation mechanisms controlling the two types of newts’ migratory behavior. Newts were

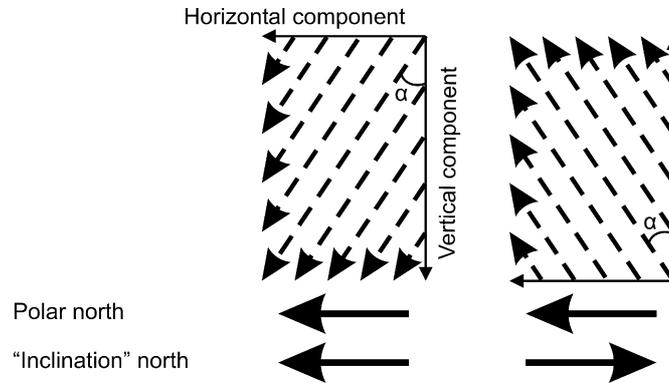


Fig. 1.13 Magnetic field vertical component reversal (adapted from Phillips 1986a)

shown to be sensitive to the inclination and direction of magnetic lines while moving shoreward and to the polarity of the lines while homing.

As has already been discussed in this chapter, the inclination compass is generally attributed to light-dependent magnetoreception mechanisms that are thought not to be sensitive to the magnetic lines polarity. In contrast, polarity sensitivity is attributed to the putative magnetite-based receptors. All these models are hypothetical, and much debate is going on concerning the real nature of the primary magnetoreceptor. Nevertheless, newts have provided still more evidence that multiple mechanisms might possibly coexist, probably as complementary ones with differing functions.

In view of the inclination sensitivity of the shoreward orientation behavior of the newts, and its insensitivity to the polarity of magnetic field lines, Phillips and Borland (1992a,b) tested their magnetic compass with respect to light dependence. Newts were oriented in their normal shoreward direction under full-spectrum light, but their orientation under near-infrared light became random. Failure to orient unimodally (or at least in any consistent direction) in the latter case raised the question of whether the absence of visible light could have affected newts' motivation to orient at all, or in other words whether the presence of light itself had any non-specific effect on newts' behavior. Under both conditions, there were individuals that had failed to show any directional preference.

Analysis of the proportion of newts that failed to show any orientation preference in each of the groups (full-spectrum and near infrared) failed to show any significant difference between them, suggesting that the absence of visible light itself had not been the likely cause of the scattered orientation pattern under near-infrared light (Phillips and Borland 1992b).

Further investigation (Phillips and Borland 1992a) revealed a direct effect of light on the orientation performance of the newts under manipulated magnetic field conditions. Orientation responses of newts heading in shoreward direction were shown to depend on the wavelength of the ambient light. Under natural conditions,

newts experience full-spectrum light, and their responses in the laboratory under full-spectrum light served as controls. It was shown that under light wavelengths of 400 and 450 nm, orientation of tested individuals was undistinguishable from that of controls.

But light of longer wavelengths (500, 550, and 600 nm) caused an anticlockwise 90° shift (perpendicular to the shoreward direction) in their magnetic compass bearings. As in the previous study, the result didn't preclude the possibility of non-specific influence of the long-wavelength light on newts' behavior. However, training newts in the outdoor tanks under long-wavelength light and subsequent testing under both light conditions (long-wavelength and full-spectrum) showed that the individuals tested under full-spectrum light oriented 90° clockwise in relation to the shoreward direction. The results support the direct light wavelength effect on magnetic orientation in newts, and, on the other hand, rule out any non-specific influence. Based on these results, the authors developed a hypothesis suggesting that newts may possess two spectral mechanisms (short- and long-wave) of light-dependent magnetoreception, as shown on Fig. 1.14.

Additional experiments were designed to test the hypothesis. As was predicted, under 475 nm light (which is midway between 450 with normal response and 500 nm with the shifted reaction) newts were disoriented, and it was supposed that the two mechanisms cancel each other out.

Now, the question was: how do these mechanisms cooperate, or coexist? The problem is that natural light is broadband and includes all of the experimental wavelengths, and newts respond to this full-spectrum light in the same way as to short-wave light. Natural "balanced" light should excite both mechanisms and cause their mutual cancellation, or at least serious degradation.

One possible explanation is that there are two types of light-dependent magnetoreceptors with different sensitivity, which transfer antagonistic inputs to some

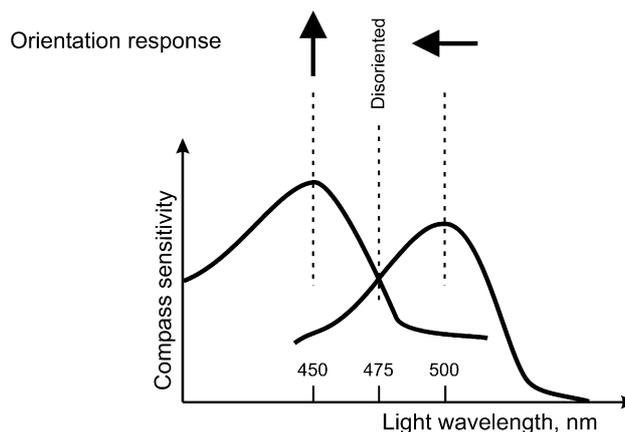


Fig. 1.14 Sensitivity and responses of the newt magnetic compass to the spectrum of light (adapted from Deutschlander et al. 1999a)

second-order cells (like spectral opponents) where the information is transformed. Another possibility includes cells with two spectral mechanisms, like photoreceptors found in the pineal complex of some lizards and amphibians (Phillips and Borland 1992b).

The latter case deserves more consideration, as the involvement of the newt pineal in light-dependent magnetoreception has been proved previously (Deutschlander et al. 1999b; Phillips et al. 2001). It is possible that under broadband exposure (natural full-spectrum light) the short-wave mechanism inhibits the long-wave counterpart, but the question remains open.

Later experiments by Phillips and Borland (1994) showed significant differences between the light-dependent orientation responses of newts heading towards shore and those homing.

The shoreward bearings produced the same results as in the previous study (with the 90° shift under long-wave light). In contrast, homing newts displayed different results. While under short-wavelength light, newts demonstrated their normal homeward orientation, and therefore were undistinguishable from controls (full-spectrum), individuals tested under long wavelengths were disoriented (oriented randomly) and didn't show any sign of a 90° shift. Thus, the study appears to indicate that the homing orientation of newts is also light-dependent (specifically, light wavelength-dependent), but with a different pattern of dependence from that of shoreward orientation. This light-dependence of magnetic orientation in homing newts is in some disagreement, as far as the sensitivity to the magnetic field polarity is concerned, with that shown in previous studies, because, as was discussed above, light-dependence and polarity sensitivity are attributed to different magnetoreception mechanisms, and are unlikely to occur otherwise.

Among possible explanations, cooperation of two mechanisms (light-dependent and magnetite-based) with different sensory inputs, and the existence of such a "hybrid" system in terrestrial vertebrates, has been proposed (Phillips and Borland 1994). The possibility that two mechanisms might coexist in terrestrial vertebrates has been discussed above, and corroborated in some other studies.

Apart from the advantages of this model, a set of questions arises here about the nature and functional properties of such interaction, as well as its necessity for homing orientation. It is also interesting whether its properties are consistent with the behavior which newts display during homing activity.

To address this problem, some theoretical speculations must be taken into account. The putative intensity sensors (see Kirschvink and Gould 1981; Kirschvink and Walker 1985) are supposed to precisely measure the magnetic field intensity by averaging signals from multiple cells (the more the better). All candidate cell types (hair cells, stretch receptors, etc) are at least partially sensitive to direction, and therefore their function may be affected if they are supposed to measure both the magnetic intensity and direction. Therefore, for accurate intensity measurements, the directional component must be eliminated or constant. One approach an animal could use to get reliable measurements is to vary the alignment of the intensity receptors on a regular basis until the maximum response is obtained. However, this would be inefficient, as each measurement would take a long time and/or require

an animal to stay motionless (see Yorke 1979; Phillips and Borland 1994) during the measurement process. An alternate option would be to utilize an independent magnetic direction detector (for example a light-dependent mechanism) which will align (or tune) the intensity detector.

Based on these speculations, Phillips and Borland (1994) formulated their “hybrid magnetoreception system” hypothesis, in which a light-dependent mechanism serves for aligning the intensity (e.g., magnetite-based) detector needed for deriving map information and, thus, allowing true navigation. “Tuning” of a predictably magnetite-based intensity (map) detector by an alternate light-dependent magnetoreception mechanism in newts is also supported by another study. Phillips et al. (2002) carried out a set of experiments to investigate the previously predicted disorientation of homing newts under preliminary exposure to long-wavelength light (> 500 nm). As in previous studies, controls trained in the outdoor tanks under natural light conditions and tested under full spectrum were oriented in their normal homeward direction. As predicted, individuals held under long-wavelength light failed to show homeward orientation when tested either under full-spectrum or long-wavelength light. But, what was new and unexpected, newts tested under full-spectrum light were indistinguishable from those tested under long-wavelength light and showed bimodal orientation along a more or less “fixed” north-northeast–south-southwest magnetic axis, although previous results demonstrated differential effects on homing (as well as on the shoreward orientation) of these two light conditions. Although the bimodal behavior of the newts tested under long-wavelength light remains enigmatic, it is interesting to note that most tests included light intensity of 45×10^{15} quanta $s^{-1} m^{-2}$ similar to that used in another study on European robins (Wiltschko and Wiltschko 2001b). However, when the robins were subjected to light of lower intensity they behaved in a different way. The behavior of newts might also have been affected by intensity of light. Unfortunately, light intensity dependence of newt magnetic orientation behavior has not been studied, which leaves the question of how to interpret the newts’ orientation responses open for future challenges.

To test the hypothesis of a possible single-domain magnetite-based mechanism of magnetoreception in newts further, Brassart et al. (1999) measured the natural remanent magnetism (NRM) of the newts and revealed that the alignments of NRM were random with respect to the newts’ head-body axis. Juxtaposing NRM alignments with the newt orientation responses didn’t show any significant relationship in the overall pool of bearings. However, the NRM alignments of the newts that showed orientation response under full-spectrum light were not random, and revealed significant clustering with the bearings. The results of the study appear to be in accordance with the hypothesis of magnetite-based intensity detector alignment by a light-dependent mechanism, since magnetite alignment in newts seems to depend on light conditions.

Although the hypothesis appears to be quite logical and supported by empirical evidence, no conclusions can be made for sure at this stage. Some non-specific effects of light on animal motivation have been ruled out, but additional research is needed to test possible other ones. For example, some researchers (Deutschlander

et al. 1999a; Kirschvink et al. 2001; Johnsen and Lohmann 2005) put forth an assumption that newts might have experienced some unexpected motivation as a result of the influence of some light spectra on photoreception mechanisms which have no relation to magnetoreception. For example, under strange, and possibly alarming, light of certain wavelengths newts might have been alerted to search for shelter instead of homing.

Melanopsin, a photopigment in the vertebrate retina and pineal, was recently shown to determine, at least in part, functioning of the circadian rhythms in vertebrates, and suspected to have blue–yellow spectral opponency mechanisms; this constitutes another reason for not hurrying with conclusions on light-dependence of magnetic orientation mechanisms (Brown and Robinson 2004; Dacey et al. 2005). Such spectral opponency is thought to be potentially capable of producing complex and unexpected effects on the circadian pacemaker system. Moreover, the recently discovered lateralization of magnetic information processing in the bird brain has provided an interesting parallel to the lateralization of circadian pacemakers (Wiltschko et al. 2002a; Johnsen and Lohmann 2005), and complex and still unknown interactions may take place between the systems. Further investigation is needed to discover possible interrelations between circadian pacemaker, photon absorption, and magnetoreception systems.

The involvement of the pineal complex in the magnetoreception sense of vertebrates, specifically in the context of light-dependent mechanisms, has been the focus of numerous studies on different vertebrates. The newt pineal gland has also been shown to play some role in magnetoreception processes. Deutschlander et al. (1999b) capped the newts' dorsal head surface with clear caps (transparent caps transmitting full spectrum light and serving as control) and filter caps transmitting only long-wavelength light. The eyes were left untreated. Magnetic orientation behavior of the capped newts was found to depend on the spectrum of light in the same way as in previous experiments (with uncapped newts), and revealed that the pineal gland may be directly involved, at least in the putative short-wavelength light-dependent magnetoreception mechanism in newts. Later, using similar manipulations with short-wavelength caps, the putative long-wavelength mechanism of newts was shown to be mediated by the pineal complex as well (Phillips et al. 2001).

Reptiles

Magnetosensitivity in reptiles has mostly been studied on alligators (Rodda 1984) and sea turtles (Light et al. 1993; Lohmann and Lohmann 1993, 1994a; Irwin and Lohmann 2003), the latter having been studied in more detail.

Inasmuch as most research has been carried out on loggerhead sea turtles, *Caretta caretta*, before discussing the available experimental results it is appropriate to briefly review their migratory biology. Loggerheads breeding on sandy beaches of Florida (USA) appear as hatchlings from their underground nests, and immediately after that they search for the oceanward direction, towards which they

move until they reach the coastline. Once having found it, they migrate into the open sea and grow there, traveling across the Atlantic Ocean up to the coasts of southwestern Europe and northwestern Africa. Then they turn southwards to the equator and back to shallow waters to forage. Females later return to the Florida beaches as adults. Growing gradually in the open sea, males never touch the land after leaving their hatching coasts; however, they return to the areas near their natal beaches to mate. Thus, moving along their tremendous migratory route, loggerheads, following major Atlantic water currents, encircle the so-called North Atlantic gyre, and spend several years in the open sea before returning to their nesting sites. The turtles have been shown to use different orientation and navigation cues on different stages of their journey.

The question of the primary mechanism operating during sea turtle magnetic orientation has hardly been defined as yet (just like those of all the other vertebrates). Different studies have produced dissimilar and, sometimes, controversial results, the most important of which are discussed below.

The debate over the question of the nature of primary magnetoreceptors in vertebrates is applied to sea turtles (and predictably reptiles) as well, since the experimental evidence available so far suggests that turtles may possess a system of magnetoreception peculiar to the group. Although turtle magnetoreception demonstrates features similar to those we find in birds (i.e., insensitivity to magnetic polarity and sensitivity to inclination), experiments on some species show that turtles are, unlike birds, able to orient in a magnetic field in complete darkness. Therefore, the putative light dependence of inclination sensors in vertebrates may well not be universal. How this inclination-sensitive light-independent system might function – whether it is similar to that of birds or completely different – remains a question.

As revealed by experimental studies, loggerhead sea turtles possess an inclination compass (Light et al. 1993), and furthermore they are able to detect changes in the magnetic inclination angle (Lohmann and Lohmann 1994a). In the first study, hatchling loggerheads were placed in a water tank surrounded by a coil system designed so that it was possible to reverse the vertical and horizontal components of the ambient magnetic field. A special harness was put on the hatchlings tethered by lashes to a direction-sensitive device located in the center of the study arena (the tank) and transmitting information about turtle's headings to a computer. Hatchlings tested in complete darkness and in the unaltered Earth's magnetic field demonstrated their normal eastward (seaward) orientation (see also Lohmann 1991). However, reversal of the vertical component of the ambient magnetic field lines caused a correspondent reversal of the hatchlings' orientation to the opposite (westward) direction. Reversal of both vertical and horizontal components (altering polarity but not inclination) didn't affect their normal eastward orientation. As was shown by the results, the reversal of the vertical component caused the same effect on hatchlings' orientation as reversals of horizontal component carried out in earlier studies (Lohmann 1991). The results of this study suggest that sea turtles possess an inclination compass similar to that of birds (this will be discussed later). Moreover, the experiments provide some evidence that the magnetic compass of

loggerheads relies upon inclination and is not sensitive to the polarity of the field lines, which is another similarity of the bird and turtle compasses. In contrast to some other animal groups, both birds and turtles fail to orient in horizontal magnetic fields (Light et al. 1993; Wiltschko and Wiltschko 1972). Such characteristics are not universal in the animal kingdom, and here we see that the orientation behavior of turtles and birds differs from that of some fishes (Quinn 1980; Quinn et al. 1981) and mammals (Burda et al. 1990; Marhold et al. 1997) able to perceive the polarity of magnetic lines and unaffected by reversals of the vertical component.

In the second study (Lohmann and Lohmann 1994a), loggerhead sea turtle hatchlings were tested for their migratory orientation in magnetic fields with different inclinations. Taking into account that inclination angles of the geomagnetic field are roughly specific to latitudes, experiments were carried out to test whether turtles are able to distinguish between different inclination angles, and thus potentially derive latitudinal information in this way. For this purpose, hatchling loggerhead sea turtles (Lohmann and Lohmann 1994a) were exposed to different magnetic fields with inclinations corresponding to various sites of their natural migratory route – the North Atlantic gyre (see Fig. 1.15). In these experiments, hatchlings exposed to the natural field of their native beaches demonstrated their normal eastward orientation. Those subjected to a field with an inclination specific to the extreme northern point of the North Atlantic gyre directed south-southwest. Under the field inclination characteristic of the southern limits of the gyre, hatchlings swam in a northeasterly direction. And finally, when the turtles were exposed to a field with inclinations they do not normally encounter in nature, or one specific to areas well within the gyre, they failed to show any significant orientation. Therefore,

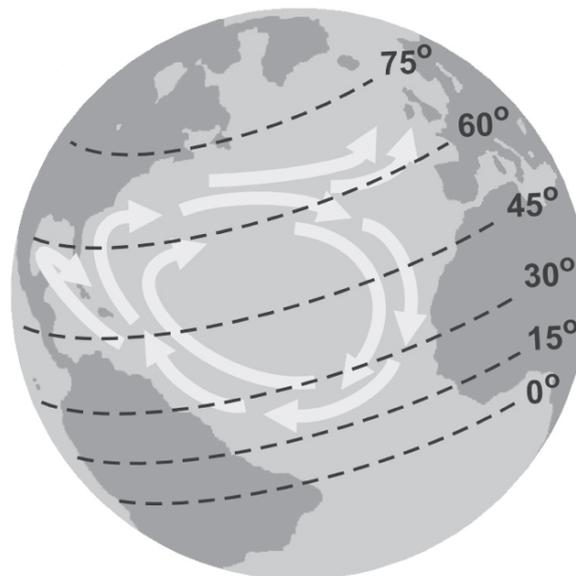


Fig. 1.15 An approximated scheme of the distribution of the geomagnetic inclination angles across the North Atlantic gyre (adapted from Lohmann and Lohmann 1994a)

hatchling loggerhead sea turtles seem to be able to distinguish between different inclination angles of the Earth-strength magnetic fields, and their orientation under the described conditions supports the hypothesis that the turtles follow the North Atlantic gyre during their open-sea migration using the geomagnetic inclination as a source of positional information.

Meanwhile, inclination sensitivity of the turtle magnetic compass discovered in these studies is supposed to explain the enigmatic site fidelity of the loggerhead females which, after a long journey in the Atlantic Ocean lasting several years, return for breeding to the area close to the beaches where they were born years ago (see Bowen et al. 1993; Limpus et al. 1992). Their most important breeding coasts are oriented roughly along the north–south axis so that the gradient of inclination angles along the beaches is very steep, and this possibly helps females discern between differences of the dip angle and, therefore, identify the latitude of their hatching site, provided that they imprint its value as hatchlings (Lohmann and Lohmann 1994a). The involvement of other cues assisting in native beach identification, however, is not excluded.

Thus, we can suggest, based on the inferred properties of different putative mechanisms of the vertebrate primary magnetoreceptors, that perception of the Earth's magnetic field in turtles (and possibly reptiles) is similar to that of birds. The turtle compass is an inclination compass, which in its turn implies that it is likely to be a chemical compass. Moreover, in the inclination sensitivity tests (Lohmann and Lohmann 1994a), turtles' responses to different dip angles with the same intensity support this assumption.

In addition, several other studies suggest the presence of magnetite (and, therefore, magnetite-based magnetoreceptors) in the bodies of turtles.

First of all, it has been clearly shown (Lohmann and Lohmann 1993) that turtles are able to orient using Earth's magnetic field in complete darkness, and, therefore, their magnetic compass is independent of light. Thus, leatherback sea turtle, *Dermochelys coriacea*, hatchlings from a Florida beach were subjected to an earth-strength magnetic field using a Rubens' cube coil system imitating Earth's magnetic field and capable of reversing it. Under natural magnetic field conditions and in complete darkness, hatchlings oriented significantly eastwards (i.e., towards the open ocean, as expected in nature). When the horizontal component of the field was reversed, the hatchlings turned their orientation correspondingly in the opposite direction, suggesting that light is not necessary for their magnetic orientation. This evidence, however, doesn't directly demonstrate involvement of magnetite, and, as stated above, may indicate some group-specific mechanism of magnetoreception, which either is of chemical light-independent nature, or is magnetite-based while sensitive to inclination.

Additionally, mineral magnetite found in some other groups of vertebrates has also been detected in sea turtles. Histological methods have allowed detection of magnetite in the turtle cephalic tissues (Perry et al. 1985).

Attachment of magnets to the carapace of loggerhead hatchlings from Florida beaches (Irwin and Lohmann 2003) revealed that the presence of magnets caused significant disorientation of the juveniles, which otherwise oriented in the ocean-

ward direction. No tests have been carried out with attachment of small magnets to different parts of the turtle body, which is expected to bring more information on the location of the putative magnetoreceptor (for details see Irwin and Lohmann 2003) and its nature.

Sea turtles have also been found to be very sensitive to the intensity of the magnetic field (Lohmann and Lohmann 1996a). Under the total field intensity of 52,000 nT (the intensity replicating that near South and North Carolina, USA) turtles from Florida were shown to orient with the mean compass angle of 69°, but the intensity of 43,000 nT (encountered on the eastern part of the Atlantic near Portugal) caused their mean orientation to turn towards 280°, both suggesting that turtle hatchlings are able to distinguish between different intensities of the geomagnetic field, which possibly could serve as navigational markers helping them keep within the warm waters of the North Atlantic gyre (Lohmann et al. 1999).

Nevertheless, in experiments on inclination (Lohmann and Lohmann 1994a) and intensity (Lohmann and Lohmann 1996a) sensitivity in sea turtles, one of the parameters was held constant and the other varied, in order to test perception of each specific parameter separately. Pairs of these parameters that were used in each experiment didn't correspond to the actual pairs of values found in any location on the turtles' migratory path. Therefore, a question whether turtles are able to recognize the actual values in combinations which they meet during migration at specific locations arose. In order to test this possibility, further experiments were conducted (Lohmann et al. 2001). In these trials, turtles were subjected to magnetic fields which replicated (inclination and intensity combined) those at three actual locations on their migratory route. As a result, turtles subjected to a field corresponding to that near Florida headed east-southeast, those tested under a field found near the north-eastern edge of the route directed southwards, and finally under a field replicating that of the southernmost part of the gyre, oriented west-northwest. These results are in accordance with the previous studies already mentioned, and provide corroboration for the hypothesis that young sea turtles are able to use regional characteristics of the geomagnetic field as navigational markers that possibly help them keep within their migratory route.

Combined intensity and inclination sensitivities, taking into account their astonishing resolution (inclination sensitivity of 1° for 100 km displacement; Lohmann and Lohmann 1994a, 1996a) might probably constitute a magnetic bicoordinate map gauge, which allows turtles to approximate their global position at any given time. Nevertheless, this is just a hypothesis, as the mechanism has not been clearly demonstrated so far (Lohmann et al. 1999; Lohmann and Lohmann 2006).

There is one more interesting point in turtle magnetoreception. Since all hatchlings tested in these experiments (including those tested for regional magnetic features) had no migratory experience, the ability of hatchlings to discern between different regional features of the geomagnetic field with predictable orientation suggests that reactions to different magnetic field values may be inherited by turtles. In view of the fact that the geomagnetic field has dramatically changed during the last millennia and in fact is continuously changing, turtle magnetic navigation

abilities, specifically their responses to signals from the putative magnetoreceptors, must evolve together with changes in the field (Courtyllot et al. 1997).

Although the possibility of such rapid (in evolutionary terms) changes might seem unlikely at first glance, some researchers suggest that similar facts of rapid evolution of migratory strategies do take place in nature. As an example, some populations of blackcaps in Europe have dramatically changed their migratory route within just three decades. Monarch butterflies introduced into Australia a century ago have so far evolved new migratory routes with the locally appropriate timing of migration. In the case of magnetoreception in turtles, such evolution may be driven by severe natural selection pressure, favoring individuals that keep within the North Atlantic gyre, as those moving astray soon die, and thus do not participate in reproduction. On the contrary, those that correctly orient in response to the encountered field values survive, and later generations are represented only by genes of this selected group (Lohmann et al. 1999).

Birds

Birds, being obviously one of the “most migratory” groups among vertebrates, are perhaps the most extensively studied group in regard to their navigation abilities. And nowadays it is common knowledge that the geomagnetic field is a very important source of directional and positional information for birds during their migratory movements, which sometimes reach up to several tens of thousand kilometers in length.

Considering the nature of bird magnetoreception, it is appropriate to say that contemporary data, combined, suggest a rather mixed (chemical and magnetite-based) magnetoreception system, both components being present and functioning on a complementary basis.

There is no need to present here modern views on the structure of the birds’ putative magnetoreceptor candidates, because the topic has largely been covered in the above parts of the chapter while highlighting magnetoreception models, since birds have been a classical modeling object in this respect. Therefore, here we will try to concentrate primarily on the experimental evidence that supports or disputes particular views.

Experimental data supporting the magnetite-based magnetoreception hypothesis are diverse, but it should be stated again that actually there are two main magnetite hypotheses: based on single-domain magnetite and superparamagnetics.

Early studies (Presti and Pettigrew 1980; Ueda et al. 1982; Beason and Brennan 1986; Edwards et al. 1992) on bird natural remanent magnetization (NRM) and isothermal-induced remanent magnetization (IRM), measured on several bird species, showed the presence of magnetite in the bodies of studied birds. In the last study, measurements in the head and neck of 21 species showed that most of the magnetic material in birds is represented by single-domain and pseudo single-domain grains of ferromagnetic nature, although several species might contain superparamagnetite. Three-quarters of the IRM in European starlings, *Sturnus vulgaris*, and common

grackles, *Quiscalus quiscula*, are located in the head, and one quarter in the neck. In several other species, the proportion of the IRM in the head is even higher. Measurements of the mean NRM values have revealed significant differences among bird species; however, no difference has been detected between migratory and non-migratory species. No differences have been shown in the mean magnetic vector directions among species as well. Interestingly, linear regression has demonstrated that the average intensity of remanent magnetism is dependent on the mean body mass, and is greater in bigger species (Edwards et al. 1992).

Later, a series of experiments with a short but powerful magnetic pulse provided further support for the magnetite-based magnetoreception in birds. The main studies of this series included bobolinks (Beason et al. 1995; Beason and Semm 1996) and Australian silvereyes (Wiltschko et al. 1998a, 2002b). In these tests, birds orienting in their normal migratory direction were treated with a short and powerful magnetic pulse directed differently from the natural north. The birds reacted by changing their migratory directional preference correspondingly, scattering along the east–west axis that is perpendicular to their normal orientation, and the effect, gradually diminishing, lasted for several days (Wiltschko et al. 1998a). Treatment of two groups with differently oriented magnetic pulses caused a corresponding difference between the groups' directional preferences, and treatment with a second pulse of the opposite polarity produced random orientation (Beason et al. 1995). The results are consistent with the presence of magnetizable material with a stable magnetic moment such as SD magnetite. However, taking into account the hypothesis that the putative magnetite-based magnetoreceptor may have a complex structure including SD magnetite as well as superparamagnetite, it is interesting to compare the results with another recent study. In this experiment (Wiltschko et al. 2007), Australian silvereyes changed their migratory headings after a treatment with a short powerful magnetic pulse. The effect lasted for 3 days, and after 10 days the birds restored normal orientation. A second pulse treatment 16 days after the first one, however, evoked unexpectedly different behavior. The birds were disoriented for just 2 days and then returned to the seasonally appropriate headings. This result now suggested that they got used to the alteration, and learned to recover faster. Such behavior cannot be explained in terms of pure SD magnetoreceptors, and provides further evidence for the involvement of superparamagnetic materials, at least as a part of a complex (“mixed”) structure, the input of which can be evaluated differently by a bird.

In another study (Beason and Semm 1996), bobolinks treated with a similar pulse responded by a change in their orientation direction. Blocking the ophthalmic branch of the trigeminal nerve completely abolished the effect of the pulse magnetization, and the birds returned to their normal orientation (they didn't disorient). Thus, blocking of the ophthalmic nerve obviously interrupted the link between magnetizable material and the central nervous system of the birds, but they remained able to orient, apparently using some other source of magnetic information. Therefore, the results of this study suggest that bobolinks (and, perhaps, birds overall) might use two independent magnetoreceptor systems, which are complementary.

Although no study has unequivocally proved or disproved this suggestion and further research is needed, another experiment has provided some complementary data to the issue. In all the above experiments, only adult experienced birds were used. But based on the contemporary view of bird navigation, we suggest that birds employ two mechanisms for magnetic orientation – one for estimation of a proper direction towards the destination, and another one for detection of their present position. Determining the latter requires having a mental representation, or a “map” of the territory in question, and is available only for experienced adults, who have accomplished their migration at least once in their life and remembered the magnetic field parameters along the entire migratory route. In a study with juvenile inexperienced Australian silvereyes (Munro et al. 1997a,b) mist-netted right after fledging, the birds’ orientation was unaffected by a magnetic pulse and they continued their normal migratory orientation, obviously relying upon their light-dependent chemical compass or other cues. Investigation of light-dependent properties of birds’ orientation revealed no differences between the responses of adults and inexperienced juveniles (Munro et al. 1997b). In general, these results may indicate that magnetic pulse only affects the “map” sense of birds. Therefore, it seems that the putative “map” sense of birds may be of magnetite-based nature, and the “compass” sense is light-dependent and employs a different mechanism (Munro et al. 1997a,b; Beason et al. 1995; Beason 2005).

Light-dependence of the bird magnetic compass orientation has been well documented in numerous studies (Wiltschko and Wiltschko 2001b; Muheim et al. 2002; Wiltschko et al. 2003, 2004).

European robins tested under different wavelengths and intensities of light (Wiltschko and Wiltschko 2001b) show that their magnetic compass orientation is dependent on both parameters. Under relatively low light intensity of 7×10^{15} quanta $s^{-1} m^{-2}$ birds oriented in their normal northeast migratory direction under either 424 nm (blue), 510 nm (turquoise), or 565 nm (green) light, while disoriented under 590 nm (yellow) light. But increasing light intensity to 43×10^{15} quanta $s^{-1} m^{-2}$ (compare with experiments on newts described above) led to a change in the birds’ behavior: under blue light they oriented along the west–east axis (predominantly to the west), and under turquoise they showed a unimodal orientation slightly west of the north. Under the yellow, they continued to be disoriented.

A more detailed study on European robins (Muheim et al. 2002) provides evidence for some additional characteristics of their light-dependent magnetoreception. In this study, robins were also appropriately oriented under 560.5 nm (green) light, but were completely disoriented under 567.5 nm (green–yellow) light under a broad range of various intensities. Interestingly, the birds were able to orient under red (617 nm) light, but only at low intensity, and they responded in a direction shifted from normal by approximately 90° . Analysis of these data supports the prediction of two antagonistically acting light-dependent mechanisms of magnetic orientation in birds. One high-sensitive short-wavelength mechanism and one low-sensitive long-wavelength mechanism with the predicted transition zone at about 567.5–590 nm wavelengths (Muheim et al. 2002; Wiltschko and Wiltschko 2001b).

An amazing fact is that the responses of robins suggest a system consisting of two light-dependent mechanisms, very similar to that found in newts. The putative long-wavelength mechanism of newts appears to be less sensitive and shifted by 90° , just as we see in birds but with a slightly different effective wavelength. Birds show a hypothetical mutual cancellation of both mechanisms similar to that of newts in a particular transition zone, which is a wavelength in between the peaks of the two mechanisms. Robins pre-exposed to red light during 1 h immediately before testing were able to orient under red spectrum in their appropriate migratory direction (Wiltschko et al. 2004). As a control, pre-exposure to darkness didn't induce proper orientation under red light. Therefore, it seems that birds adapt to red light (learn to orient under new light conditions), which is very similar to the results obtained on newts after training them (pre-exposure) under long wavelengths before testing.

Further, migratory Australian silvereyes were tested under monochromatic blue (424 nm) and green (565 nm) light, and under two intensity conditions – low intensity (7×10^{15} quanta $s^{-1} m^{-2}$) and high intensity (43×10^{15} quanta $s^{-1} m^{-2}$). Additionally, inclination inversion was applied to test whether the birds used their normal inclination compass. Under low intensity of light the birds were seasonally appropriately oriented under both wavelength conditions, reversing their direction of orientation to the opposite in response to field inclination reversal. However, at high intensity they directed along the east–west axis under blue and west–northwest under green, and they didn't reverse their orientation after the field inclination was reversed. Such behavior suggests that under the latter conditions (high intensity of light) the birds didn't employ their inclination compass. The phenomenon still remains unexplained. The birds' activity under high intensity light was even slightly higher than under low intensity – therefore the intensity itself didn't oppress their migratory motivation. Testing was carried out in the same room as other tests, so artifacts resulting from the testing conditions are excluded. Moreover, significant bearing vectors indicate that it was rather common behavior implying some accord among the birds, and was not a non-specific deviation. The behavior cannot be attributed to excessive light intensity itself, because full-spectrum experiments have involved even higher intensities without any strange responses, and the high intensity applied in this study corresponds to ambient light conditions immediately after the sunset or before the dawn (Wiltschko et al. 2003). Unfortunately, lack of studies on the light-intensity dependence of newt magnetoreception significantly restricts our ability to compare the results from these two groups, which would potentially give more room for speculation.

One explanation put forth by the authors is that the change in behavior might have been caused by the fact that test light was monochromatic (narrow band), in contrast to natural conditions where light has a wide-band spectrum. Then, if it is supposed that two different photoreceptors are normally used by a bird to produce a reliable orientation pattern, the birds might have got into a situation in which increased difference between the two photoreceptor inputs (neural signals) due to the discrete narrow-banded wavelengths might have affected signal processing at

higher neural levels, and led to the birds' inability to interpret it. It is interesting that the silveryeyes in this study showed somewhat different responses to high-intensity light to those exhibited by robins (Wiltschko and Wiltschko 2001b), which responded identically to both blue and green light.

Thus, the exact properties of bird light-dependent magnetoreception are still far from being understood clearly. Many points, like the light intensity threshold at which birds switch to abnormal patterns of orientation (see Wiltschko et al. 2003), still have to be addressed. In addition, the present-day status of theory on light-dependent compasses is rather fragmentary. And in this situation, some standard sets of questions to be answered and generalized approaches devoted to find similarities and dissimilarities in different groups of vertebrates would potentially give more room for comparison, and therefore much more understanding of the topic.

In addition to the nature and properties of the primary magnetoreceptor, the studies just presented suggest it may be located in the head. Another recent work (Mouritsen et al. 2004b) provides additional support for this assumption. In this study, birds were investigated for their initial behavior before they had chosen a certain flight direction after release. It was revealed that garden warblers use special head scans before they are able to choose their migratory direction. The scans consist of turning the head in different directions, fixing it in each direction for a short time. It is suggested that the behavior is dedicated to estimation of the direction of the ambient magnetic lines, and thus identification of the proper migratory course. It was shown that in a zero magnetic field, birds almost triple the frequency of the scans, but the resulting bearings are undistinguishable from random (i.e., they are unable to orient). It is noteworthy that the study provides not only support for in-head location of the magnetoreceptors, but supplies us with a behavioral response that somewhat complements other studies on light-dependent magnetoreception. The abovementioned pre-exposure of newts and birds to the light spectra that cause changes in normal orientation produced proper orientation under these spectra, and abnormal behavior under the spectra that under normal conditions provide reliable reference for proper orientation. So, it has been suggested that birds and newts "learn" to orient using new light conditions. Now, considering the head scans observed on warblers, we could suppose that the scans may represent the same "learning" to orient in the ambient field. The mechanism of such "learning" is still unclear and requires future investigation.

And finally, it should be mentioned that not only migrant birds are supposed to use magnetism for orientation. In recent studies, researchers have been able to elicit predictable spatial behavior by domestic chickens (Freire et al. 2005) and zebra finches, *Taeniopygia guttata* (Voss et al. 2007). As the Wiltschkos suggest (Wiltschko and Wiltschko 2007), the last work is a breakthrough against a background of many unsuccessful attempts with magnetic conditioning in birds, as the object can easily be grown in the laboratory and can be tested whenever needed, independently of the short migration periods of migratory birds, opening a new perspective for investigation of bird magnetoreception.

Mammals

The involvement of magnetic information in mammal orientation has been suggested for a number of species, predominantly including rodents, whales, and bats. But as yet it has been proved experimentally only for a few genera of rodents, such as *Spalax* (Kimchi and Terkel 2001, Kimchi et al. 2004), *Fukomys* (Marhold et al. 1997; Thalau et al. 2006; Wegner et al. 2006), *Mus* (Muheim et al. 2006c) etc, and two genera of bats – *Eptesicus* (Holland et al. 2006) and *Nyctalus* (Wang et al. 2007).

The blind mole rat, *Spalax ehrenbergi*, is a small mammal that lives under the ground in a system of branching channels dug by the animal. The animal never leaves the channel system, i.e., it doesn't create aboveground exits, and thus never appears above ground level. At first glance, living in such a spatially restricted environment doesn't require powerful navigational abilities. But, on the other hand, digging is a very energetically costly activity. Therefore, construction of a pattern of properly spatially distributed and branched channels will save much energy and time for an animal. This requires excellent navigation. This is particularly the case in view of the absence (or extreme scarcity) of orientation cues under ground. Here, a sense of magnetic field would be of great help. Experiments show that some underground animals, including the species just mentioned, are experts at it.

In experiments with blind mole rats (Kimchi and Terkel 2001), an eight-armed maze was employed to study the use of magnetic cues by the animals as shown in Fig. 1.16. With the help of the Helmholtz coil system, it was possible to change the magnetic field direction. In the first stage, the animals under study were divided into two groups. One group was tested under the natural magnetic field conditions, in order to reveal whether the rats have any directional preferences for placing their nests and cache rooms. The results demonstrated that the animals preferred southern boxes for the rooms. The other group was tested for the same task, but after the ambient magnetic field was reversed by 180°. As a consequence, the animals chose

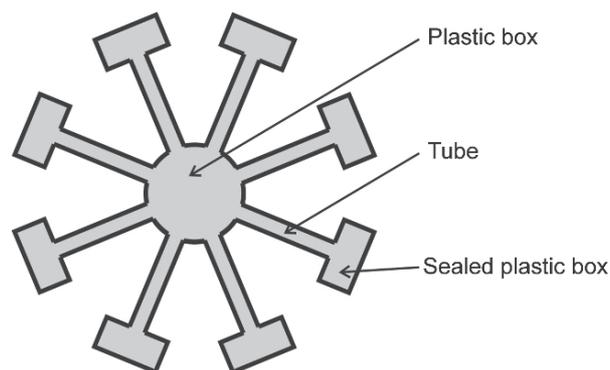


Fig. 1.16 A schematic view of the eight-armed maze used to investigate magnetic orientation in blind mole rats (adapted from Kimchi and Terkel 2001)

northern sectors of the maze for the rooms, which indicated that they had used magnetic cues while choosing. After similar testing in complete darkness, it was shown that light is not necessary for the rats to use magnetic orientation successfully (which seems logical in case of a functionally blind underground animal). In the second part of these experiments, the animals were trained to orient in a labyrinth and finally reach a goal box. After the whole group learned to find the goal box, the group was divided in two – one tested under the natural magnetic field, and the other tested under a field with its horizontal component (polarity) shifted by 180° in respect to the first. Results showed a significant impairment of orientation function in the second group, which indicates that the rats may have a magnetic compass. However, it should be mentioned that several studies have shown that the magnetic compass of blind mole rats is not an independent and primary orientation gauge, and that it interacts with other mechanisms to form the so-called path integration system (Kimchi et al. 2004) which will be discussed later.

Another similar experiment has recently been carried out on big brown bats, *Eptesicus fuscus* (Holland et al. 2006). The bats were divided into three groups. The control group was allowed to home from the release site in unmanipulated (ambient) magnetic conditions. The other two groups were held in manipulated magnetic fields during a period from 45 min before sunset to 45 min after it. One of the experimental groups was held in a magnetic field turned by 90° clockwise in relation to the ambient geomagnetic field, and the other one in a field shifted 90° anticlockwise. Radio telemetry was applied to track the directions of flight of the animals. As a result, controls headed southwards in their appropriate homing direction, while two experimental groups moved eastwards and westwards, corresponding to the magnetic field shift conditions they had experienced before release.

In addition to such convincing data, much is confusing while analyzing magnetic orientation in mammals, and several studies on rodents have failed to reveal any use of magnetic cues by these animals (Madden and Phillips 1987; Schleich and Antinuchi 2004). There may be two possible explanations. Magnetic orientation may be well-developed only in some mammals (such as subterranean rodents that have little other orientation cues available), or the experimental animals combined magnetic orientation with other cues during those failed experiments.

While due to an insufficient amount of data on different groups it's too early to speculate on how widespread magnetic orientation is among mammals, the second possible explanation seems to have received some experimental support. A recent study of magnetic orientation in Siberian hamsters, *Rhodopus sungorus* (Deutschlander et al. 2003), shows that some cues learned prior to testing can interfere with hamsters' behavioral responses to magnetic cues. For this purpose, hamsters were tested in a circular arena inside a cube coil system for magnetic field manipulations. Magnetic field was the only orientation reference available. It was clearly demonstrated that in the ambient magnetic field hamsters preferred to build their nests bimodally along the southeast–northwest magnetic axis, without any preference for either end of the axis. But when magnetic north was rotated to coincide with either the geographical east, west, or south, hamsters failed to show any directional preferences, and built their nests randomly. Having been held in an

adjacent room before testing, they were suspected to have been influenced by some other type of directional reference. So, in the second experiment their ability to orient in the magnetic field was tested in combination with some visual cues available prior to testing. The hamsters were separated into two groups held in cages located along two perpendicular walls in a room, and subsequent testing revealed that their nest-building directions were different (approximately perpendicular) in each group, and corresponded to the long axes of the walls their cages had been held against before the testing. The results suggest that magnetic cues may be not of first priority for hamsters, and learned visual information may play some role.

Therefore, debates over the ability of mammals to orient in the geomagnetic field are not appropriate at this time because of too scarce experimental data obtained on just a few species. Nevertheless, the data available suggest that at least some mammals are capable of orienting with the use of magnetic cues.

Laboratory rats subjected to a strong magnetic field (Haupt et al. 2003) demonstrated a circling locomotor activity, and the direction of this activity (clockwise or counterclockwise) depended on the direction of the field lines applied. The central neural system of mammals is very highly organized, and it is obviously the limbic system of the brain that is the primary part responsible for orientation and navigation tasks (this will be discussed later). But the location of neurons responsible for analysis of magnetic sensory input has not been clearly identified to date. Nevertheless, there are some experimental and anatomical data suggesting the involvement of the superior colliculus in this process. In a recent study (Nemec et al. 2001), blind mole rats were tested under different magnetic field conditions for expression of the transcription factor c-Fos, which is a good marker of neuronal activity. The expression level of c-Fos in the superior colliculus of the rats was then compared to the environmental conditions a rat had experienced. Magnetic stimuli seemed to activate collicular c-Fos expression compared to controls untreated magnetically. The results also allowed the suggestion that sensory input from an external field aligned in different directions or with different polarity is analyzed in the colliculi by an ordered array of neurons probably capable of “map-like” representation of the external field parameters.

On the other hand, the exact location of the putative magnetoreceptors in mammals has not been determined. However, there are some indications that the cornea may contain the hypothesized magnetite-based magnetoreceptors in mammals. Recent experiments on the gray mole rats, *Fukomys anselli*, show that animals normally able to orient with the help of magnetic information disorient under conditions of local anesthesia of the cornea (Wegner et al. 2006). It was additionally shown that light perception by the experimental animals had not been affected by the treatment, suggesting therefore no involvement of the retina.

In addition to experimental studies on rodents and bats, there is indirect evidence that cetaceans are also capable of detecting the geomagnetic field stimuli. Observations on fin whales, *Balaenoptera physalus*, migrating along the northeastern shores of the United States (Walker et al. 1992) have revealed random distribution of the animals in relation to bottom depth, bottom slope, and the intensity and gradient of the local geomagnetic field. However, an additional analysis of seasonal

distribution of the population showed a statistically reliable association of the whales to areas with low magnetic field gradient and intensity during fall and winter, respectively, with still no association with the parameters of the sea bottom. When feeding individuals were excluded from counts of these migrating population, association with the same parameters of the geomagnetic field was observed during spring and winter, respectively. The data suggest that whales may be sensitive to the geomagnetic field, but so far there is no direct evidence. Unfortunately, whales are too big and are not suited for such detailed experiments as those carried out on rodents. Therefore, close study of their magnetoreception will require some completely different methods, specific to the group and still not developed.

Therefore, at the present day we have some experimental and indirect (observational) data supporting the hypothesis that mammals possess a magnetoreception system and use it as an orientation reference. Unlike that in birds, amphibians, and reptiles, sensitivity to the geomagnetic field in mammals has not been ultimately proven. Its properties and extent are poorly understood as yet. What seems more or less evident today is that the mammal magnetic compass, unlike that in non-mammalian groups, apparently relies on magnetic field polarity and is insensitive to inclination. Among other experiments, direct testing of the nature of mammalian magnetic compass has recently been conducted on bats *Nyctalus plancyi* (Wang et al. 2007). In normal ambient magnetic conditions, the bats preferred hanging at the northern part of their roosting basket. When the vertical component of the magnetic field was reversed, they didn't alter this preference. But they began hanging at the southern end of the basket when magnetic polarity was reversed. This provides additional evidence that bats (and probably other mammals) are insensitive to the inclination of magnetic field lines, but instead use magnetic polarity for orientation.

It is possible that magnetic orientation is well developed in only some mammals, while others have lost it in the process of evolution, or at least greatly reduced its function so that it is left as a secondary orientation reference. True magnetic navigation by mammals has not been shown so far, although the "map-like" representation of sensory inputs by the mammal central nervous system suggests that magnetic "map" sense in mammals is theoretically possible. So the topic requires further research.

1.2 Celestial Cues

Although the geomagnetic field has been shown to be a significant cue contributing to navigation and orientation in various groups of vertebrates, there are several other types of external orientational information sources thought to play a significant role in some cases, and often to be of primary use. Those are celestial cues (like the Sun and star constellations), polarized light, and odors. Likewise, whether migrating over long distances or orienting within a small-range area, vertebrates use familiar landmarks that help them create a map representation of the territory

they inhabit. The use of landmarks and the previously mentioned path integration system will be highlighted in more detail in the next chapter.

Visibility of the Sun during the day, skylight polarization, and star constellations in the night have been shown to provide an important orientation reference for variety of vertebrates.

The general principle of celestial orientation is derived from the fact that the Sun, stars, and the Moon have their fixed unique time-dependent position in the sky if seen from the Earth's surface from a given global position. Further, due to Earth's rotation around its axis, these objects in the sky perform a rotation along some path (perceptually to an Earth-based observer) with the characteristic timing of the movement. The path they move along changes on a regular basis depending on the season. Therefore, it is theoretically possible to calculate where you are and where to move based on the position of a given celestial cue at a given moment. Animals are supposed to use such cues in much the same way, the only difference being that their "knowledge" and "calculator" (called also the internal "clock") seem to be inherited. The very peculiar feature of the celestial cues is that they are closely connected with timing, having a rather precisely regular schedule of movement.

Experiments designed to contribute to the issue are carried out on systems involving outdoor studies of the homing and migration of animals, as well as laboratory experiments employing artificial sky in planetariums where the position of celestial cues can easily be manipulated.

First evidence that avian orientation behavior depends on celestial stimuli came as early as in 1950 as revealed from conditioning experiments on European starlings (Kramer and Saint Paul 1950), where food location in a round cage was detected by the birds depending on the sun position, which could be altered by mirrors. Later, the proposed sun compass orientation by birds was corroborated by experiments with "clock-shifted" pigeons (Schmidt-Koenig 1958a,b, 1960, 1961). In general, these experiments showed that pigeons in which the day-night internal clock phases were artificially shifted deviated from a selected orientation direction by degrees predicted by the clock shifts.

Somewhere in that period, Franz Sauer complemented the theory of celestial orientation in birds by discovering stellar orientation in blackcaps, *Sylvia atricapilla*, garden warblers, and lesser whitethroats, *Sylvia curruca* (Sauer 1956, 1957). Later, Stephen Emlen used the so-called Emlen funnels, called after the name of the inventors (Emlen and Emlen 1966), to record the bearing vectors of the studied animals, and conducted further experiments on bird stellar orientation studying indigo buntings, *Passerina cyanea*, in a planetarium (Emlen 1967a and b, 1970, 1975). The principle of the funnel is simple. During their migratory restlessness, birds captured in a funnel-shaped cage will demonstrate their migratory direction by jumping against the walls of the funnel. If the bottom of the funnel is soaked with ink or the touch-sensitive walls are connected to a computer, birds will leave marks on the walls corresponding to the direction they choose. Methods of circular statistics allow calculation of their preferred direction. This method was tested by comparing funnel bearings of redstarts, *Phoenicurus phoenicurus*, with the directions of disappearance of released birds (Mouritsen 1998a) and proved to be

adequate. Nevertheless, this method should be used with care, since any results obtained from Emlen funnels will be much stronger if there is any corroboration obtained using other methods, especially telemetric data providing the advantage of analyzing the whole track of an animal, or at least major part of it. The results of Emlen's studies have provided early scientific evidence that vertebrates are able to use celestial cues for compass orientation for their migration, by revealing the fact that birds' orientation during their migratory restlessness (also called Zugunruhe) depends on the position of stars.

Also, in those early years of experimental exploration of celestial navigation by animals, Gustav Kramer (1957) was the first to propose the hypothesis that interpretation of the position of celestial cues by birds may depend on time, formulating thus the hypothesis of time-compensated celestial compass orientation.

Combined with later works by a number of other researchers, the celestial orientation hypothesis received ample experimental support, both for sun and stellar compasses. Later, it was revealed by conducting orientation experiments on birds in non-directional magnetic fields that stellar orientation is commonly employed as a cue by savannah sparrows, *Passerculus sandwichensis*, pied flycatchers, garden warblers, and some other species (see Bingman 1983, 1984; Wiltschko et al. 1987a).

A number of outdoor studies under overcast and clear sky have been carried out, and also support the use of celestial cues. It was shown that pigeons not trained to home from a certain site (Keeton and Gobert 1970) were not able to orient in the homeward direction under overcast sky, while they oriented well when the Sun was visible, which suggested the use of the Sun for orientation. Orientation of pigeons trained to home from a particular location was not affected by the overcast sky, indicating that they most likely used other cues, like the geomagnetic field, familiar landmarks or odors.

A recent study on marbled newts, *Triturus marmoratus* (Diego-Rasilla and Luengo 2002), showed that the newts were able to orient in the appropriate homeward direction only if stars were visible. The newts were tested under three experimental conditions: under clear sky, overcast sky, and clear sky with a magnetic field with an artificially altered direction. The animals oriented in the homeward direction (towards their pond) under clear sky conditions, but failed to orient appropriately under overcast sky, although the ambient geomagnetic field was available. What is more interesting, the newts were significantly oriented homewards under clear sky even when the magnetic field direction had been changed. The results suggest that celestial cues may provide more important orientational information for this species, which contrasts with the data obtained on red-spotted newts (already discussed), for which magnetic cues have been found to be important. It can be concluded, therefore, that magnetic orientation seems not to be a prerequisite for all amphibians able to home, and many species may use mostly celestial or other cues. But there is another possibility. Red-spotted newts were tested inside a coil system, a tool for manipulations with magnetic fields. This device has been proven as a reliable system for such tests by numerous studies. Instead, manipulations in the study being discussed were achieved by the use of magnets attached to

the testing arena. We cannot exclude the possibility that this system is not well suited for studying magnetic orientation, and thus that stellar cues might have been a complementary cue source increasing newt orientation preciseness, but not the ultimate cue, in this study and for this species. The topic needs further investigation.

A similar study on Australian sleepy lizards, *Tiliqua rugosa* (Freake 2001), demonstrates that the lizards devoid of any visual information were unable to orient homewards, in contrast to those with full visual sensing. Moreover, the lizards were able to orient appropriately even when their vision range was restricted only to the sky. But preventing their parietal eye sensory input, even if the lateral eyes functioned normally, disabled their homing, suggesting that their homing orientation may highly depend on celestial cues and be mediated by the parietal eye. However, conducting such experiments probably requires concurrent testing for magnetic orientation, in view of the light dependence of magnetic orientation found in many vertebrates. In some species, like that same red-spotted newt, the lateral eyes are not of primary importance in relation to light-dependent magnetoreception. In the case of the sleepy lizard, its parietal eye might be responsible for the light-dependent magnetic compass, and covering the organ with caps might switch it off.

Therefore, although these investigations support the use of celestial cues for migratory orientation by some vertebrates, they are of a rather inconclusive nature, because the putative light-dependent magnetic compass and use of celestial cues both refer largely to the same organs, if not receptors, of vision. Thus, techniques allowing discrimination between magnetic and celestial inputs while carrying out combined studies would be of major help here.

Another approach has been employed in several other studies examining the use of the sun compass in birds (Muheim and Akesson 2002; Wiltschko et al. 2000, Munro and Wiltschko 1993) by changing the birds' internal "clock." This "clock" in terms of celestial navigation means the ability of birds (and other animals) to calculate the expected position of the Sun depending on the time of day. To test this ability, as well as the existence of such a time-dependent sun compass, birds are "clock-shifted" by several hours and then their orientation is observed. "Clock-shifting" is achieved by holding birds indoors in a light-darkness regime shifted by a certain time period in relation to the ambient regime of the local territory. After the treatment, birds, released or tested in funnels, have been shown to orient in a direction shifted approximately by the number of degrees the Sun is expected to move for the period of the clock shift, although in reality the directions of the birds' bearings do not correspond accurately to the values indicated, and a certain scattering or deflection often takes place. It occurs as a result of the impact of several factors, including a bird's probable confusion when its magnetic compass and "clock-shifted" sun compass inputs do not coincide, or if wild birds are tested soon after capturing and, therefore, are too distressed (Muheim et al. 1999) to show their normal responses. But the effect of clock shift has generally been reported for several species, and indicates that the putative internal clock of birds compensates for the change of the Sun's position with time, and thus a selected direction of flight can be maintained during the whole day. Moreover, it has recently been shown

(Wiltschko et al. 2000) that this compensation is probably highly attuned to the speed of Sun movement. The problem is that the Sun moves with its visible angular position change at different rates during the day, being fastest near noon and slowest in the morning and evening. Dividing of pigeons into several groups released for orientation tests at different times of the day, with subsequent comparison of their headings, revealed that pigeons compensate with different rates depending on the time of the day, indicating that their internal clock functions in a rather integral way, gradually changing the compensation rate during the day.

Experiments like this one provide yet stronger proof of sun compass orientation in animals. However, the extent of its use is still unknown for sure, since some studies suggest that it is a rather accessory orientation system. Studies on yellow-faced honeyeaters, *Lichenostomus chrysops* (Munro and Wiltschko 1993), demonstrate that the birds seem to prefer the magnetic compass. For this purpose, the orientation behavior of the birds under clear sky and overcast was compared. Under an overcast sky, honeyeaters oriented in their naturally expected direction, probably relying on their magnetic compass. Birds clock-shifted by several hours slow or fast deviated from their normal direction, but the deviations were not what they had been theoretically expected to be, indicating that the sun compass doesn't act alone and most probably interacts with the magnetic compass. Similar deviations from the orientation expected if only the sun compass had been employed were observed in savannah sparrows (Muheim and Akesson 2002), with the same seeming preference given to the magnetic compass.

Moreover, pied flycatchers tested on simultaneous use of magnetic and sun compass information (Akesson and Backman 1999) failed to show any obvious preference, but nevertheless their orientation direction shifted markedly when the position of the Sun was artificially changed with the help of mirrors. This fact implies that the sun compass does function in birds when the Sun is visible. Otherwise, (overcast) birds switch to other reliable sources, such as the geomagnetic field, etc.

But, nevertheless, we cannot state that the sun compass is never used independently and as a primary mechanism. Some studies on pigeon homing (Bonadonna et al. 2000) have reported significant correlation between the headings of clock-shifted birds (homing pigeons) and the value of clock-shifts, implying that the Sun provided a major reference for the orientation of the pigeons. They deviated from their home direction by the angle expected theoretically based on the clock shifts, even regardless of the fact that they were released inside an area that was familiar, and that familiarity to the local area had previously been shown to influence pigeon sun compass orientation significantly (Wallraff et al. 1999). It may appear conclusive, but the result was obtained in only one of the two release sites, and the other group of birds failed to show anything commensurable.

Some more striking data were obtained when pigeons were tested under conditions of partial exposure to the sun arc (Budzynski et al. 2000). For this purpose, pigeons were raised so that they had never seen the Sun. Then the group was divided in two – control birds allowed to see the Sun during the whole day, and tested birds placed so that they could see the Sun only after noon till sunset. Both

groups were trained to find food in a specific direction in an outdoor arena allowing them to see the sky, but not the surrounding landmarks. After some period, the groups were tested in the morning for their foraging headings. There was no behavioral difference between the two, suggesting that the second group, that had never seen the position of the Sun in the morning, was still able to compensate their compass orientation in relation to Sun movement. Further, the groups were tested in the morning under complete overcast, and both showed random orientation.

A similar limitation on seeing the sun arc was imposed on pigeons in an earlier study (Wiltschko and Wiltschko 1980). As in the experiment discussed above, there was no difference in homing orientation between the “full arc” and “partial arc” groups.

It is difficult to draw an unambiguous conclusion from these results. The problem is that most probably pigeons with partial sun arc exposure cannot orient with the sun compass in the morning, and their good homing suggests the use of other cues. In another study, such birds were disoriented if released with attached magnets that disrupted their inherent magnetic orientation (Wiltschko et al. 1981). This suggests that they indeed use the magnetic compass mechanism if celestial reference is unavailable or unreliable. But the disorientation of both – control and experimental – groups under overcast skies (in Budzynski et al. 2000) cannot be explained in this way. One possible resolution may be that conditioning applied in this study may not be a reliable approach, as some researchers reveal problems with interpreting conditioning experimental results in the context of sun compass orientation (Rawson 1954; Kramer 1957; Schmidt-Koenig 1958b).

These studies are related to a series of other experiments, the results of which provide some more details on the development and functioning of the sun compass in birds (conducted primarily on pigeons). Altogether, these studies suggest that at least in pigeons (and possibly in other birds) celestial compass is a learned mechanism. Experiments with pigeons of different ages (Wiltschko and Wiltschko 1981a) have shown that young inexperienced pigeons under the age of near 2 months do not rely on the Sun for compass orientation, but are still able to return home from distant release sites, probably orienting with the help of other cues. At the age of approximately 3 months they acquire (learn) the ability to use the sun compass, which becomes evident from the shifted orientation at release sites by homing pigeons reared in clock-shifted conditions. The most evident cue younger pigeons might use for navigation is probably the geomagnetic field (see Keeton 1971; Wiltschko et al. 1983), as other references, such as landmarks and odors, also have to be learned.

Another remarkable evidence of the learned nature of sun compass orientation in pigeons was obtained when young pigeons that had never seen the sun and had been raised in a 6-h-slow shifted photoperiod didn't depart from the release sites with the 90° deviation from the homeward course expected for 6-h clock-shifted birds, but instead were properly oriented homewards (Wiltschko et al. 1976). However, later exposure of these birds to normal time produced the same effect as a 6-h-fast clock-shift on normal birds. This suggested the learned nature of the responses. After some time the birds resumed normal orientation. However, when subjected after 1 to 3 months later again to the 6-h-slow clock-shift, the birds didn't

show the response expected under the clock-shift, which was interpreted by the authors as indication that the birds might have downgraded the importance of the cue and relied upon other orientation references, which indeed seems evident from the results. Nevertheless, after being kept in normal conditions for a year and then subjected to a 6-h-slow photoperiod shift, the birds reacted with the orientation deflection expected for the clock-shift, which may mean that during the long period of stable photoperiod conditions they had recalibrated the sun compass and the cue had become important again. Altogether, this suggests that the sun compass of birds (at least that of pigeons) is a learned mechanism which is calibrated (and may be recalibrated, even in adults, under certain circumstances) with the help of other navigation reference cues (see also Wiltschko et al. 1984).

Stars have also been shown to be an independent and important orientation cue for nocturnally migrating birds (Sauer 1956, 1957; Emlen 1967a). In Emlen's experiments, indigo buntings were tested both in the planetarium and outdoors. Outdoor testing was carried out in the absence of the moon, and planetarium tests didn't include planets on the artificial firmament, which suggested that the birds responded to the movement of the stars solely.

Orientation of reed warblers, *Acrocephalus scirpaceus*, when they start their nocturnal migration was shown to be highly dependent on visibility of celestial cues at dusk, and stars in particular (Akesson et al. 2001a). In this study, radio telemetry revealed that the warblers departed with less scatter in orientation under clear sky night conditions than under overcast. The main departures were undertaken during clear sky nights, while in the overcast nights significantly lower numbers of warblers initiated their migratory flight.

In fact, there are three main hypotheses proposed to describe exactly how birds use stellar cues. In the first hypothesis, it is suggested that birds possess true stellar navigation. This means that they are able to deduce their global position from the pattern of the stars at a given time and region. Theoretically, latitude can be deduced from the height of the stars above the horizon (say, the North Star is suitable for this task, but any other visible star will also qualify if taken in relation to a specific time). Longitude, in its turn, can be calculated by detecting the rotational phase of certain stars, which is highly specific for the time of the night in any given location, because stars also move along an arc-like track in the sky during the night, and are found in a constant location if seen at the same time for a number of consecutive nights. Their location, however, also depends on the season, but birds migrate at specific periods and may be adjusted to this. Using this navigational information, they migrate (orient) to their destination (wintering areas or stop-over spots) along the routes dictated by their inner compass program (loxodrome course). There are some variations of this hypothesis. For instance, there are suggestions saying that birds reach their goal along orthodrome routes – shortest distances between two points on the globe, or that they do not head for goals, but to the locations they expect to be at this time of the season.

The second hypothesis suggests that birds use stellar cues much like the Sun and form a similar stellar time-compensated compass, but are unable to determine their global positions with the help of stars (their rotational phase).

And finally, the third hypothesis assumes that birds possess a time-independent stellar compass and estimate north from the geometrical pattern of the stars, regardless of the rotation of stars (for more detailed description of these hypotheses see Emlen 1975; Alerstam et al. 2001; Mouritsen and Larsen 2001).

The actual manner in which birds use these cues remains debatable. This field also lacks studies. But some results supporting this or that particular hypothesis have been obtained and can be discussed.

First of all, it should be mentioned that solar and stellar orientation systems are somewhat different in respect to the demands imposed on a bird's mental processing of the cues. Instead of one reference during the day (solar) for orientation, the night sky contains a huge number of stars, and a bird has to identify those important for orientation. Moreover, different stars move with different linear speeds. If the North Star rotates around a minute circle, other stars move faster, the more distant from the North Star the faster. Therefore, in addition to identifying the key stars or constellations, a bird needs to compensate differentially for different stars, and this compensation will be antiparallel in the southern hemisphere – clockwise in the northern hemisphere, and anticlockwise in the southern (Emlen 1967a,b).

Various experiments have been carried out to test these hypotheses. Clock shifts, just like those designed for solar orientation, are much easier to achieve in a planetarium, because it doesn't require rearing birds in "shifted" regimes. The artificial sky of a planetarium is exposed to birds during testing in a phase corresponding to certain hours of the night. Say, we need an advanced 3-h clock shift. Now it is 2:00 a.m.. A bird is shown the sky rotated so that it corresponds to the natural 11:00 p.m.. A bird "feels" itself being advanced by 3 h, because its internal clock tells it that it's 2:00 a.m., but the sky is as if it were 11:00 p.m.. If birds rely on a time-compensated stellar compass, such a shift will produce a shift in their directional preference. However, it should be stressed that the effect is to take place only if birds use stars for true navigation. In this case, it is easy to imagine, that if now it is 2:00 a.m., and we see the sky as if it were only 11:00 p.m., we should take to the east for a distance corresponding to 3 h, and at some longitude we will find the "normal" sky. Thus, for a bird such a shift would mean that the bird is located at an inappropriate longitude. Then a bird would undertake to compensate for the "displacement" and take a more eastward direction. It is somewhat misleading to build experimental setups based on the assumption that birds will directionally respond to stellar clock shifts in case they use a time-compensated compass corresponding to the second hypothesis presented above. A mere compensation of star rotation will not result in a change of direction unless a bird has a mental representation of the longitude it is located at. Such a change will only result if a bird at least is aware of its longitudinal displacement relative to the longitude of its destination (say, wintering quarters).

A study of stellar orientation in buntings (Emlen 1967b) revealed that the birds didn't respond by a change of heading when they were subjected to a shifted starry sky, neither advanced nor retarded. Emlen concluded that the only explanation consistent with the results is that birds do not use any time-compensated stellar compass, and hypothesized that the geometry of constellations distributed constantly

relative to each other could be a possible candidate reference. But experiments with selected constellations presented to the birds (even with the Polaris invisible) failed to support the suggestion.

In a later study, Emlen (1970) conducted an experiment dedicated to further clarify the mechanism of stellar orientation in birds on indigo buntings, *Passerina cyanea*. Juvenile birds that had never seen the night sky were divided into three groups. Individuals of group A were raised under conditions in which they couldn't see any celestial cues. Those of group B were raised so that they periodically could see the planetarium artificial night "sky" that duplicated the natural sky with the corresponding rotation direction and speed. And finally birds of group C were raised in a way similar to group B, except for the artificial night sky of the planetarium rotated around the Betelgeuse star in the Orion constellation instead of the North Star. All this took place during the summer premigratory period of the birds' first migration. Later, during the migratory period, when the birds started exhibiting their migratory restlessness common for this period, they were tested for migratory orientation in Emlen funnels under the artificial planetarium sky which now was stationary. The logic of such testing was the following. Emlen aimed to test several hypotheses on how migratory birds use the night sky. Sauer (1957) had previously suggested that birds might have a genetically predetermined map of the star patterns. If that was true, either true stellar navigation or stellar compass navigation based on these patterns might be suggested. On the other hand, based on his own and others' observation, Emlen also suggested that the ability to use stars might be learned by birds and that birds may not have a star map, but instead use celestial rotation as a reference mechanism assisting them in learning the necessary stellar cues, which they later use as a compass.

The result of the study was as follows. The orientation of group A, that had never seen the starry sky in the first premigratory period, was indistinguishable from random. The birds from group B, which had previously experienced exposition to the normal sky, oriented towards the south, their normal migratory direction. As foreseen by Emlen, the birds of group C directed towards the new "south" in respect to the Betelgeuse star, which they obviously interpreted as the indicator of the true north, as can be deduced from the experimental setup for this group.

This behavior is inconsistent with the hypothesis of a preprogrammed star template (map), otherwise the birds of group C should head for true stellar south deduced from the star patterns. The fact that all birds were tested under a stationary artificial sky, and thus were unable to calculate the axis of rotation, together with the expected difference between headings of group B and group C, suggests that they had learned the position of the axis of rotation from their premigratory experience. Taken together these results seem to exclude the possibility of any preprogrammed star map in the tested birds, and suggest that birds rather observe the axis of rotation of the night star pattern and remember the position of least rotation (which in the case of natural sky coincides with the position of the North star) and use this part of the sky as an indicator of the geographic north. This, in turn, is supposed to provide them with a stellar compass which they use during migration.

Additionally, testing pied flycatchers' and blackcaps' stellar orientation (Mouritsen and Larsen 2001) shows that the birds respond by the expected orientation shift only when the position of the Polaris (the North Star) was changed.

Figure 1.17 shows the principal design of the experiments with Emlen funnels. The funnels with birds are subjected to experimental conditions (stellar orientation manipulated in a planetarium, in this case). The reading of the results may also be computer-controlled. No clock-shifted rotational phase evoked any shift in their orientation. The authors' conclusion was similar to that of Emlen (for more

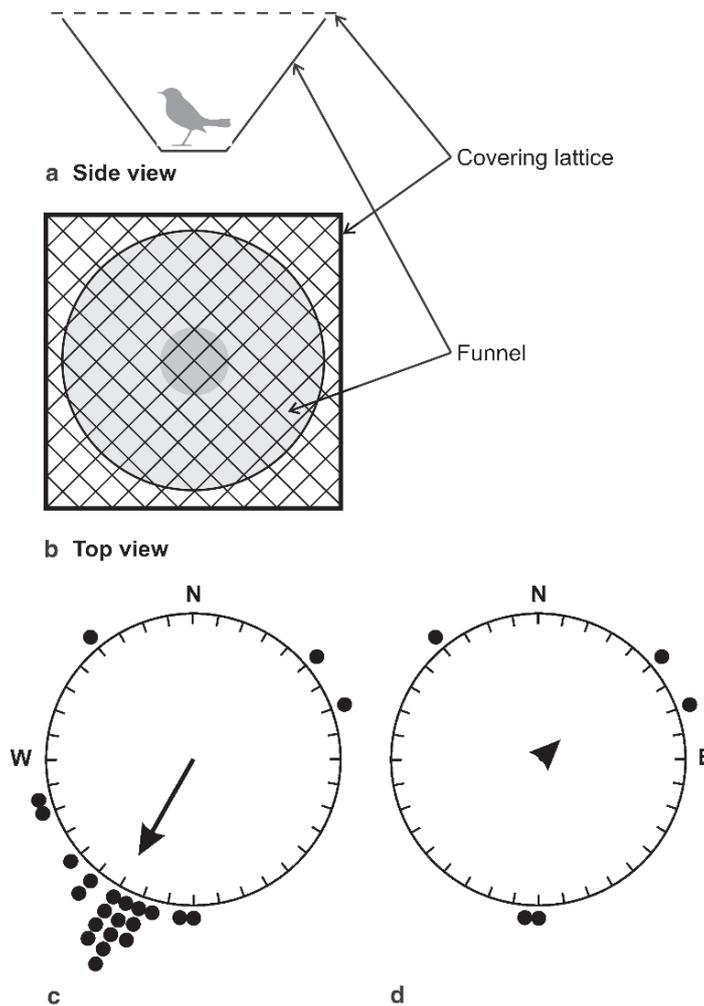


Fig. 1.17 Principal design of the Emlen funnel (**a** and **b**) with an example of the readings chart (**c** and **d**). By jumping into different directions a bird leaves marks on the walls of the funnel. This marks are recorded (*black dots* on **c** and **d**) with respect to direction on the readings chart and analyzed by means of circular statistics (**c** and **d** modified from Akesson et al. 2001a)

analysis, see also Emlen 1969, 1970, 1971), suggesting that the avian stellar compass functions without time compensation which has been observed for the bird sun compass. Several other studies, like conditioning of mallards, *Anas platyrhynchos*, to directionally respond to artificial sky patterns (Wallraff 1968), also failed to show any use of time compensation during stellar orientation by birds.

It is interesting to note that approaches to studying stellar time-compensated orientation should differ from those for a solar time-compensated compass. There seems to be a significant difference between the principles of the two types of compasses. The Sun is the only celestial orientation cue for birds during their day orientation, and the cue moves along an arc-like track in the sky. So, this reference is motile, changing the location of the "point of origin." During nocturnal orientation, birds seem to use the North Star as the point of origin (based on most studies), and it is almost motionless, maintaining a constant position during the whole night. Therefore, clock-shift experiments suitable for sun compass studies do not apply in some cases for stellar orientation, because birds appear to compensate for the time-dependent difference in star locations relative to the Polaris. The geometry of constellations most probably helps birds identify the North Star, and this ability may be programmed genetically. Again, there are no data proving that birds are ultimately able to identify the North Star, and most probably they identify a region encircling the star in some vicinity of it. However, this is only a speculation and the topic requires further studies.

By this time, it is hard to speculate on what criteria birds use, or better what factors or triggers help birds in selecting the stable region of the night sky. What part of this learning process is preprogrammed, and what cues are being sought by birds while they learn star patterns and their motion, remains enigmatic. Nevertheless, based on the results and conclusions from the work just mentioned and several similar studies, it can be suggested that birds use star patterns just like any other visual landmarks they learn to use during their life. However, it is obvious that there is some most probably genetically predetermined mechanism that ensures selection of individual stars or patterns based on some criterion. Interestingly, landmark stability has been demonstrated to be an important feature for visual landmark-based navigation in some fishes (Odling-Smee and Braithwaite 2003) and rats (Biegler and Morris 1996). The positional stability of the region near the North Star in the night sky may well be one of the factors prompting selection of this region as a compass reference. A bird might memorize (imprint) this cue and develop a kind of negative phototaxis urging it to head away from this cue. This suggestion is particularly supported by a study on garden warblers, in which experimental birds tested for migratory orientation just headed away from stable stars (Weindler et al. 1997).

In this experiment, the birds were hand-raised in the ambient geomagnetic field and, during their pre-migratory period, exposed to an artificial sky in a planetarium. The warblers were divided into four groups. The first group (serving as control) was presented a sky resembling the natural sky (with "north" coinciding with that in nature) and rotating in its natural direction. The other three groups were exposed to a sky rotating in the opposite direction under three arrangements: north coinciding

with natural, located at east, and located at west, respectively. All the birds were tested in the absence of magnetic field. As a result, the control group was significantly oriented in their naturally appropriate southwest direction. All the others directed due south in respect to their particular “north.” Among these three groups, the one exposed to “north” coinciding with natural demonstrated the least scatter. Analyzing the results, it’s easy to behold that the birds’ orientation depended only on the direction of celestial rotation (normal or reversed). The difference in behavior between the control group and all the others cannot be explained based solely on geometrical relations between stars, because there was no difference, and the sky had identical star patterns for all groups. It seemed as if the birds used the North Star as a coordinate reference and compared its position with other stars. All three experimental groups showed directions just leading them away from their north, except for the control group, which may indicate that stellar orientation might have interacted with some other cues. These experiments also argue against pure true stellar navigation in birds, otherwise the birds would have headed in opposite directions depending on the experimental direction of celestial rotation.

Interaction of the avian stellar orientation system with at least one other cue, namely the geomagnetic field, has been shown in a number of studies which will be discussed in the next chapter. In short, these studies have demonstrated that it is interaction of stellar and magnetic information that allows birds to accurately locate their migratory course.

Another question is: when do birds learn a stellar reference system? Initially, Emlen (1970, 1972) suggested that based on his observations birds seem to have a sensitive period during their first premigratory period, and this may be the time when they learn (or imprint) this cue and use this information ever afterwards. This suggestion was particularly suggested by a study following the 1970 experiments. The birds studied under Betelgeuse conditions as was described above overwintered indoors, but were kept in open-air aviaries through the following summer, having thus had an opportunity to investigate the normal night sky before the next autumn testing. After that they were tested again under a stationary planetarium sky and continued to orient away from the Betelgeuse star. Thus, Emlen (1972) concluded that they had not relearned the reference system and continued using the “old” Betelgeuse reference star. Indeed, one-time imprinting during the first premigratory period by birds may take place in nature. However, some researchers (e.g., Liepa 1994) advise not to take this conclusion as unambiguous truth. The point is that the natural and planetarium skies are in many aspects different (e.g., the spectrum of light), and birds may well perceive these as two different conditions and respond differently according to the pattern memorized for each case – the North Star as the reference for the natural sky, and Betelgeuse as the reference for the experimental planetarium sky. Whether or not this is the case, the problem appears to need more research to clarify the issue.

Birds are most probably not the only group of vertebrates capable of celestial navigation. Some other vertebrates, like migrating salmon, are also suggested to employ the cues. Nevertheless, data on other vertebrates is rather scarce, and much research is still needed.

1.3 Sensitivity to Polarized Light

Light from the Sun enters our atmosphere and undergoes a process called polarization. Light possesses the properties of electromagnetic waves, and perpendicularly arranged electric and magnetic oscillating fields are registered in a light wave. If light is not polarized, a light beam includes (roughly speaking for simplicity) a set of pairs of mutually perpendicular waves oriented at different angles, forming a circle on an imaginary cross-section plane with the origin point positioned at their intersection. As a result of polarization when light passes through polarizing substances, only waves under certain angles with respect to an imaginary horizontal plane are allowed to move further. The angle of the electrical field vector (e-vector) is usually referred to in navigation literature as the angle of light polarization, and it is possible to detect this plane (angle). Humans use special devices to detect it, but many animals appear to register it by “unaided eye.”

The pattern of light polarization in the atmosphere or under water has been found to be highly regular depending on the position of the Sun in the sky, which suggests that the pattern of light polarization may constitute a reliable source of orientational information for many animals. Polarized light has been shown to have multiple uses in the animal kingdom, ranging from foraging, defense, and communication to orientation and navigation (see Wehner 2001).

Various vertebrates are assumed (in many cases it has been proved experimentally) to possess a navigation system based on the pattern of light polarization, taking into account the regular distribution of it through the globe (Cronin and Shashar 2001). Several properties of polarization of natural light make it potentially highly proper for this task. For example, the light polarization pattern is substantially conserved even if the sky is overcast and light passes through thick layers of clouds (Pomozi et al. 2001). Water environments are also known to contain polarized light, most of which is concentrated in shallow waters (Shashar et al. 2004). Polarization patterns in the air and under water differ, but light reflected by water surfaces is, as a rule, horizontally polarized and can serve as a navigational marker for terrestrial animals trying to locate water bodies from some distance. Even if water is not visible, it can be detected by the horizontally polarized light pattern above it, which is detectable from many kilometers away. If terrestrial animals have a system of polarized light discrimination, the remarkable ability of some of them (turtles, for instance; suggested by Gibbons et al. 1983; see also Yeomans 1995) to find distant water bodies could easily be explained based on it. In more general application, the system would serve for orientation, since different parts of the sky have a different polarization pattern depending on the current position of the Sun, and direction estimation becomes possible (Wehner 2001).

Polarization sensitivity among fishes is best studied on salmonids. Early studies on different salmonid species (Dill 1971) have revealed that they are able to discriminate between differently polarized lights. More recent experiments support this evidence (Parkyn and Hawryshyn 1993, 2000; Coughlin and Hawryshyn 1995).

Juvenile rainbow trout, steelheads, and brook charrs, *Salvelinus fontinalis*, were trained to orient according to the axis of linearly polarized light (Parkyn et al. 2003). As a result, rainbow trout oriented predictably depending on the axis of light polarization in 70% of cases (other species also demonstrated axis-dependent orientation). By contrast, untrained rainbow trout didn't show any preferred direction and oriented randomly. The fish trained under laboratory conditions showed the expected orientation under natural conditions as well. When a diffuser causing light depolarization was applied, trained fish failed to orient parallel to the plane of incident light polarization.

The distances up to which fishes are able to detect prey were also shown to increase significantly under polarized light conditions compared to diffuse illumination in juvenile rainbow trout (Novales-Flamarique and Browman 2001), which also suggests discrimination between polarized and unpolarized light in juvenile trout on the one hand, and the possible important function of polarization sensitivity in fishes on the other.

Electrophysiological recordings from the optic nerve have confirmed sensitivity to both vertically and horizontally polarized light in many salmonids species, suggesting that this feature may possibly be widespread among fishes (Parkyn and Hawryshyn 2000).

All the studies quoted above investigated juveniles. Interestingly, ultraviolet receptors supposed to take part in polarization sensitivity in salmonids have a specific cycle during a fish's lifespan. As a juvenile undergoes the smoltification transformation, its UV receptors disappear from some parts of the retina and reappear in adults. This strange cycle has been proposed to relate to the fish's foraging strategies, since the UV receptors are most abundant at periods of intensive feeding on zooplankton or small fish, which are assumed to be more visible for the fish under polarized UV light. Receptors of other spectra do not change throughout the fish's lifecycle (Novales-Flamarique 2000; Deutschlander et al. 2001; Hawryshyn et al. 2003).

Such a transition cycle of UV photoreceptors has led to a suspicion that polarized light sensitivity probably serves primarily for prey detection, since navigation by polarized light has yet not been shown conclusively (Losey et al. 1999). Moreover, the stages of salmonid development coinciding with better UV-sensitivity are known to occur mostly in shallow waters where polarized light is most abundant. Nevertheless, navigation by fishes based on polarized light patterns still needs more research, since the hypothesis hasn't been disproved and has some potential to be challenged in future.

Evidence for polarization sensitivity in terrestrial vertebrates is also scarce. Most of it has been obtained by using the same methodology – training animals to respond in a certain directional orientation depending on the direction of the axis of the light polarization, and subsequent testing of their orientation under other directions of polarized illumination, either under natural or laboratory conditions.

Using this principle, polarization sensitivity was found in amphibians, such as the tiger salamander, *Ambystoma tigrinum* (Adler 1976; Taylor and Adler 1973,

1978), and reptiles, such as sleepy lizards (Freake 1999), for which the parietal eye and the pineal were shown to be of primary importance for the process (Taylor and Adler 1978; Freake 2001).

Experiments on birds are disputable. On the one hand, we have some evidence that birds use the light polarization pattern of the early morning sky to get directional information while they perform their seasonal migration. Nocturnally migrating passerines are known to migrate shortly after sunrise in the early morning, often regaining their appropriate direction after displacement during the night (Gauthreaux 1978). This interesting habit allowed speculations that birds might use polarization of the skylight at this morning time to calibrate the direction of their flight. Several species of North American migrating warblers were tested in cages, and observation showed that the birds are much better oriented in their seasonally appropriate direction in the early morning under clear sky than under overcast conditions (Moore 1986). Application of polarizing material in this study made it possible to evoke predictable patterns of birds' headings depending on the axis of polarization. Similar results supporting this study were obtained in a few other experiments (Able and Able 1993, 1995a). However, application of artificial polarizers to manipulate orientational responses in birds has, itself, been questioned as a proper method in the context of navigation research, since at least in one study on black-caps (Helbig and Wiltschko 1989) birds' responses to artificially polarized light were reported to differ from that to natural light, although their general sensitivity to polarized light was evident.

Meanwhile, in view of some unsuccessful attempts to evoke polarization sensitivity response in birds, some researchers are inclined to explain these failures in terms of the experimental conditions. A recent study by Muheim et al. (2006a) has demonstrated that savannah sparrows allowed to view the natural sky above the horizon seemed to recalibrate their magnetic compass by collating its information with the patterns of the sky light polarization above the horizon. The results became evident when orientation headings of birds tested in the ambient magnetic field without viewing the sky were compared with those obtained on individuals that had had the access to the sunset and sunrise polarized light during the pretesting period.

Therefore, despite the fact that most data obtained so far are not sufficiently convincing, we have some evidence indicating that birds are able to perceive polarized light. There is more evidence that birds use polarization patterns of the sky for orientation than for other groups of vertebrates. Whether all birds or only some of them have this capability remains a question, since, again, some studies have failed to find polarization sensitivity in several other bird species.

For example, studies on pigeon bearings in respect to orientation of the e-vector of linearly polarized light (Coemans et al. 1994) failed to show any detection of polarization by the birds. Electroretinographical recordings from pigeons experiencing flashes of polarized light of different spectra (including white and UV) directed at the yellow field were compared to those under unpolarized illumination, and revealed no difference between the two conditions, which also suggested that the pigeons were not sensitive to polarization of light (Hzn et al. 1995). In addition

to pigeons, European starlings and Japanese quails, *Coturnix coturnix japonica*, trained to find food depending on polarization pattern have also failed to show any signs of polarization sensitivity (Greenwood et al. 2003).

Therefore, at this time it has not been convincingly shown that birds use polarized light as an orientation cue, though some empirical indications of polarization sensitivity in birds have been obtained. A huge field for future experiments and observations exists here.

1.4 Olfactory Cues

The use of olfactory cues for navigation by animals remains one of the most debatable topics over the past decades. Much evidence supporting the employment of olfaction has been obtained, though most of this evidence is indirect and involves orientation tests with animals (mostly birds) deprived of olfactory function. The prevention is achieved in several ways, the most popular of which are dissection of the olfactory nerve, anesthesia with the help of chemicals, and direct occlusion of the sense by filling the bird's nostrils with wax. Regardless of the seeming evidence supporting the involvement of olfaction in animal navigation, one should analyze such data carefully, since we also have some evidence that olfactory organs may be important for magnetic navigation (responsible for the putative magnetic "map" sense). Therefore, manipulations with olfaction in many studies on birds might theoretically have disabled or impaired its putative magnetic application, with the exception, however, of those studies in which olfaction was precluded by inserting cotton plugs.

Nevertheless, the ever growing body of evidence indicates that olfaction may be crucial at least during short- and middle-scale navigation, like homing in pigeons or the final stages of the migration of green turtles finding the tiny Ascension Island in the middle of the Atlantic ocean (for details see Able 1996; Wallraff 2004). Some more recent approaches, like manipulations with air content or wind direction perceived by experimental animals seem to have added some additional weight to the results supporting the hypothesis.

Empirical evidence supporting the use of olfactory cues for orientation and navigation purposes has been collected for exemplary representatives of several major groups of vertebrates.

1.4.1 Fishes

Migratory salmon are supposed to considerably rely upon olfactory cues while returning to their breeding streams. Anadromous forms of salmonids hatching in springs and rivers spend some time (often up to several years) in fresh waters, and then migrate to the open sea for growing into adults. As adults, they return to their

home hatching sites to spawn. During this lifecycle, they face significant navigational demands laid upon them by the huge distances they cover in the open ocean before entering the exact river mouth they left during the seaward migration. Then they move along these rivers to reach their specific home tributaries to spawn. Their way in rivers may be as long as their sea migration, and constitutes an environment where navigation might require other approaches than those applied in the sea (for review see Dittman and Quinn 1996). Nevertheless, in most cases their homing is amazingly precise. While salmon open sea navigation is generally supposed to rely upon diverse cues, like magnetic and celestial (Quinn 1980; Quinn and Brannon 1982), or polarized light (Hawryshyn et al. 1990), olfaction has been shown to play an important role during the salmonid in-river homing. Once a fish enters coastal and estuarine waters it is supposed to “switch” its orientation system to that used in fresh waters (presumably olfactory). The process may be gradual and include “mixed” orientation cue use while at the river mouth (Pascual and Quinn 1991).

It has been proposed (Hasler and Wisby 1951) that salmon smolts imprint the odor of their natal stream and later use it as the key feature for locating their stream while migrating as adults for spawning (for review also see Hasler et al. 1978). This hypothesis is based on three main prerequisite assumptions: (1) streams have different chemical features that are relatively stable over time, (2) salmonids are able to discriminate these differences, and (3) salmonids memorize these features while migrating toward the sea and remember them through all their oceanic life until the reverse homing migration starts (Dittman and Quinn 1996).

Most experiments in this context have included transplantation of hatched fish into different streams. It was proposed (Hasler and Scholz 1983) and subsequently corroborated by experimental evidence that if the imprinting does occur, it is rapid and confined to a very short period before the smolt stage. It is also connected with the parr-smolt transformation involving physiological changes of the fish body preparing it to life in the sea (in salt waters) and accompanied on the endocrine level by an increase in thyroxine concentration (Scholz et al. 1992). Thyroxine seems to be responsible for salmon odor memory, since coho salmon, *Oncorhynchus kisutch*, pre-smolts with artificially raised thyroxine levels demonstrate the ability of long-term odor memory, in contrast to untreated control individuals (Scholz 1980).

Since the process of remembering natal river odor seems to be irreversible and has its confined sensitive period, just as in the case of visual imprinting in birds, the term “imprinting” is also applied here (Dittman and Quinn 1996).

When salmon were taken away from their hatching streams as smolts and released at other reservoirs, they returned to the sites of release while migrating for spawning as adults (Shirahata and Tanaka 1969; Jensen and Duncan 1971). It was also shown that 4 h were sufficient for coho salmon smolts to imprint their new home and consequently return to it. Coho salmon released in other rivers several weeks after their smolt transformation, by contrast, failed to show such consistent returns (Peck 1970). Another study provides additional support of such a rapid imprinting in brown trout, *Salmo trutta*. Trout raised in Dunalastair Reservoir (Scotland) migrate to spawn in the lake’s tributaries. Two groups of trout taken

from their natal tributaries were transplanted to another stream, one group before their smolt transformation, and the other after it. The fish transferred before their smolt stage returned to the site of release, while those transplanted after smoltification migrated to their natal (original) spots (Stuart 1959). These and many other similar studies provide sufficient evidence for imprinting of hatching sites by salmon, however only in the case that they remember odors, since fish may possibly remember some other site-specific cues as well.

Many studies indicate that imprinting for chemicals concurs with the period of smolt stage formation in several species. Thus, steelhead trout, *O. mykiss* (Cooper and Scholz 1976) and coho salmon (Cooper et al. 1976; Johnsen and Hasler 1980) imprinted as smolts for artificial chemicals which didn't naturally occur in rivers tended to select for spawning streams where such chemicals had been dispersed artificially.

More recent studies (Tilson et al. 1994, 1995) on kokanee salmon (the non-anadromous form of sockeye salmon, *Oncorhynchus nerka*) have shown, however, that this form is able to imprint odors also as alevins and fry.

Additionally, coho salmon taken from their natural hatching river site and kept during smoltification in a holding facility in spring water (Jensen and Duncan 1971) were tagged and released into the river. At the time of spawning they were recaptured near a spring-water discharge 0.8 km downstream from the point of release, artificially created so that it alternated with river-water discharges on a daily basis. No salmon were caught when river water was released. No marked individuals were recaptured at the hatchery site (for a brief review, see also Scholz et al. 1992).

Therefore, the studies just presented provide experimental evidence that homing salmonids use imprinted olfactory cues while migrating to their spawning streams.

Nevertheless, in natural conditions salmon olfactory imprinting may be more complex than that revealed in laboratory or field studies. Single odorant applied in many tests to manipulate the fish odor imprinting may not necessarily reflect what is going on in nature, where complex patterns of different odors occur. It has been shown that fish recognition of odor mixtures may differ from that of a single odorant (Dodson and Bitterman 1989). Moreover, the diversity of lifecycles among salmon may also have produced some variations in imprinting strategies in different species. Thus, if pink, *Oncorhynchus gorbuscha*, and chum, *Oncorhynchus keta*, salmon migrate to the sea right after hatching, chinooks, *Oncorhynchus tshawytscha*, remain for some period in their native springs, and sockeyes grow in lakes (Groot and Margolis 1991). Such variations in salmonid lifecycles may have impacted their odor imprinting. Thus, imprinting before smolt transformation might be expected in, for instance, sockeyes, which migrate a year or more before the parr-smolt transformation starts (see Dittman and Quinn 1996; Peterson 1982).

It has been proposed (Harden Jones 1968) that salmon memorize several odors of several sequential sites along their seaward migration and, later, recollect those sites in the reversed sequence. This system, therefore, may have been changed evolutionarily, according to the migration pattern of a particular species or population. This point of view is supported by the fact that salmon migration towards spawning

sites is not continuous, and includes many stopover sites where fish may stay for months before entering their precise spawning quarters (Berman and Quinn 1991). Chemical characteristics of these stopovers may possibly be memorized by migrating salmonids as well. In addition, revision of transplantation experiments reveals that salmonid smolts imprinted to a release site (see above) demonstrate better homing to the site if it is close to their natal hatching site, the closer the better (Johnson et al. 1990), which is also consistent with the hypothesis of sequential imprinting, as closer sites are expected to be more similar to the original in chemical composition.

1.4.2 Turtles

Sea turtles are known to possess an excellent sense of smell (Owens et al. 1986). Therefore, several species migrating over long distances have been suggested to use wind-borne smells as orientation markers.

Green turtles, *Chelonia mydas*, forage along the eastern coasts of Brasilia and move over 2,000 km to breed on the beaches of Ascension Island in the middle of the Atlantic Ocean several times a season. This long journey requires outstanding navigational abilities in order to find such a tiny island in the vast monotonous ocean. It has been proposed that olfaction is among the orientation mechanisms controlling their migration (Luschi et al. 2001; Hays et al. 2003).

The core of experiments with green turtles have been those involving removing females (right after egg laying) away from the island in different directions. At the time of turtle nesting, stable trade winds blow from the southeast. Experiments with females displaced for 50 and more kilometers away from the island have shown that the turtles do not return directly to the island and move in multiple changing directions before estimating the appropriate course towards the island. Closer to the island they finally catch the sought direction and approach along a straight route. More importantly, only downwind-displaced females have been able to locate the island fast. Those removed upwind returned considerably later and only after crossing the downwind line, and not all individuals found the island – several females after a short search abandoned the island-finding activity and headed for their foraging grounds near Brazil. Disorientation of all females at initial stages of homing, as well as the return of only downwind-displaced individuals, is difficult to explain by means of the magnetic navigation hypothesis. The results are in better accordance with olfactory orientation.

Birds

Bird olfactory orientation and navigation is, perhaps, the best studied case among vertebrates, and has evoked much debate over whether they use smells for navigation, which has finally led to formulation of the olfactory navigational map hypothesis.

Whether or not this is the case, however, there is some experimental evidence supporting the importance of olfactory cues in bird orientation. Most studies in this field have been carried out on homing pigeons, and involve rather short-range navigation. However, several other species, such as some *Procellariidae*, have been addressed as well.

Several approaches have been applied to investigate the role of olfaction in pigeon orientation and navigation. The main methods have included: (1) blocking pigeons' sense of smell, (2) manipulations with air contents, (3) olfactory "simulation" of certain sites in question, and (4) changing wind directions at the pigeons' home loft location (for review see Wallraff 2004, 2005).

Deprivation of the olfactory sense by dissection of the olfactory nerve in pigeons, initiated by Papi and his team (Papi et al. 1971) and followed by several other research schools, demonstrates that anosmic pigeons' homing is significantly impaired compared to untreated individuals. A series of subsequent studies with similar approaches have supported these results. Taking into account that dissection of the olfactory nerve might have caused some non-specific effects on pigeons' behavior, another set of experiments was designed. Pigeons were treated in two ways. The control group was subjected to unilateral dissection of the olfactory nerve and ipsilateral (on the same side) sealing of one nostril with wax. The experimental group was treated in the same two ways but contralaterally (nostril sealing on one side, and nerve dissection on the other). In this way, neither traumatic impact nor breathing differed between the groups. As a result, only control birds were able to orient appropriately in their home direction, suggesting that nerve dissection had not produced any significant non-specific behavioral impact on the birds, but rather olfaction impairment had directly affected the homing ability of the pigeons (Papi et al. 1980). Ideas have been expressed that dissection of the olfactory nerve may simultaneously impair the magnetic sense (e.g., Mora et al. 2004) in case the putative magnetoreceptors are located within the nasal cavity or are somehow affiliated with the olfactory nerve, as pigeons with dissected ophthalmic branch of the trigeminal nerve, which is located in proximity to the olfactory nerve, seem not to discriminate between the presence and absence of magnetic fields. However, dissection of the olfactory nerve itself didn't cause magnetic indiscrimination. In contrast, an intact olfactory nerve has been shown to be crucial for homing performance in pigeons in another study (Gagliardo et al. 2006), suggesting that the homing success with intact olfactory nerve is most likely due to its direct olfactory function.

To investigate further the question of whether anosmia treatment produces specific olfactory impact on pigeons' orientation or whether they are generally harmed by the treatment, pigeons were divided into three groups (Benvenuti and Gagliardo 1996): (1) unmanipulated controls, (2) controls deprived of olfaction by unilateral zinc sulfate application and ipsilateral nasal plugs, and (3) experimental birds with unilateral $ZnSO_4$ and contralateral nostril plugging. After release at 55–79 km (a range exceeding pigeons' familiar area) their homing was assessed. The results showed that the experimental group had demonstrated significantly worse homing performance than both control groups. Difference in homing efficiency between the

two control groups was not significant, which supported the idea that blocking the sense of olfaction by zinc sulfate produced a direct effect on the pigeons' orientation by impairing their olfaction as an orientation reference, and it imposed no general damage for their brain functioning.

It has been revealed that pigeons also use landmarks while homing, but the range where this type of cue is effective usually approximates to 30–40 km (Wallraff 2004; Guilford et al. 1998). So when pigeons are released within this area, results may suffer from some cue interplay, and pure olfactory orientation or navigation experiments are difficult to designate. The importance of this point has been well documented during some olfactory orientation experiments where trained and inexperienced birds were compared. Once trained to home from certain release sites pigeons home far better. Trained pigeons have been shown to home well from familiar release sites regardless of whether they were treated with zinc sulfate or left unmanipulated (Bingman et al. 1998a). However, when released from unfamiliar sites, only untreated birds oriented properly. Afterwards, two groups (anosmic and untreated) of inexperienced birds were released at unfamiliar sites, and both homed poorly, although untreated pigeons performed better and the difference was statistically significant. Their poor performance suggested that being inexperienced they lacked some other than olfactory cues (obviously learned landmarks), but the statistically different results between the anosmic and innate birds in this group supported the use of olfaction for homing.

Another indicative set of experiments conducted in southern England (Guilford et al. 1998) have provided further evidence on this point. Homing of experienced (trained) pigeons released between 30 and 39 km from their home loft was not significantly affected by zinc sulfate-induced anosmia. But when released from a site as distant as 66 km, only untreated individuals were able to home. Untrained pigeons, both anosmic and intact, released from 25, 36, and 39 km demonstrated poor homing, contributing thus to the evidence that within close range from home experienced pigeons may rely more on landmarks or other cues (for example, a training effect has also been hypothesized for magnetic orientation). Nevertheless, pooled data revealed a significant difference between intact and anosmic birds.

Similar results were obtained in some other studies. Half of the pigeons deprived of olfaction by nerve sectioning homed successfully within 30 km from their loft, but only untreated birds were able to home when released from 150 km (Papi et al. 1980; Wallraff 2003, 2004) and from 54–70 km (Schmid and Schlund 1993).

All the experiments with anosmia discussed above suggest the use of olfactory cues for orientation by pigeons. But how air-borne information interplays with other proposed orientation mechanisms remains enigmatic. More studies are needed to discriminate between different stages of the process of homing orientation from different distances. Cue interplay analysis would be of particular benefit. In this context, pigeons were reared constantly anosmic, and their orientation behavior was compared to zinc sulfate-treated birds and untreated controls (Schmid and Schlund 1993). Birds were released from 15–24 km from their home loft. As a result, good initial homeward orientation was demonstrated by all birds except for those deprived of olfaction just before release; i.e., those reared anosmic were well

oriented. But no ZnSO_4 -treated individuals (neither permanently nor before release) homed well. Thus, ontogenetic experience with zinc sulfate anosmia produced little effect on pigeons' initial orientation, but nevertheless considerably affected their overall homing performance. The results suggest that pigeons may use different mechanisms at different stages of homing, which in turn emphasizes the importance of further studies focused on the role of olfaction compared with the impacts of other possible cues also supported by substantial experimental proof. The problem is particularly evident in view of some findings suggesting that olfactory deprivation may affect pigeons' natural response to other cues, like the sun compass. For example, it has been documented that anosmia affects pigeons' homing speed only when the Sun is visible, but it has no effect under overcast sky (cited in Wiltschko 1996). Also pigeons' normal reaction to clock shifts may be impaired by anosmia (Bingman and Ioale 1989). Therefore, at this time, unequivocal conclusions from experiments in birds with anosmia produced by olfactory nerve dissection or chemical anaesthetics cannot be made, and more research is needed to clarify their overall or specific impacts on bird senses.

As it has already been mentioned, several other approaches besides simple anesthesia exist which are based on manipulations with air content. In one of such experiments, pigeons were divided into two groups: one transported to release site with natural air available en-route, and the other transported in containers with filtered air. The filter changed the composition of the ambient air, and was supposed to deprive pigeons of putative air-borne orientational information. Immediately before release pigeons of both groups underwent anesthesia of their sense of smell. Only control birds (the first group) were statistically oriented in their home direction (Wallraff and Foa 1981). In this case, birds of both groups were treated equally except for access to natural air during transportation – those having had it theoretically might possess a mental representation of where they were in respect to home based on these air-borne cues. This experiment also suggests that the putative odor information may function in cooperation with other sense (or senses) which provide compass information, and this information is bound to local distribution of odors, so that odor gradients are superimposed on compass direction obtained from other sources.

Further evidence became available from the so-called olfactory site simulation studies when pigeons were divided into three groups transported in filter boxes (without access to the ambient air). One group was transported to the site of release (T), and the other two to a "false" release site (F) located in the opposite direction from the loft. Then the first group and one of the remaining two (at site F) were allowed to smell the natural air, after which the groups from site F were transported with filters to the site T from where all three groups were released. Pigeons allowed to smell the ambient air at site F flew in the direction corresponding to home direction from site F (roughly opposite to the real home from the release site T). The first group (having smelled the environmental air at site T) was oriented in the actual homeward direction. Those that never smelled the ambient air demonstrated no significant orientation, and their headings dispersed among those of the two other groups (Benvenuti and Wallraff 1985).

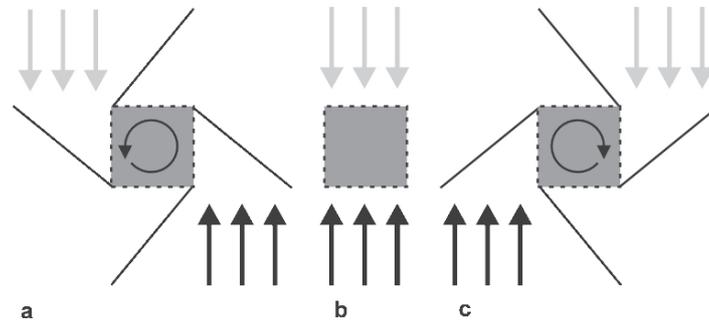


Fig. 1.18 A schematic view of deflector lofts (top view) rotating wind direction counterclockwise (a), clockwise (c), and leaving it without changes (b). *Black and gray arrows* represent different odors that mix inside a loft (adapted from Waldvogel and Phillips 1991)

A special device called “deflector loft” constitutes another possibility of studying pigeon olfactory orientation. A deflector loft is a loft fenced with screens attached to special deflector panels designed so that it is possible to manipulate the direction of artificial or natural winds passing through the loft. The device is designed so that it makes it possible to turn the wind direction clockwise, counterclockwise, or leave it without changes, as shown on Fig. 1.18. It is possible to produce a mixture of odors coming from different directions inside such a loft. Evidence from experiments in deflector lofts, however, is contradictory. On the one hand, some researchers (Baldaccini et al. 1975; Ioale et al. 1978; Kiepenheuer 1978a; Waldvogel et al. 1978) have reported that pigeons raised in deflector lofts and subjected to wind-direction manipulations changed their orientation upon release corresponding to the changed wind directions and odor composition in the loft, which seems to unambiguously suggest a direct involvement of olfaction in their homing. But, again, if cue interplay is concerned, such an interpretation of the results is not so evident. For instance, when “resident” (raised in the loft from fledgling) pigeons were prevented from viewing the natural sky horizon (Waldvogel and Phillips 1991), similar wind manipulations at the home loft didn’t produce homing orientation deflection upon release (or at least such a deflection was not at a significant level). These results provide additional evidence that the homing direction deflections observed after wind manipulations might actually have been caused by other factors.

In addition, an interesting point in the controversy of olfactory homing experimental results appears when results obtained by different research schools are compared. The main bulk of data supporting the importance of olfactory cues during homing in pigeons have been obtained by two schools – the Italian group initiated by Floriano Papi’s pioneering pigeon olfactory homing research and one German school led by Hans Wallraff. A series of experiments in the USA (e.g., Keeton and Brown 1976; Keeton et al. 1977), and even one performed by an American and Italian combined group in the USA (Papi et al. 1978), failed to corroborate the critical effect of olfactory cues during homing in pigeons. Wolfgang

and Roswitha Wiltschko, also leading a German animal navigation research group, point out that their results also do not strongly support the dominant roles of olfaction during pigeon homing. Such a discrepancy has evoked much debate over the plausibility of the hypothesis of olfactory navigation in birds. But one approach seems to have come close to the gist of the problem (at least partially). The Wiltschkos, together with the American ornithologist Charles Walcott, published a work (Wiltschko et al. 1987b) in which results of olfactory deprivation on pigeon homing performance from different schools were compared. The analysis showed that the most conclusive effects of manipulations with olfaction on homing success were obtained in Italy, but experiments in Germany and the USA produced more or less controversial output. It seemed like pigeons from different locations use different strategies to home. Further experiments (Wiltschko et al. 1989), however, revealed that the reason for the discrepancy in results may originate from the experimental procedure itself, namely from the way pigeons are held in captivity before experiments. In this study, the effect of olfactory manipulation on the homing of two groups of pigeons was compared. The study groups were held under two different captivity styles, called the “Italian” style and the “Frankfurt” style after the locations of the two respective research schools. These two styles of captivity differ generally in two ways: (1) the Italian pigeons are raised in an open aviary placed high on the roof of a building with good wind exposition, unlike the Frankfurt birds that are kept in a wind protected loft in a garden, and (2) Italian-style pigeons have significantly less training experience. In this study, the Italian-style pigeons demonstrated poor homing as a result of olfactory deprivation, while the Frankfurt birds seemed to be unaffected by anosmia. Tests for the effect of these two factors – wind exposition and training – have shown that wind exposure is the critical factor, and differences in training demonstrate far less influence on pigeon homing. Thus, the results of this study indirectly support the hypothesis of the importance of olfactory cues during pigeon homing, but on the other hand, the study demonstrates that the olfactory homing strategy may or may not develop or function depending on a bird’s previous experience. This allows the suggestion that, indeed, different pigeons may give higher priority to different homing navigation cues depending on the environment, which if supported by further research may potentially resolve the debate. However, in general the importance of olfactory cues for avian short-range navigation is not denied by the majority of researchers – the question as to which way they use smells still represents a much more difficult problem.

Therefore, we have rather conflicting evidence concerning the involvement and role of odors in avian orientation and navigation. The olfactory hypothesis itself is based on the assumption that more or less stable spatial gradients of different trace substances exist in the atmosphere (Wallraff 1989, 2004). Such gradients would provide a bird with an olfactory “map” of gas concentrations unique to a particular region. But the possibility of such a mechanism seems to be doubtful at its core. Meteorologists and other researchers of the atmosphere appear to deny the existence of such stable gradients (Becker and Raden 1986; Ganzhorn and Raffrath 1995; Waldvogel 1987). Air composition, in addition, varies greatly over time,

changing on a secular basis, and is hardly reliable for the millions of years of evolution obviously needed to develop navigational mechanisms.

Moreover, if regarded theoretically, pigeon homing is hardly based on mechanisms completely different from those ruling other birds' navigation and orientation. On the other hand, looking at the problem from another point of view, we can suggest that olfactory cues might provide the basis for some kind of a mosaic map (a map with irregularly distributed components) and function during short-range navigation, as in the case of pigeon homing, or serve as an additional or maybe even primary source of navigational information at the final stages of long-distance migrations of other bird species. Indeed, although hypotheses of the universal use of olfaction for navigation have been raised, the most logical and safe conclusion we can make at present is that olfaction may serve for short-range navigation. Even if long-distance migrants are supposed to rely on other cues with more regular global occurrence, odors as well as visual landmarks may constitute significant navigational markers at closer distances. The final stage of any long-distance migration, per se, may be considered as short-range navigation with the same navigational challenges. In this context, more critical analyses are needed to detect possible non-olfactory impacts of the manipulations with olfaction described above (see Wiltschko 1996), in order to tell these effects from pure olfactory impacts. New methods and approaches would be helpful.

In addition, olfaction has been shown to play an important role in the foraging and nocturnal homing for many sea birds, like *Procellariidae* (Bonadonna et al. 2001, 2003; Bonadonna and Bretagnolle 2002; Nevitt 2000), which are known to possess an excellent sense of smell. Olfaction is known to play an important role in foraging over vast stretches of ocean where prey-specific smells concentrate in regions of huge prey accumulations (like fish and krill). These accumulations are known to often occur at certain locations tethered to water upwelling sites dependent on the orography of the sea bottom and the configuration of currents.

In addition to the manipulations with the olfactory sense (i.e., olfactory deprivation) already described, lesions of specific brain compartments provide further evidence. Pigeons, for instance, with an ablated pyriform cortex, a part of the vertebrate brain responsible for olfaction, were found to be unable to home from unfamiliar areas (Papi and Cassini 1990). Therefore, whatever mechanisms are involved in long-distance migratory navigation, the cumulative evidence we have at this time suggests that olfactory navigation may indeed play a significant role in avian navigation, but that its significance is probably restricted to short-range navigation. In fact, despite the huge amount of experimental evidence on the involvement of olfactory cues in avian navigation, this problem remains one of the most debated issues in animal navigation. Therefore, any unequivocal statements in this field would, probably, be premature as yet. Further research is still needed.

2 Navigation and Cue Interplay

Abstract Whatever cues animals make use of during navigation, impressive attempts have been made over the past decades to look inside the very process of animal navigation. Actually, this is not a process but a complex of processes, with any specific group of animals employing its own strategy. Animals have been found to make use of many mechanisms of navigation, which generally reside upon three main phenomena – compass, map, and internal clock. These three basic constituents are building blocks of practically any navigational strategy. Animals have been found to use different compass systems, such as the magnetic and celestial compasses, several types of maps, such as the olfactory map or magnetic map by the nature of the underlying cues, or gradient or mosaic maps by the characteristics of spatial distribution of a cue, etc. The internal clock serves for temporal aspects of navigation, such as, for instance, for proper interpretation of the Sun or star position in the sky. In this chapter, the diversity of navigation strategies employed by different groups of animals while completing various navigational tasks is discussed.

2.1 Mechanisms of Navigation

There are many definitions of navigation in literature, but in simple words navigation is the ability to determine one's relative position and proper direction to a selected destination. Describing navigation in vertebrates, we have to mention that depending on the habitat a certain group lives in, and its evolutionary relations, the navigation systems employed may differ. Several different navigation systems have been proposed in vertebrates. As we have seen in the previous chapter, there is much debate on which sense of vertebrates is primarily responsible for detection of orientational cues. Concerning some senses proposed, agreement on the exact nature of the primary mechanism (or mechanisms) of orientation and navigation has not yet been achieved. Stellar, magnetic, and olfactory orientation systems are among the most substantiated models proposed so far. But often we have no clear understanding even within one of these (remember the multiple hypotheses proposed for, say, magnetic orientation). Every single mechanism or model proposed has its experimental or theoretical proof upon which it is based, so that at this

time we cannot deny any one for sure. But further in-depth analyses reveal that multiple mechanisms may really exist in nature. For instance, the electromagnetic induction mechanism of magnetic orientation proposed for some fishes (aquatic medium) is almost certainly impossible for birds (dry air medium). Another example deals with the functional characteristics of some systems – there is strong evidence supporting use of local landmarks during homing by pigeons, and almost equally as strong evidence for magnetic orientation in this group. While visual piloting (use of landmarks) may be problematic over great distances, changes in magnetic field characteristics may be indiscernible within a small range (usually close to home loft), particularly within regions with magnetic anomalies. Thus, the use of particular mechanism here will depend on the range in question. Again, if stellar navigation is probably common among birds, it is not feasible for subterranean mammals, simply due to unavailability of the cues underground. Based on all this, we have every right to suppose that navigational strategies and mechanisms may also be multiple. And this view is supported by the available experimental and theoretical evidence.

But in addition to such discrepancies in the mechanisms hypothesized, navigation as a phenomenon has some general principles that must be common in all cases, whatever mechanism is employed. First of all, it should be mentioned that navigation is supposed to be performed based on two general types of sensory input. Navigation based on internal reference (also called dead reckoning, or path integration) is achieved with the help of an animal's mental (internal) representation of a path it moves along. In such a case, an animal is able to approximately determine its relative position even in the absence of external cues, and reconstruct its movement based on motion-derived information. This type of navigation is possible due to the function of several key structures of the limbic system of the vertebrate brain. Alternatively, vertebrates can benefit in their orientation needs from various external cues described in the previous chapter. And here we will try to look into some possible mechanisms and strategies vertebrates seem to employ based on the available external and internal references.

In reality, animals seem to use both these types of information as complementary ones. In addition, although most of the evidence obtained so far relates to mechanisms of navigation employed by individuals, we have some incentive theory and experiments indicating that social relationships in groups of conspecifics may also play some role in the process of navigation.

2.1.1 Navigation on the Individual Level

The “Map and Compass” Model

In case of long-distance navigation, e.g., during long migrations when direct learning of landmarks is problematic due to excessive amount of information, navigation requires the ability to deduce one's relative position from local cues. The task is

only possible when the references involved are regularly distributed in space and/or time. In other words, the reference has to form a kind of imaginary grid with (ideally) orthogonally changing gradients giving an animal the opportunity of bicoordinate orientation. There are several examples of such cues on the global scale. The geomagnetic field, although having some minor deviations, demonstrates overall regular distribution of the intensity and inclination across the surface of the Earth. Another example is celestial cues (like the Sun and stars), which have not only regular spatial occurrence but are characterized by precise timing of movement across the sky. Such characteristics put these cues among the most probable on which to base long-distance navigation. For example, if you measure your local geomagnetic field intensity and inclination with sufficient precision, you can derive the global latitude of your position. And certainly this is what some animals might do, too. The measurement may be performed with the mechanisms discussed in the previous chapter. But the values obtained are not useful for an animal unless they are compared to other values, e.g., those at home range or wintering ground or any other destination of movement. At this stage, an animal needs to interpret the value and “retrieve” navigational information from it.

The “Map and Compass” model originally introduced by Kramer (1957, 1959) was formulated in order to explain the logic of such an interpretation. The model describes navigation as a two-step process. In the first step, an animal (a bird in Kramer’s original explanation) needs to determine the compass course to the goal of its movement. In other words, it needs to establish its relative position with respect to the goal. For example, “I am east of my home, so I need to move westwards.” This is the “map” step. The second step is to determine the course using a putative sense of compass. It is like “the west is there, or in that direction.” This one is the “compass” step. Sampling the local value of some cue, such as, for instance, local magnetic field intensity or inclination, and comparing it with the destination value at the first step does the trick. For example, if the value regularly decreases to the south, and the local one is less than that at home, this means that you are south of your home. Comparing the position/direction of the cues involved in relation to geographical directions makes the compass step. In the most primitive explanation, if you look at the North Star, then west is to the left, east is to the right, and south is behind you. But these are very primitive representations of the process, which may be more complicated in nature, sometimes involving time-compensated mechanisms for interpreting the position of moving objects, like the Sun or stars.

Compass Orientation

Among possible compass mechanisms, those based on the geomagnetic field and celestial cues are among the best substantiated, particularly for such relatively well-studied groups as birds and sea turtles.

Magnetic compass orientation has been well documented for about 18 bird species (Wiltschko and Wiltschko 1996) and at least several species of sea turtles (see in the previous chapter). Magnetic compasses of both birds and sea turtles seem to

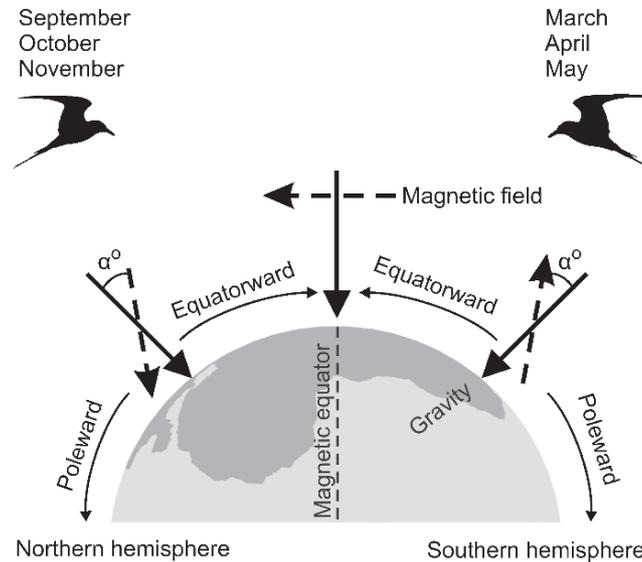


Fig. 2.1 A schematic representation of the inclination compass of birds and sea turtles (adapted from Wiltschko and Wiltschko 1996)

function as inclination compasses (Wiltschko 1997; Wiltschko and Wiltschko 1972, 1996; Light et al. 1993; Lohmann and Lohmann 1994a). As has already been discussed in the previous chapter, they are able to detect the inclination angle of the local geomagnetic field, and based on these data establish the “equatorward” and “poleward” direction, instead of magnetic “north” and “south,” estimation of which requires sensitivity to the magnetic polarity (Fig. 2.1). Birds and turtles are not sensitive to the polarity of magnetic lines (Beason 2005; Lohmann et al. 1999); this is supported by experiments in which reversal of the polarity of the field lines without changes in their inclination (achieved by simultaneous reversal of both the vertical and horizontal components) didn’t produce any effect on the orientation of experimental individuals (Wiltschko and Wiltschko 1996). Therefore, for a bird from the Northern hemisphere the spring migration is “equatorward,” and fall migration is “poleward,” and vice versa for Southern hemisphere migrants.

Many birds, though, are transequatorial migrants, and the compass, in order to guide such a bird in the proper direction, needs switching to the opposite when a bird crosses the magnetic equator. It has been shown on garden warblers (Wiltschko and Wiltschko 1992) and bobolinks (Beason 1992) that experience with artificially created horizontal magnetic fields (like that we encounter near the magnetic equator) “reverses” their directional responses, so that a Northern hemisphere migrant continues its, say, spring migration, in a southward direction after crossing the equator, although now its movement is “poleward.” During the reverse fall migration, the switching near the equator is supposed to repeat. This

hypothetical compass switch has been proposed to explain how transequatorial migrants using the putative magnetic inclination compass cross the magnetic equator and continue their flight without any obvious confusion.

Nevertheless, it will be appropriate to carefully note that the experimental evidence on which this hypothesis is based is still scarce and needs further investigation.

Not all vertebrates are assumed to possess this type of compass. As was shown in the previous chapter, some subterranean mammals are sensitive to the polarity of magnetic lines, and therefore are supposed to be able to distinguish between the magnetic “north” and “south” irrespective of inclination. We will not analyze their navigational system in this context, because the data are scarce. The compass sense of these animals probably relies on other mechanisms of magnetosensitivity and their sense of “map,” if it exists, may be based on a different source of spatial information. Perhaps dead reckoning or some combination of magnetic information with path integration (dead reckoning) applies here.

The magnetic compass of birds seems to be tuned to the geomagnetic field parameters, particularly to intensity. Thus, European robins were unable to orient in fields the total intensities of which were outside the range of 34,000–46,000 nT (the normal range of the geomagnetic field); however, the ability to orient returned to them after they were exposed to such out-of-range fields for at least 3 days (Wiltschko 1978), which obviously means that they may be able to adapt to unusual values after some time. This suggestion seems logical if we take into account that a first-year migrant may have no idea about the magnetic intensity and/or inclination of their wintering quarters, and that they learn these values afterwards as they perform their first migration. Therefore, adaptation to unusual magnetic parameters may well be normal among birds.

Magnetic compass orientation, unlike the “map” component of navigation, seems to be innate in vertebrates (Wiltschko and Wiltschko 2003). In migratory species, these innate directions of migration are obviously regulated in a complex way, as migratory programs seem to also include timing of migration. Navigation based on such innate programs of direction, distance, and timing of flight is called “vector navigation.” The terms “vector orientation,” “genetically-based orientation” (Papi 1990a), and “time-and-direction program” (Berthold 1996) refer to the same principle, but “vector navigation” is now more widely accepted (see Able 2000).

A clear and now classical indication of this type of navigation was first obtained by Perdeck (1958). He found that young first time migrating European starlings heading for their winter quarters didn't compensate if displaced off their migratory route. Instead they continued flying in the direction of their initial departure from home. As a result, they reached an area away from their wintering range. The vector between the area reached and the normal wintering range was similar in length and direction to that from the home range to the place of release, indicating that the young continued their migration in their normal (pre-programmed) direction and distance as if they hadn't been displaced. In contrast, experienced adult individuals did make a correction in flight direction following displacement and reached their normal wintering quarters, which meant that their innate compass was interfered with by some other type of information probably gained with experience.

Another exemplary experiment supporting this view has been conducted on garden warblers, a European migratory species that performs its fall migration to the south, and winters in Africa south of Sahara. This route, however, is not straight, and the birds fly first in a southwestern direction to Spain, and then southeast to the wintering quarters. In this experiment, individuals reared in cages demonstrated southwest orientation at the time their wild conspecifics were flying to Spain and southeast orientation at the time of the second stage of migration of their wild-reared counterparts (Gwinner and Wiltschko 1978). This behavior was in accordance with the hypothesis of genetically inherited programs of migration in birds.

Further, cross-breeding experiments with two differently migrating groups of blackcaps, *Sylvia atricapilla*, and subsequent analysis of their migratory headings revealed that their compass directions connected with timing of migration and distances was intermediate between the two original populations, and might have been inherited (Helbig 1991).

Time-compensated sun and stellar compasses have also been shown to play an important role in bird orientation during day and night, respectively (Keeton 1974; Schmidt-Koenig 1965; Wiltschko and Wiltschko 1996). It was shown that pigeons preferred the sun compass while homing during day under clear sky conditions. But under overcast they seemed to refer to the geomagnetic cues. The fact was revealed by the observation that magnets attached to the pigeons' back prevented proper homing orientation under overcast, but didn't have any effect on orientation under clear sky (Keeton 1971; Ioale 1984). These results are also supported by artificial magnetic field manipulations that produced reorientation of pigeons under overcast sky (Walcott and Green 1974).

Unlike in the case with the magnetic compass, celestial compasses, according to most studies, have to be learned during early stages of individual development. Nevertheless, we should note separately that what seems to be innate (inherited) is the axis of celestial rotation at night (Wiltschko et al. 1987a). Birds learn to use celestial cues as young. It seems that the magnetic compass takes part in this learning process when pigeons establish their sun compass (Wiltschko and Wiltschko 1996) using magnetic information as reference. It was shown that pigeons use a magnetic compass prior to the time they establish their sun compass, and the magnetic compass sense obviously serves as a directional reference system – a kind of “origin” or “scale” on which to base the learning of sun compass orientation (Wiltschko and Wiltschko 1981a; Wiltschko et al. 1983). However, experiments with clock-shifted pigeons (individuals with an artificially altered internal clock) show that later the sun compass becomes important, since clock-shifted birds demonstrate characteristic deflections from their home direction while homing (Schmidt-Koenig 1961). The direction of orientation of clock-shifted birds is theoretically predictable, which has been observed many times on pigeons, and in the case of practical proof suggests the valuable role of the sun compass. Similar results have also been obtained on clock-shifted savannah sparrows (Muheim and Akesson 2002) and Australian yellow-faced honeyeaters, *Lichenostomus chrysops* (Munro and Wiltschko 1993), but in the latter case the studied honeyeaters, although they demonstrated deflection from normal orientation, failed to show any predictable pattern. Moreover,

the effect of clock shift ceased with time, and the birds regained their normal pattern of orientation. These latter data may indicate that the sun compass is not the only important compass reference in birds, and its calibration by magnetic stimuli or other cues may be possible. This suggestion is in agreement with a few other studies. In one such study (Wiltschko et al. 1994a), analysis of 103 pigeon releases with 6-h clock-shifted pigeons revealed that in roughly half of the releases the clock-shift imposed deviations from the homeward course which were significantly smaller than predicted theoretically. Interestingly, that reliance on the sun compass seemed to correlate with age, with more experienced pigeons deviating less than younger individuals. This implies that experienced pigeons do not rely so heavily on the sun compass, and calibrate its guidance with the help of other cues. Another series of experiments provides some corroboration to this latter suggestion. In this study (Wiltschko and Wiltschko 2001a), released 6-h clock-shifted pigeons deviated approximately 60% of the theoretically expected deviation. But once tiny magnets distorting “readings” from their magnetic compass were attached to their body, the deviation increased up to 90% of the expected. This implies that, indeed, adult pigeons with an “intact” magnetic compass may in some way counter-calibrate their magnetic and solar compasses and choose a compromising direction based on the averaged reading from the two mechanisms, since deprived of magnetic information they seem to rely more heavily on their clock-shifted solar compass. However, pigeon homing is a case for short-range navigation in birds, and there might be a more complex scheme of navigation in experienced birds. Nevertheless, such studies may be valuable if applied to avian long-distance migrants, for which the importance of the magnetic compass is supported by a stronger body of evidence.

We observe a more complicated pattern in the interaction of the magnetic and the star compasses. The star compass of birds requires developing (learning) just as in the case of the sun compass, but most data suggest that it develops independently of the magnetic compass (Wiltschko et al. 1987a; Emlen 1970). In case of a conflicting situation between information from the magnetic cues and that of the star compass, birds behave in different ways depending on the phase of the annual life cycle (Wiltschko and Wiltschko 1996). Celestial cues prove to dominate over the magnetic compass when a bird is in the premigratory state (Able and Able 1990a; Prinz and Wiltschko 1992). The indications of this fact were obtained in a simple way – altering celestial rotation produced changes in orientation in premigratory birds irrespective of the pattern of the magnetic field applied. By contrast, a series of experiments showed that during migration magnetic information becomes more important, and the magnetic compass dominates over the celestial in case of conflicting input in European warblers and European robins (Wiltschko and Wiltschko 1975a,b; Bingman 1987). This pattern in general has been documented also for several other bird species like red-eyed vireo, *Vireo olivaceus*, northern waterthrush, *Seiurus noveboracensis*, etc. (Sandberg et al. 2000). Interestingly, in the latter study carried out during fall migration, the researchers found some interspecific differences in responses of the experimental birds. The species just mentioned demonstrated typical orientation responses that were in agreement with the statements above. But two other species, namely

indigo buntings, *Passerina cyanea*, and grey catbirds, *Dumetella carolinensis*, originally directing towards the sunset, failed to change their orientation in artificially altered magnetic fields. In other words, they failed to demonstrate any calibration of celestial information by the magnetic compass sense. However, these were cage tests. In release experiments, all four species revealed such calibration. While there is no clear explanation for such deviation in behavior, the authors suggest that there may be some species-specific preferences. The confusion becomes even more pronounced in view of some other studies, in which savannah sparrows were exposed to a conflict between celestial and magnetic information (Moore 1982, 1985; Able and Able 1995b) and seemed to calibrate their magnetic compass on the basis of celestial information. Taken together, this indicates that, indeed, some interspecific variation in calibration of orientational information using several available cues may take place in nature. Vertebrates are diverse, each group with its specific method of space utilization, and among this diversity of migration types taking place in different regions of the Earth, with different cues available or “desirable” for any specific migrant or migration type, some variation in cue interplay strategies can naturally be expected. Unfortunately the “ecology” of navigation is a field that has hardly been touched in scientific literature with proper scrutiny so far, and its future potential appears vast. In addition, we should not discard the possibility that these experimental results may suffer from some methodological inconsistencies (such as problems with caged tests, where the behavior of birds may be altered by various unexpected factors, etc.), in view of which we have to be careful in interpreting any particular results. Further research is needed to clarify the problem.

There are also contradictory data on the way in which the polarization compass develops. Some early experiments indicate that a putative compass based on polarized light pattern develops with calibration from the magnetic compass in birds at the time of migration (Bingman and Wiltschko 1988), because the parameters of the magnetic field applied changed polarization compass responses in dunnocks, *Prunella modularis*. However, it is difficult to come to an indubitable conclusion concerning the relative importance of the natural sky polarization pattern itself. Some experiments suggest the opposite. Pied flycatchers cage-tested under overcast conditions during migration showed random orientation unrelated to the direction of the magnetic fields applied (Akesson and Backman 1999). They only produced the normal pattern of orientation when both a magnetic field and polarized sky light were available. The controversy is that this very species has demonstrated proper orientation in other studies (e.g., Beck and Wiltschko 1981) when a magnetic field was the only cue.

In another experiment (Able and Able 1997), savannah sparrows were divided into two groups and reared in different magnetic conditions (the normal geomagnetic field and one of which the direction was altered by 90° clockwise). When tested under clear sky at the time of sunset, no significant difference in directions of headings between the two groups was found, which suggested no calibration from the magnetic field, and independent development of a polarized light compass was supposed. An earlier set of tests (Able and Able 1993, 1995a) provide evidence

that the polarization compass in birds is not only independently developed, but calibrates magnetic information in birds. Such a discrepancy in data may be explained if we take into account that some early conclusions were drawn from experiments with small sample sizes (Able and Able 1990b). Moreover, it should be noted that the polarization pattern of the sky may play different roles and have different weight compared to other compass mechanisms depending on the time of day. Recent studies indicate that polarization of the sky light may be most important at the times of sunrise and sunset. Experiments with caged savannah sparrows show that sky polarization is especially important at these early morning and evening times when birds must see the parts of the sky near the horizon. The information from sunrise/sunset polarization cues they derived was shown to recalibrate their magnetic compass (Muheim et al. 2006a, 2007).

Therefore, we have debatable but predominant evidence that the polarization pattern of the sky, especially during early morning and evening, may also constitute a very important source of directional information for terrestrial vertebrates, and the polarization compass either develops independently or is innate. Although most studies have been carried out on birds, we can suggest these properties for other terrestrial groups as well, since polarization sensitivity has been shown for many groups other than birds.

In the case of celestial compasses, orientational information retrieved gives true geographical coordinates. In this respect, the magnetic compass is somewhat different, since the accuracy of measurement is supposed to be significantly lower. Although in general the geomagnetic field parameters (such as the total intensity or inclination) show regular spatial distribution throughout the surface of the Earth, this regularity is far from being as strict as the spatial and temporal distribution of celestial bodies. Therefore, many researchers assume that the accuracy of the magnetic compass is less than that of the celestial one. However, this view has mostly been derived from cage experiments, and from the data pooled from tests of many different individuals. In short, the accuracy of about $\pm 40^\circ$ in vector bearings was concluded in general for the magnetic compass in birds (Wiltschko and Wiltschko 1996). Nevertheless, a set of homing studies carried out outdoors on pigeons showed no significant difference in accuracy between the magnetic and celestial compasses (Keeton 1969, 1974). In view of the scarcity of clear-cut experimental evidence in this respect, it is difficult to discuss the relative accuracy, importance, and, in some cases, even existence of different animal compasses at this time. Much of the issue remains for future investigation.

The Map Component

The notion of “map” in animal navigation carries a broader sense than the maps which we humans use in our navigational practice. True navigation, itself, is thought to be map-based navigation (Griffin 1952; Phillips 1996). In animals, a navigational map means the mental representation of spatial and/or temporal relationships between different objects within a certain area. Animals are mainly

supposed to achieve it in two ways – by direct remembering of the relative position of various objects, and/or through spatial interpretation of environmental gradients. The area usually includes the territory an animal moves within during its life. The areas of interest greatly vary in size depending on a particular animal's lifestyle. In the case of vertebrates, it may be as small as several hundred meters for some subterranean mammals, or as large as several tens of thousands of kilometers for such migrants as arctic terns, *Sterna paradisaea*, or some open-ocean migrants. Therefore, the corresponding “maps” will differ not only in size, they may also be different in structure.

So, nowadays we consider two main types of navigational map in vertebrates: (1) the “grid map,” and (2) the “mosaic map” (Biro et al. 2004; Wiltschko and Wiltschko 2003). The “grid map” represents a map sense built on the regular spatial and/or temporal gradients of some environmental factors. The geomagnetic field and, in some cases, odors (the hypothesized regular spatial distribution of some airborne substances) are assumed to constitute the basis for “grid maps” (although the putative grid-like nature of odor maps is often questioned). The other type of mental map – the “mosaic map” – is nothing other than a set of landmark characteristics (constant) for any local territory, the spatial relationship of which is memorized by an animal inhabiting the area, as shown on Fig. 2.2. This mental representation of the spatial relationship between local objects is juxtaposed by an animal with the position of a destination of movement, and guides the animal aiming to get there.

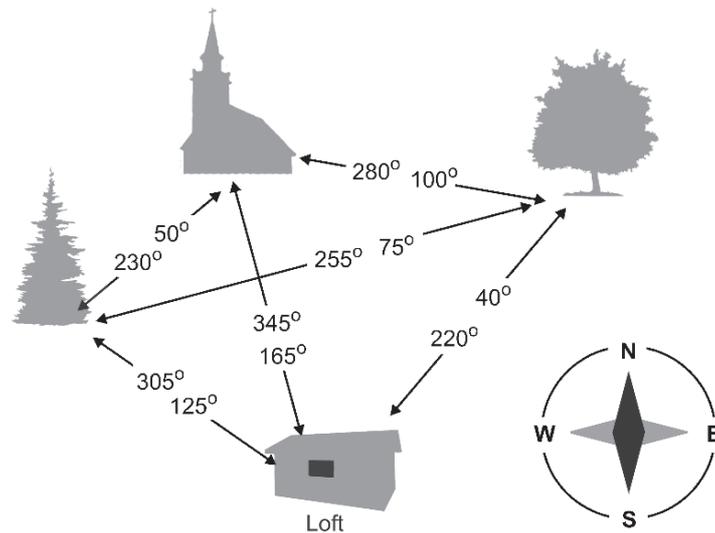


Fig. 2.2 An example of a compass-dependent “mosaic map” animals are supposed to use during short-range navigation (adapted from Wiltschko 1997)

The term “mosaic” implies the absence of rigid regular patterns of distribution of this type of navigational markers, in contrast to the previous types of map based on gradients. Animals navigating locally are generally supposed to use mosaic maps. Long-distance navigation (during, say, migrations) probably requires a grid map. Nonetheless, both types of map are based on remembering whatever it be – objects or gradients. Observing an object or “measuring” local gradient value, an animal compares it with what is stored in its memory, and thus deduces its relative position. Meanwhile, the huge volume of material to remember during long-distance migrations is thought to impede direct learning of objects and formation of a mosaic map. This is the point that makes the two types of map principally different. The interpretation of spatial data deduced from grid maps is based on the so called “map sense” (Gould 1998). Often, long-distance migrants moving beyond the range of their familiar area are still able to deduce their relative position and the position of a selected destination point. This is possible only when some spatial gradient (for instance, the inclination of the geomagnetic field) changes predictably in certain defined directions, and extrapolation of its values beyond the familiar area is feasible. For example, if you stay in the Northern hemisphere, and the local inclination angle is greater than you have ever experienced, you are most probably north of your familiar range of movement. If you have any cues to measure longitude as well, you can extrapolate, and deduce your relative position on a bicoordinate map. This process of extrapolation is not a mere reference to memory; it’s more like creation of an extended map based on the properties of your familiar area map (e.g., based on directionally predictable change in the inclination angle of the geomagnetic field or any other factor within your familiar area). So, whereas mosaic maps are, in principle, based on learned material, grid maps include additional innate analytical components that ensure the map sense.

The magnetic map concept is one of the best-developed map hypotheses. As has already been stated in the previous chapter, at the present time we don’t have any unified theory of the magnetic sense in animals, and we don’t know what the exact nature of magnetoreceptors is. But based on most evidence, it can be suggested that at least in birds (and maybe in other terrestrial vertebrates) the magnetic map sense seems to operate with the help of magnetite-based magnetoreceptors. The presence of a specialized receptor system sets another principal difference between grid maps (in case of magnetic maps) and mosaic maps based on memory.

In the case of the olfactory map hypothesis, according to that summarized by Wallraff (2004), there are no specialized receptors employed. But the properties of this type of map indicate that we may essentially consider it as a grid map in some cases. The olfactory navigation hypothesis has obtained some experimental evidence from studies on migratory sea turtles, but is formed based mainly on investigations of pigeon homing. Although pigeon homing is generally short-range navigation, there is some evidence that pigeons are able to home from unfamiliar sites with the help of olfaction, and this ability is thought to operate based on extrapolation of spatial distribution of some trace substances (gases) in the atmosphere (also reviewed in Wallraff 1996). Another feature indicating its “grid-like” nature is some evidence that spatial distribution of some gaseous substances (odors)

may be constant for large areas (see Wallraff 2004), and thus allows extrapolation on directionally predictable gradual changes in concentration of these substances in the air. However, it should be noted once more that, unlike the geomagnetic field, odor gradients are not directionally predictable on the global scale and, therefore, cannot serve as a map reference for long-distance migrants. Some adherents of the olfactory navigation hypothesis state that navigation of other birds must not essentially differ from that of homing pigeons and, therefore, should be based on olfaction. But, since the influence of the magnetic field on the orientation of many terrestrial vertebrates has been convincingly demonstrated, the putative olfactory navigation on the global scale may be questioned. At this point, migration of sea turtles and many birds stretching for tens of thousands of kilometers is more likely to be explained from the point of view of the magnetic and celestial navigation hypotheses, which are potentially suitable candidates to mediate the formation of true grid maps in long-distance migrants on up to the global level. Nevertheless, as has already been stated, olfactory navigation may play an important (or even dominating) role in the final stages of long-distance migration, when a small and familiar area is being approached by a migrant.

But regardless of the system on which navigation is based, it requires one condition in any case. This condition is a bicoordinate map in cases where grid maps apply. This means that an animal, in order to orient properly, needs at least two gradients to change in a directionally predictable manner. The directions of change of these gradients have to be different. The ideal situation is when two factors change in directions that are perpendicular (the angle between them is 90°). In this case, position detection is most precise. In the case of global positioning, it should give an animal the longitude and the latitude of its location. However, position detection in a case where the gradients differ by a different angle (a sharp one) is theoretically possible. In such a case, the precision is expected to be lower. The more acute the angle, the less will be the precision. Gradients with different directions are observed in some parameters of the geomagnetic field. Theoretically, not only spatial gradients can exist. Employment of temporal gradients is also theoretically possible. Nevertheless, the putative celestial and magnetic navigation systems as basis for the grid maps mentioned above remain to some degree a mystery today. There are several cues (like magnetic intensity, inclination, location of the Sun or stars) potentially capable of indicating the latitude of one's position, but detection of longitude by animals is not clearly understood to date (Gould 1998). Two theoretical approaches to solving this problem have been explored. One is that the altitude of the Sun above the horizon at the same moment is longitude-dependent. So, an animal presented with a strange position of the Sun in relation to its internal clock (a clock-shifted animal) is expected to treat the situation as if it were at a different longitude. But the complication is that sometimes clock-shifted birds behave as if their compasses had been rotated, but not as if they had been moved to another longitude. However, in other cases the direction of orientation expected if the birds' compass had been rotated was not observed (Munro and Wiltschko 1993). In some studies, the results of clock shift were rather complicated, as some birds did show the expected deflections in orientation, while other did not (Muheim and Akesson

2002). Therefore, the issue requires more extensive investigation, and the possibility that celestial cues may serve as indicators of longitude has not yet been rejected. This means that employment of temporal gradients in navigation is possible, and may play a role in longitude determination by long-distance migrants.

Another assumption is that some parameters of the geomagnetic field may constitute a sufficient basis for both longitude and latitude identification. The involvement of the geomagnetic field in the map component of navigation has been demonstrated for many vertebrates belonging to different groups (reviewed by Gould 1998; Phillips 1996; Beason 2005). Thus, young (inexperienced) American alligators have been found to rely on route-based information (dead reckoning) while homing (Rodda 1985). However, navigation by older individuals was different and seemed to rely on site-based cues, which suggested that they used a map. Further, the apparent correlation between deflections in their orientation from homeward direction and variations in the geomagnetic field (inclination and horizontal intensity) pointed out a possible role of the geomagnetic field in this map, suggesting overall that the alligators used a true (at least bicoordinate) magnetic map (Rodda 1984). Yearlings didn't show that correlation, and served as control.

A very strong set of evidence was obtained on sea turtles (Lohmann and Lohmann 1994a). Hatchling loggerhead sea turtles exposed to magnetic fields with inclination angles corresponding to different locations of their subsequent migratory path turned their headings in the directions naturally expected in those locations. These experiments indicate that the hatchlings possess an innate sense of inclination (giving latitudinal positioning) which they use as they move through their huge migratory route encircling the North Atlantic gyre. What is interesting is that the turtles fail to demonstrate any consistent orientation when exposed to inclinations that do not occur on their migratory route. It may indicate that they are unable to extrapolate unusual inclination values, which strengthens the idea that their probable magnetic map sense is an innate behavioral program.

A study on Australian silvereyes with simulated northern and southern exposure (Fischer et al. 2003) provides even more interesting evidence. Silvereyes breeding on Tasmania and migrating northwards to their wintering grounds were transported to Australia (to a point in the middle of their migratory route). Then the birds were divided into three groups. The first group was held in a magnetic field the inclination of which corresponded to that of their Tasmanian breeding grounds. The second group was held under magnetic conditions close to that of their northern wintering quarters. And the last group was held in the local geomagnetic field and served as control. As a result, birds that experienced southern magnetic conditions and controls were oriented toward north-northeast (their usual fall migratory direction). Controls demonstrated a little weaker response than the "southern exposure" group. By contrast, the group exposed to the field conditions corresponding to their wintering grounds failed to show any consistent orientation and scattered randomly. Their migratory motivation had significantly diminished. The behavior of the last group is best explained by the assumption that birds subjected to conditions similar to those of their wintering quarters (destination of their migration) naturally lost

their motivation to migrate further. The phenomenon most probably can only be explained if the birds retrieve positional (map) information (or at least its latitudinal component) from inclination angles of the Earth's magnetic field. This experiment provides additional support for the hypothesis of the existence of magnetic grid maps in long-distance migrants.

The list of experiments presented above is far from being exhaustive. There is much more additional data supporting the magnetic map hypothesis. But the key question in this hypothesis still remains open. If latitude can possibly be calculated with the help of inclination angles or/and total intensity (which also is latitude-dependent), how do animals determine longitude? Where do they get information about the second coordinate?

One possible solution to the problem is the fact that the values of both the total intensity and the vertical intensity of the geomagnetic field lines increase toward the poles (see Fig. 2.3), but the directions of their gradients differ by up to 30° (Gould 1998). Theoretically, this discrepancy can be used as a bicoordinate map, and provides a system sufficient to base navigation on (Gould 1980, 1982). As stated above, an ideal bicoordinate map would contain two coordinates changing in perpendicular directions. It was theoretically calculated (Gould 1998) that in case of magnetic coordinates an angle of only 20° would require a sensitivity capable of discriminating magnetic fields with increments of about 0.01%, which doesn't exceed the theoretically possible sensitivity of magnetite-based magnetoreceptors (Kirschvink and Gould 1981; Gould 1982); and thus the hypothesis above is theoretically plausible.

A more recent hypothesis, often called "the vector summation model" (Walker 1998), proposes a more explicit assumption of how birds might use the geomagnetic

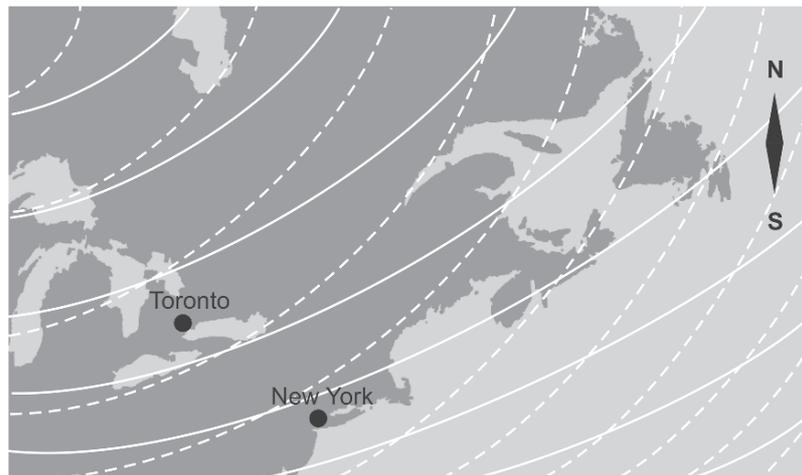


Fig. 2.3 Discrepancy between gradient directions of the total (*solid lines*) and vertical (*dashed lines*) of the geomagnetic field in the northwestern part of North America (adapted from Gould 1998)

total intensity to derive the second coordinate. In this hypothesis, the direction of the steepest gradient of total intensity is proposed as the second coordinate. Analysis of departure directions of released homing pigeons in North America and Europe has shown that clockwise and counter-clockwise deflections from the true home direction at the release site are regularly distributed, and literally divided by a straight line separating the release sites into two domains.

Predominantly clockwise deflections are observed from release sites located on one side of the line, and counter-clockwise biases on the other. Another fact that was noted was that most accurate flights (least deflections) had been performed from sites located on or close to this line, and the true homing direction more or less coincided with the line. When these lines, both in Europe and North America, were superimposed on the map of global total intensity distribution, it was discovered that they crossed the contours of equal total intensity at the angle of approximately 90° , which meant that the imaginary lines dividing the release site deflections coincided with the local directions of steepest gradients (slopes) of the total intensity of the geomagnetic field. Similarity of the symmetries at locations as distant as North America and Europe suggested that local landmarks did not cause these symmetries, but rather that some regularly distributed global factors produced the patterns. The geomagnetic total field intensity seemed the most obvious candidate. Therefore, the local total field intensity and the direction (provided by the compass sense) of the steepest total intensity slope are suggested to form the map sense of pigeons (and, perhaps, of many other animals). It is suggested that pigeons perform detection of the steepest gradient shortly after release, when they fly in different directions (presumably measuring the field intensity in different locations). Orientation in that way, according to the author of the hypothesis, is like finding home on a hill, when one is located at a certain point on the hill and measures the height (analogous to total intensity of the field) and compass direction of the steepest slope, compares it to the corresponding parameters of its home position (which the homer keeps in memory) and deduces the required compass direction towards the home. In a similar way, animal navigation might be based on the “magnetic relief” (or “intensity relief”). An animal measures the parameters at the site of its position, and then compares the values with those of its home. Therefore, the model proposes that pigeons might use the local total intensity and the direction of the steepest slope of intensity as vector coordinates. These vectors can be reproduced geometrically, where a geometrical vector will have its direction (actually, steepest slope direction) and length (the local field intensity). Comparison of release and home vectors (imagine a simple geometrical vector summation) gives a bird the compass course towards its home, as demonstrated in Fig. 2.4.

Although the use of these parameters (total intensity and direction of slope) is suggested for homing (short- and middle-range navigation), its employment by long-distance migrants might also be possible (for details, see Walker 1998).

Another hypothesis suggesting the use of a magnetic grid map by long-distance migrants was generated, based on many studies of magnetic sensitivity in sea turtles (reviewed in the previous chapter) and satellite tracking of sea turtles and albatrosses as they migrate to distant destinations in the vast featureless ocean. As has

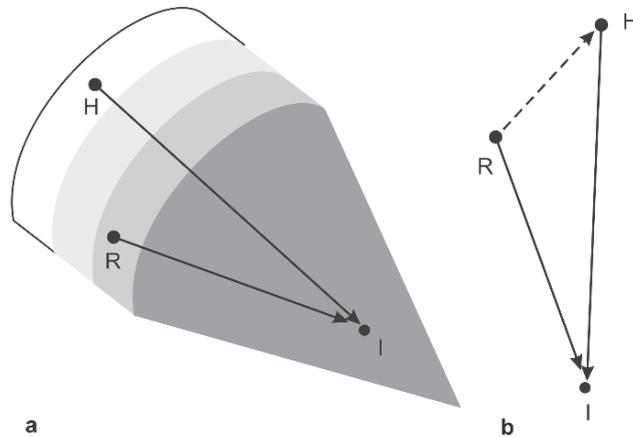


Fig. 2.4 A geometric representation of the vector summation model applied to magnetic navigation. *Shaded areas (a)* represent regions of different intensity increasing towards more heavily shaded parts. *R*, release site; *H*, home; *I*, point of intersection of the vectors *HI* and *RI*. Vector direction is determined as the direction of the steepest intensity gradient, and its length is defined by the intensity difference between locations *H* and *I*, and *R* and *I* respectively. Homing direction and distance (**b**) are deduced geometrically (adapted from Walker 1998)

already been discussed, sea turtles have been shown to be sensitive to inclination and total intensity of the geomagnetic field. In view of this ability, a magnetic grid map based on inclination and intensity coordinates was proposed. Excluding some areas where the gradient directions of these two parameters coincide, and locations near the poles where inclination is close to 90° (vertical field) and its use in navigation is not feasible, inclination and intensity form a grid of intersecting gradients, and allow (theoretically) accurate navigation when any given place has its unique combination of two values. Keeping this fact in mind, navigation based on these parameters was proposed for green turtles feeding near the Atlantic shores of Brasilia and migrating over 2,000km to the beaches of Ascension Island to breed. In this region, the magnetic field intensity and inclination contours of equal value (isolines) intercross nearly orthogonally (Fig. 2.5), which potentially may provide an excellent basis for grid map formation (Akesson 1996).

In addition to numerous experiments corroborating the ability of many animals to detect the geomagnetic field inclination and intensity, hypotheses of the use of grid map-based navigation are also supported by satellite tracking of long-distant migrations. Thus, tracking of albatrosses and sea turtles (Jouventin and Wiemerskirch 1990; Papi et al. 1995; Papi and Luschi 1996) has shown that they are able to reach distant goals in the open ocean moving along relatively straight trajectories. This fact supports the assumption that these migrants are able to accurately measure the navigational cues they make use of (for additional discussion on the nature of the geomagnetic maps in animals, see Lohmann et al. 2007).



Fig. 2.5 Intersection of the inclination angle (*dashed lines*) and total intensity (*solid lines*) equal value contours in southern parts of the Atlantic Ocean (adapted from Lohmann and Lohmann 1996b)

Finally, it should be mentioned that evident map-based navigation may be not limited to the groups of vertebrates discussed above. Similar empirical support for the use of maps has been found for some amphibians (Phillips et al. 1995; Fischer et al. 2001), fin whales (Walker et al. 1992) etc., and this seems to indicate that navigational maps may be widespread among vertebrates.

An alternative to the grid map-based navigation hypothesis is navigation with the involvement of mosaic maps (use of landmarks) and path integration (information obtained from movements of an animal's own body). These types of navigation will be covered separately below.

Use of Landmarks

In short-range navigation, e.g., homing, salient features of a landscape may play a significant role by helping an animal to navigate accurately within its familiar terrains. The use of local landmarks for navigation was first discussed by Griffin (1952). Later, Schmidt-Koenig (1965) coined the term "piloting" to refer to the landmark-based type of navigation. This term is generally accepted nowadays. There have been many definitions of piloting. These definitions were primarily aimed at determining how exactly landmarks may be used for short-range navigation, and

there has been much debate over the topic. Today, the most widely accepted understanding of piloting (see Wallraff and Neumann 1989; Wallraff et al. 1994; Holland 2003) is related to the concept of mosaic maps (spatial representation of familiar terrains with irregularly distributed prominent objects). The simplest explanation of the notion is that piloting is the use of local landmarks, the spatial relationships among which are remembered by an animal and employed to deduce the location of a remote goal within a familiar area. The phenomenon is also known as the “familiar area map.”

However evident the use of landmarks may seem intuitively, this topic remains the focus of eager debates and is poorly studied. Some researchers have come to the conclusion that landmarks are often not necessary for navigation (Wiltschko and Wiltschko 1998b; Walker et al. 2002), whereas others argue that evidence supports landmark-based navigation being rather wide-spread among animals (Bingman et al. 1998b).

But regardless of the scarcity of and contradiction in empirical evidence, the use of landmarks during homing is becoming more and more supported by empirical evidence, and several patterns can be traced.

One of the most debatable questions in regard to landmark-based navigation is whether it is integrated with the putative map-and-compass mechanism or is an independent type of behavior (Able 2000; Holland 2003). In the first case, landmark navigation should involve compass bearings from one object to another, and in total should form a kind of a mosaic map where compass directions between objects are memorized and used for navigation. By contrast, if landmarks provide a kind of navigational guide independent of compass mechanisms, the reference system should function based on guides like “fly to that object,” or “fly between those objects” and so on. Another possibility of this type of landmark navigation (as soon as homing, for example, is concerned) would be remembering a sequence of landmarks and then flying the route in reverse direction in order to get home. Often, the compass-independent system is called piloting, as opposed to the mosaic map that is attributed to the first (compass-dependent) system. Each of these two strategies is supposed to have its advantages. The first obviously would need smaller memory size. The second (without compass) is assumed to be of benefit when for some reason compass cues are unavailable or bring too imprecise information (Holland 2003).

One of the complications arguing against piloting independent of compass is that if it takes place in nature, then clock shifts should produce no effect on the initial orientation of homing animals (Able 2000). Nevertheless, studies on clock-shifted pigeons, a classical object for homing experiments, do not support this type of navigation. It is possible, however, that compass-independent piloting (piloting *sensu stricto*) functions along with the map-and-compass mechanism, and is employed when, as suggested above, the use of the compass is troublesome.

An interesting and productive method of testing these two principal models is to analyze the routes clock-shifted pigeons choose to home along. Comparison of releases from familiar and unfamiliar sites proves to be particularly useful. Experiments show that clock-shifted pigeons released from unfamiliar sites, as a

rule, demonstrate initial orientation turned by an angle predicted by the degree of the experimental clock shift (Schmidt-Koenig 1960; Neuss and Wallraff 1988; Holland 1998). Results of the studies where pigeons were released from familiar sites are equivocal. In some experiments, clock-shifted birds demonstrated full deflection, as in the case of those released from beyond their familiar area (Keeton 1969; Fuller et al. 1983). However, the birds' headings from familiar release sites may be expected to vary in principle, depending on the local features of landscapes, distance from the loft, degree of familiarity with the area, the age of an individual, and possibly some other factors. Therefore, the results of any single study are not likely to describe the actual behavior of pigeons. And there is plentiful evidence that landmarks influence the initial orientation of pigeons released to home within their familiar area. Indeed, in many trials clock-shifted pigeons did not deviate as expected based on the clock shifts, but instead made "corrections" of their homeward routes. These corrections varied by degree, showing compromising directions in some cases, and no deflection in other (Wallraff et al. 1994, 1999; Gagliardo et al. 1999, 2002, 2005). However, the majority of the clock-shift setups by these and some other authors have involved occlusion of the olfactory sense. Olfaction has been shown to participate in at least short- and middle-scale navigation in pigeons, and blocking this sense certainly imposes a navigational challenge for homing birds. Landmarks may also be supposed to provide an additional reference system in such cases. However, a recent attempt to find a difference in clock-shift responses by pigeons based on site familiarity failed to do so (Wiltschko et al. 2005). Deflections of pigeons familiar with the release area and those unfamiliar with it didn't differ statistically, suggesting that landmark familiarity does not improve compensation for clock shifting and that pigeons use other cues.

Therefore, there is no unambiguous evidence on what navigational system dominates in homing pigeons. Although some researchers insist on the dominant role of piloting, the safest conclusion so far will obviously be that piloting, in the case that it does work, is more a complementary means.

Meanwhile, clock-shift designs are thought to provide rather indirect evidence. Several other approaches providing support for homing pigeon navigation by means of piloting have been employed. For example, some studies show that pigeons allowed to preview familiar sites for at least 5 min before release home faster (Burt et al. 1997). This effect has not been reported for releases from unfamiliar sites (Braithwaite and Newman 1994). Further, pigeons trained to home from a release site several times, and allowed to see only a segment of the surrounding landscape, demonstrated better homing performance if allowed to preview the area in the angle range in which they had previously been trained. Previewing other angular aspects from the same release site didn't ensure better navigation (Biro et al. 2003), which suggested that the previews provided some visual recognition of the release site, and allowed birds to head in the preliminarily learned direction without the necessity to investigate the area once more. As expected, previewing other aspects of the terrain didn't cause the recollected site recognition.

A more detailed analysis of pigeon homing routes with the use of GPS tracking technology has demonstrated that the difference in orientation between individuals

allowed a preliminary view of landscapes and those released without it is significant only within about 1 km of homing flight starting from a release site. At this stage, “previewing” pigeons were shown to choose more straight courses. In contrast, individuals that had been denied a preview of a familiar area flew along a more complicated route, including circling supposed to play a direction search role. However, at distances greater than 1,000 m from the release site there was no evident difference (Biro et al. 2002). These data suggest that viewing a familiar area before release provides some orientation features for pigeons which allow them to orient before starting to fly. Moreover, the discrepancy in behavior along the first kilometer additionally suggests that landscape preview influences the initial orientation of pigeons rather than having any non-specific effect.

In view of the fact that homing pigeons do not fly along a straight line but that, on the contrary, their routes are often quite complicated, detection of birds’ initial bearing provides a limited basis for interpretation of results. Employment of the GPS technologies which are becoming more and more popular has made it possible to track the entire homing route of released pigeons by attaching tiny transmitters to the birds. This approach has brought yet another set of evidence. Thus, in many cases clock-shifted pigeons were shown to fly in the “shifted” (wrong) direction some part of the way and then correct their direction (Bonadonna et al. 2000). In this study, a possible role of terrain features has also been supposed.

But more convincing support appeared when pigeon tracks were juxtaposed on prominent landscape features of the experimental area. For instance, when homing tracks obtained with the help of GPS near Rome, Italy, were overlaid on a map of the study area, they were found to correlate significantly with the pattern of the local major highways (Lipp et al. 2004), which suggested that roads might have provided some guidance for the pigeons in these experiments. This suggestion is supported yet in another study. Observations show that pigeons released several times from the same site tend to adhere to the routes they have followed in previous trials. Even when afterwards released from another site off-route they often find the shortest way to the remembered route and once located follow it in the homeward direction (Biro et al. 2004), which supports their reliance on learned visual stimuli patterns rather than on compass information or a remembered sequence of compass bearings.

Nevertheless, most of the research presented so far provides indirect evidence. More direct approaches require experimental manipulations with landmarks or senses that perceive them. There is no need to describe the complications connected with manipulations of prominent features on a large-scale terrain to test pigeons’ reaction during homing trials. Manipulations of the visual sense are much more convenient. However, the results are not always conclusive. The visual sense is, for instance, also hypothesized to participate in the putative light-dependent magnetoreception mechanism, and therefore interpretation of homing behavior in animals with altered vision is often complicated.

Initially, a series of studies with homing pigeons, the visual sense of which was impaired with frosted contact lenses so that they couldn’t see landmarks but remained able to detect the position of the Sun, showed that the birds were able to

home successfully even without viewing the surrounding landscape (Schmidt-Koenig and Schlichte 1972; Schmidt-Koenig and Walcott 1978). The only effect of the lenses was that the pigeons were not able to locate their loft when close to it, where the role of visual cues obviously becomes significant. Based on these studies, many early students have formed the conclusion that the visual sense doesn't play any role in pigeon homing. But nowadays this interpretation is usually denied. The only safe suggestion that can be made from these experiments is that the use of visual landmarks is not an exclusive mechanism employed by homing pigeons.

Therefore, landmark-based navigation by homing animals, and its relative importance compared to other mechanisms proposed, depend on many factors. Availability of other cues and distance to travel are thought to be among the most influential factors affecting the use of landmarks. Navigation in close vicinity to the goal will probably be primarily based on landmarks, and it will be independent of the compass sense. Nighttime navigation, as well as long-distance navigation, is supposed to rely mostly upon other cues, although some landmarks (e.g., city lights, etc.) may constitute a complementary source of information.

However, studies on other birds and mammals indicate that in some cases small-range landmark-based navigation may depend on compass bearings. Collett et al. (1986) carried out an experiment in which gerbils had to find sunflower seeds by digging in a certain place. Each time, the place the seeds were buried at remained at the same distance and in the same direction from a single symmetrical landmark. The position of the landmark moved from trial to trial so that its spatial relationship with the seed cache remained constant. The gerbils were able to search for the hidden cache in the proper places regardless of where the landmark stood. This indicated that gerbils learned not only the distance between the landmark and the cache but also their directional relation. If the animals had been unable to determine the direction from the landmark to the cache, they would probably have looked for it around a circle on the determined distance from the landmark. But this didn't happen. Further, when the location of the cache was defined by two landmarks, some additional support of the ability of gerbils to measure directions and distances between landmarks and cache appeared. When gerbils had remembered the spatial relationships between the goal and the two landmarks defining its position, one landmark was removed. Presented with only one landmark the animals searched in two locations defined by the distances and directions memorized, but as if gerbils didn't know which of the two landmarks was present. When both landmarks were present, but the distance between them increased, gerbils also looked for food in two places, with corresponding (remembered) directions and distances from each of the landmarks. The setup is illustrated in Fig. 2.6. These latter results also suggest that calculation of distance and direction was performed separately from each of the landmarks.

One of the mechanisms proposed for landmark-goal arrangement interpretation by gerbils (and possibly by other vertebrates) is the vector summation model previously discussed (Collett et al. 1986; see also Walker 1998; Cheng 1989). Applied to gerbils, it suggests that an animal searching a goal uses the directional and distance information about the initially remembered relation between the goal and the

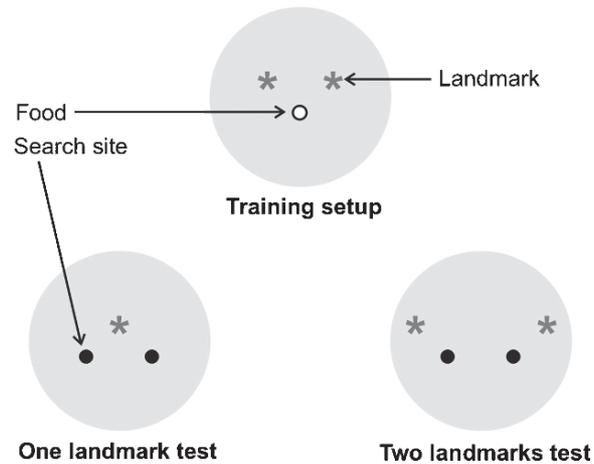


Fig. 2.6 Circular arena used to study gerbil landmark navigation (adapted from Collett et al. 1986)

landmark. The search is supposed to rely on a calculation of the animal's present position in respect to the direction and distance to the landmark. This forms a vector. Then, this vector is summed with a similar vector defining the position of the goal in relation to the landmark. This is done as a simple geometrical vector summation. The vector that results from this summation describes the direction and distance the animal has to walk in order to reach the goal. Such calculations are applied to all landmarks involved. The vector sum produced is a common vector of some direction and distance that leads to the goal.

Interestingly, in similar studies with two landmarks moved farther apart, pigeons didn't search in two places. They searched in the middle of the line connecting these predicted places (Cheng 1989). Therefore, it was suggested that pigeons do not use each spatial goal-landmark relationship separately. Instead they were supposed to use a vector calculated by averaging all the goal-landmark vectors remembered (see Cheng 1988, 1989, 1994).

Nevertheless, vector summation is not the only mechanism proposed for landmark navigation in vertebrates. The "multiple bearings" hypothesis proposes another explanation. Clark's nutcrackers, *Nucifraga columbiana*, make food provisions by storing seeds underground. They are able to bury up to 33,000 seed items in hundreds of underground locations, and months later they can still find the seeds with remarkable accuracy (Balda and Kamil 2002). Experiments show that nutcrackers use landmarks to locate their cache, and this landmark-based navigation appears to be highly dependent on the birds' compass sense (reviewed in Kamil et al. 2001).

Kamil and Jones (1997) trained nutcrackers to find a cache hidden halfway between two landmarks. If a line is drawn between two objects, then finding the point halfway will suggest they are measuring distance, whereas going astray

(displacing perpendicularly) will mean a directional bias. In this study, Kamil and Jones measured errors made by the birds in relation to distance and compass direction (bearing) measurements. They found that as the distance between the two landmarks increased the birds tended to make greater errors, but they were more accurate in determining direction.

But the accuracy of searches using only two landmarks is a challenging task in many cases, because the theoretical accuracy of search is expected to increase with the increase in the number of landmarks employed. Indeed, nutcrackers have been found to use multiple landmarks to find caches more accurately. Kamil and Cheng (2001) suggest that relying on only two landmarks might be problematic because of the compass-bearing errors. Indeed, if seed-caching birds rely on estimation of directions from a cache to the surrounding landmarks more heavily than on the correspondent distances (Kamil and Jones 2000), then directional errors will lead to a wrong point of intersection of the vectors leading from each of the landmarks to the cache (the imagined cache location).

As a result, the researchers formulated the “multiple bearings” hypothesis, which suggests that seed-caching birds use directional relationships between the buried seeds and many surrounding objects. These directions are used to find the intersection point as an indicator of cache location. This mechanism is similar to the concept of the use by homing pigeons of mosaic maps based on known directional relationships between familiar area landmarks (Wiltschko 1997).

It should be noted, however, that the multiple-bearings mechanism is not an alternative to the vector summation principle mentioned above. The vector summation mechanism can be considered as a simpler behavioral complex that probably constitutes the basis for the more complex multiple bearings model. Vector summation probably occurs as an animal compares its own position in relation to landmarks. It remembers the directions and distances from a cache to the surrounding landmarks, and compares the data with its current position. Its movement towards the goal (i.e., correction of its current position with reference to the frame stored in memory) is probably based on vector summation.

The multiple-bearings hypothesis still needs detailed testing, and is not firmly evident at the present time. But some predictions the model puts forth have already been verified experimentally.

There are five main predictions stated by the authors. First of all, if there is a single landmark to indicate the position of a cache, it is expected that the distance error will increase faster than the directional error as the distance between the landmark and the cache increases. Additionally, a correlation of distance and directional errors must take place across trials within any given individual. If there is no correlation, other mechanisms should account for the search instead of that proposed by the hypothesis.

The second prediction is that the accuracy of cache recovery will increase as the number of landmarks involved increases. This prediction seems self-evident, but still should be considered as additional support for the mechanism hypothesized.

The next point suggests that the effect on the accuracy of searches of adding another landmark must depend on the geometric relationships between the landmarks

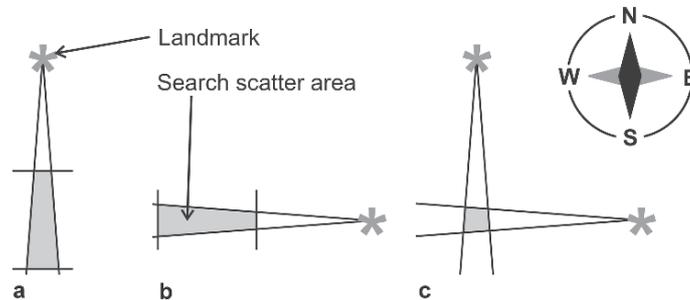


Fig. 2.7 Landmark-dependent search accuracy predicted by Kamil and Cheng (2001). See explanation in the text

involved, i.e., it depends on the geometric pattern of the locations of landmarks in relation to the goal. It is also evident, because logically if, say, three landmarks are aligned so that they form a triangle, they should produce an effect different from that when they are placed along a straight line, etc.

The fourth prediction is built on a situation where two landmarks are present, and they are located so that the lines connecting them with the goal intersect at the right angle. Kamil and Cheng (2001) depict it (see Fig. 2.7) as if the landmarks were located one due east and the other due north (*c*) of the cache. In such a case, bearing in mind that with increased distance directional error reduces, it should be expected that if only the eastern landmark is present (*b*) the search error must be greater along the east–west axis than along the north–south one. Similarly, when only the northern landmark is present (*a*) the resultant error will be greater along the north–south axis. Presence of both landmarks should equalize the east–west and north–south errors. Moreover, the resultant directional error should be the same as in single-landmark trials.

And finally, the fifth prediction states that animals navigating with the use of relative directional information should be less susceptible to directional errors than those employing an absolute compass bearing. The original illustration speculates that if birds are trained in an outdoor arena and then clock-shifted, the clock shift will produce little effect on individuals using relative directional information. But it is supposed to have a dramatic impact on the accuracy of search by those using, say, the sun compass (absolute compass measures).

So, these are the main conditions to be tested in future. More experiments will make the real mechanism clearer. Nevertheless, some tests have already been carried out. Kamil et al. (2001) made a setup in which nutcrackers were trained to recover seeds the position of which was defined by four landmarks. These landmarks were placed so that the lines between the cache and each of the landmarks intersected orthogonally (at right angles). Then 600 trials were carried out on five birds. Each fifth trial was performed with no seed in the cache to preclude the use of olfactory cues. The 15 possible arrangements of the landmarks were employed, including one

four-landmark setup, the four possible combinations with three landmarks, the six positions possible for a pair of landmarks, and the four arrangements with a single landmark. Landmarks were set up at different distances, and therefore the whole experiment provided substantial sample sizes to test several predictions put forth in the multiple-bearings hypothesis. As a result, four of the predictions obtained experimental proof. Namely, the accuracy of searches was found to increase as the number of landmarks increased; distance errors increased faster than directional errors as the cache–landmark distance increased; directional error represented in angle degrees was constant throughout different cache–landmark distances; and the fourth prediction (see above) was also confirmed. Therefore, based on these experiments and theoretical assumptions, we can conclude that the multiple-bearings hypothesis seems to work in natural conditions, and describes some features of the actual mechanism of at least short-distance landmark-based navigation.

Although the fifth prediction of the multiple-bearings hypothesis has obtained little experimental backup so far, some evidence supports the use of absolute compass bearings by cache-storing birds in nature. A series of studies have demonstrated that clock shifts significantly affect the accuracy of cache finding by nutcrackers (Wiltschko et al. 1999) and black-capped chickadees, *Parus atricapillus* (Duff et al. 1998). These studies do not resolve the question of the differential impact of clock shifts predicted by the hypothesis, but nevertheless provide some indication of interaction between the bird sun compass and landmark-based orientation. These data contribute to the basic problem of landmark-based navigation theory – whether the use of landmarks is independent of the bird map-and-compass mechanism which is suggested to play a major role in homing. Pigeons finding their way home might use the same multiple-bearings principle for landmark navigation, based on interaction of the map-and-compass mechanism with local landmark arrangement.

Basically, it is suggested that vertebrates navigate with the help of landmarks in two main ways (Cook and Tauro 1999). The first is forming a “map” of relevant landmarks, which includes remembering the distances and directions between objects within a familiar area. Formation of such a map implies that an animal is able to interpret the position of a goal within the area covered by the map by means of deducing it based on known directional and distance relationships between the goal and different landmarks. Such maps are nothing other than the mosaic maps already described, but are often also called “cognitive maps,” as initially proposed by Tolman (1948). Both terms describe principally the same phenomenon, with the latter one more often used in neurophysiological literature. Later research on neural mechanisms of spatial representation and analysis of the vertebrate limbic system have provided further support of this hypothesis, and created a firm theoretical basis for this mechanism (O’Keefe and Nadel 1978; Poucet 1993).

The other mechanism, called “beaconing,” is based on finding a goal by approaching one landmark (beacon). This mechanism is supposed not to include remembering of distances and directional relationships between objects, and in a simple case implies learning to directly approach a beacon (Leonard and McNaughton 1990; Brown 1992).

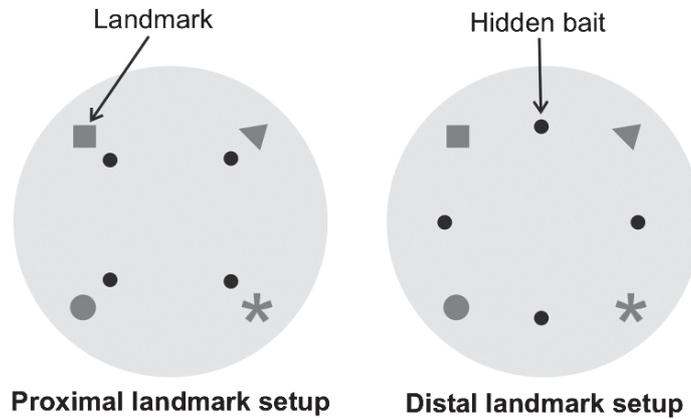


Fig. 2.8 Circular arena with different landmark–bait arrangements used to study rat landmark navigation (adapted from Cook and Tauro 1999)

Although the existence of cognitive maps is still denied by some researchers, both mechanisms are generally accepted today. It has been suggested that vertebrates (at least rats) are able to use both mechanisms as complementary ones, or any one of the two depending on the environment. Cook and Tauro (1999) designed an experimental setup in which testing the use of these two mechanisms was possible. They constructed a circular arena where four landmarks and four hidden baits (food pellets) were arranged as shown in Fig. 2.8. Two conditions were designed – the “proximal” (left plot) and the “distal” (right plot). As it can be seen from the picture, baits and landmarks are placed very closely in the proximal setup, and with baits roughly midway between two neighboring landmarks in the distal setup. Rats were divided into two groups (“proximal” and “distal,” respectively) and trained to locate the hidden baits. The results showed that the rats of the proximal group learned to find their baits significantly faster. Different rearrangements of the proximal and distal landmark–bait arrays revealed that rats of the two groups employed different strategies to locate their goals. While simply approaching a landmark and finding food nearby guided the proximal group (beaconing), their counterparts memorized the geometric relationships between the landmarks and the baits (formation of cognitive maps). The latter took a longer time. Therefore, the experiment has provided support for the notion that beaconing and map-based landmark navigation can be used differently within the same species depending on the environment.

But what factor defines the choice of strategy? Several studies (including the one just mentioned) suggest that this choice may be dependent on distances between landmarks and goals (for discussion, see Cook and Tauro 1999). Pigeons have been found to prefer landmarks placed closer to the goal (Spetch 1995). Similarly rufous hummingbirds, *Selasforus rufus*, have been found to learn spatial tasks faster when landmarks were closer to the goal (Brown 1994). Dependence on cue proximity in choosing between beaconing and map-based landmark navigation is probably

explained in terms of saving time and energy. Indeed, it seems easier to remember one close landmark as a beacon than to keep in memory the geometrical relations among several cues. As the distance between a landmark and a goal increases, however, beaconing becomes more and more inefficient due to increased risk of error.

The simplest example of beaconing was presented in a study by Morris (1981). In this experiment, rats placed in a water-filled circular arena were able to escape the water only by swimming towards a platform set above water level and climbing onto it. The animals quickly learned this behavior, since it required just approaching the platform.

However, it should be noted that beaconing is not restricted just to approaching a visual landmark. In some cases, vertebrates may use a gradient cue that gradually changes in one direction as a beacon. Green sea turtles nesting on the beaches of Ascension Island, and displaced from the island downwind, returned faster and more often than those displaced upwind (Luschi et al. 2001). Obviously odors emanating from the island formed a gradient of odor intensity increasing towards the island. Such gradients are also considered as beacons (Collett 1987). *Oceanodroma*, *Halobaena*, and *Hydrobates* petrels were found to employ this mechanism while searching for their burrow nests at night after foraging in the open ocean (Grubb 1974; Minguez 1977; Bonadonna et al. 2001). Among other experiments, diving petrels *Pelecanoides* and thin-billed prions *Pachyptila* studied in a T-shaped maze were found to prefer the scent of their own nest to that of their conspecifics (Bonadonna et al. 2003). Some classical setups with plugged nostrils and zinc sulfate-induced anosmia have also been performed. Anosmic petrels of seven burrowing species have demonstrated impaired nest recognition (Bonadonna and Bretagnolle 2002).

Navigation by landmarks is, obviously, not restricted just to the groups mentioned above, and must be wide-spread among animals. However, experimental evidence for many groups is scarce. The hatchlings of some sea turtles have been shown to orient with the help of visual cues during their initial seaward stage of migration (this will be discussed in more detail later). Some populations of humpback whales, *Megaptera novaeangliae*, migrate across the Atlantic and Pacific oceans, covering sometimes more than 8,000 km (Stone et al. 1990). Some populations of humpbacks migrate parallel to coasts, and are supposed to keep in contact with the coastal line (Bingman and Cheng 2005). But other populations (those migrating from Hawaii to Alaska, or from Antarctica to Australia) seem not to require coastlines for guidance. However, it has been proposed that magnetic anomalies, a typical feature of the ocean bottom, also serve as “landmarks” for navigation by whales of these populations. Nevertheless, these are just speculations that need testing.

In fact, landmarks can be of different types. Visual landmarks are only a particular, though maybe the most common, case. Magnetic landmarks hypothesized above for whales, as well as infrasound supposed to also guide homing pigeons (Hagstrum 2000), represent some of the other putative types of landmarks. The common feature defining a cue as a landmark is probably its irregular distribution.

Therefore, odors, magnetic field anomalies, infrasound, etc., can be considered as landmarks in view of their irregular spatial distribution. Mosaic maps are thought to be based on landmarks, and build up as an animal remembers their spatial relationships within a constant (familiar) territory.

Moreover, some animals are able to perceive visually detectable objects with the help of other senses. For instance, some whales are supposed to use their sonar system in order to monitor features of underwater landscape at the time of migration. Although in the case of whales the mechanism has not yet been proved, a similar system can be illustrated on the example of bats known to employ echolocation as they hunt. It is well known that bats emit ultrasound and then monitor its reflection to locate prey. The mechanism is so accurate that a bat is able to determine the exact direction and distance to the prey – a tiny insect – from a distance up to 5 m (Kick 1982). The resolution of the bat's directional audition is as high as 1° in the horizontal plane (Simmons et al. 1983) and about 3° in the vertical (Lawrence and Simmons 1982). It has recently been shown that bats use the echolocation system to navigate by landmarks as well. Jensen et al. (2005) trained big brown bats, *Eptesicus fuscus*, to fly through a hole in a mist net to get food on the other side. The illumination was so low that it precluded visual perception of a landmark near the hole and of the hole itself by the experimental bats. A landmark was placed 10 cm to the left of the hole, and the hole and the landmark were moved so that their positions in relation to each other didn't change. In this setup, the bats quickly located the opening in the net. But once the spatial relationship between the hole and the landmarks was altered, the animals collided with the net, unable to find the opening. When the landmark was removed completely, the animals needed more time to locate the whole, and also more crashes into the net were observed. This experiment became the first one to unequivocally prove bats' ability to employ audition to estimate spatial relationships between objects for navigation.

An interesting concept is that landmarks may not only be of visible or tangible nature. Any cues that mark this or that place, the position of which can be learned and used to mark some site within a familiar area, can contribute to the animal landmark navigation system. For example, some irregular magnetic conditions like magnetic anomalies can also potentially be used by animals to mark some location. One of the typical experiments in this context was carried out on pigeons (Thalau et al. 2007). The birds were trained to find food in two places within a testing area, based on the presence of a magnetic anomaly created by the presence of a small bar magnet nearby. The food sites were visually indistinguishable, and their position was changed from time to time. During testing, it was revealed that pigeons conditioned in such a way searched food near the magnetic anomaly for a significantly longer time than near the other food site, as compared to unconditioned controls. It can be suggested that they used the local magnetic anomaly as a "landmark" indicating the presence of the food location.

An important feature that makes landmarks important for navigation is, obviously, their stability. Stable landmarks are remembered better, and cause animals relying on them to make fewer navigational errors. The factor of landmark stability makes generalizations about landmark-based navigation even more problematic

on/above the species level. Indeed, different populations of the same species can navigate differently. This phenomenon was shown, for instance, on three-spined sticklebacks, *Gasterosteus aculeatus* (Odling-Smee and Braithwaite 2003). Sticklebacks were captured from two different habitats – fast-flowing rivers and ponds – and trained to find a hidden reward in a T-maze. Individuals taken from ponds were found to navigate by relying on landmarks significantly heavier than their river counterparts. Additionally, this study has shown that landmark-based navigation can rapidly adapt to the environment a species inhabits, and can depend more on the habitat than on the species itself, thus separating the species into differently behaving populations. It seems logical that relying upon landmarks in fast-moving rivers may be quite misleading, because the majority of visual objects there often change their location under pressure from the fast-running water. Similar regularity has also been shown for rats (Biegler and Morris 1996), which seem to perform landmark navigation tasks better in stable environments. The importance of landmark stability for navigation is also supported by neurophysiological studies (Jeffery 1998). The so-called “place cells” in the rat hippocampus (will be discussed later) responsible for spatial navigation fire with patterns depending on the arrangement of external references within a familiar area. It was shown that the cells ceased firing if presented with unstable (moving) landmarks as references. Therefore, unstable references seem to be perceived as unreliable cues by navigating vertebrates.

Meanwhile, the theory of landmark navigation is still built on many hypotheses that have been tested insufficiently, and provides a fruitful field for future investigation.

Path Integration

Charles Darwin (1873) was among the first researchers to admit the existence of a special type of navigational mechanism called “dead reckoning.” Later, this type of navigation was called “path integration” (Mittelstaedt and Mittelstaedt 1980). The terms are synonymous and mean the same, but the latter one is preferred and used more widely nowadays. Path integration is the ability of animals and humans to determine a beeline course to the origin of their travel based on the information gathered during the outward journey. In view of this, there is yet another term to account for this type of navigation called “route-based navigation” (Baker 1981), which better represents the inherent nature of the mechanism but today is rarely used.

Path integration has been shown to be an important part of the navigation process in various animals, and seems to be essential in short-range navigation (for review, see Maurer and Seguinot 1995; Rodrigo 2002). There is almost no evidence supporting its role in long-distance navigation (Able 2000).

In simpler terms, when an animal, like an ant or a gerbil, undertakes a foraging trip from its nest to a forage site, it often moves along a complicated route that includes many detours and loops, particularly in cases when it doesn't realize where the food is and has to search for it. Once the place is located and the forage

collected, the animal is often able to return along the shortest straight path directly towards the nest.

This ability implies that animals are able to constantly update their position in relation to the starting point of their journey by calculating the distance and compass direction to it. It is hypothesized that animals are able to do this by using two main types of information. Based on these sources we discriminate two types of path integration, namely, the “allothetic path integration” that is fed from external navigational cues (the so called geocentric information), and the “idiothetic path integration” based on internal signals (egocentric information) generated by the animal’s body as it moves (Able 2000).

Although a series of studies on vertebrate path integration has been carried out, many fundamental points of the process have been studied on invertebrates. Therefore, in order to better highlight the existing theory we will also include evidence coming from invertebrates.

Allothetic and idiothetic path integration do not necessarily occur separately, nor are they peculiar to individual species. Often the processes are supposed to accompany each other. One of the classical examples of allothetic path integration is the use of the sun compass by foraging ants to calculate the angles of their turns during an outward foraging journey. They have also been found to estimate distances by means of optic flow as they move (Wehner et al. 1996; for review see also Collett and Collett 2000). Similarly, geese have been found to be able to detect the beeline homeward course after a passive displacement along a circuitous route only in cases when they were allowed to see at least part of the sky. Once devoid of external information, they failed to demonstrate path integration (Saint Paul 1982). Similar results were obtained in a study involving transportation of young pigeons in total darkness (Wiltschko and Wiltschko 1981b).

Among other external references, it has also been suggested that young inexperienced homing pigeons track the geomagnetic field and use it for path integration (Wiltschko and Wiltschko 1978a). As the path integration mechanism, by definition, requires the collection of navigational information en-route, experiments involved transportation of three groups of pigeons, during which one group served as untreated control, the second one was transported in an artificially altered magnetic field, and the third group was held in an altered magnetic field at the released site. As a result, only control birds and those transported normally but held at the release site in an altered magnetic field selected proper homeward courses upon release. Pigeons transported in an altered field headed randomly, i.e., proper homing directions were only observed in pigeons that had access to the ambient magnetic field during the outward journey. This, in turn, provides some evidence that young inexperienced pigeons may track the geomagnetic field during outward journeys and use it for path integration while returning home (see also Kiepenheuer 1978b,c). In agreement with these results is another study in which transportation manipulations dealt with different light conditions, some of which are thought to prevent the birds from collecting magnetic information (Wiltschko and Wiltschko 1998a). There is, however, criticism addressed by some authors (see Wallraff 2000) towards these magnetic treatments as proper methods, and dispute on this topic has

not resolved so far (see also Wiltschko and Wiltschko 2000). A careful review of these two publications can give one good insights into the prospect of future investigation of this topic, as the issue constitutes many unresolved aspects, and promises huge potential for future challenges.

However, external information is not always necessary for animals to perform path integration. As an animal moves, it analyzes internally generated information about its movement. Proprioceptive reafferences from muscles and joints, efference copies (stored information about motor commands) interacting with vestibular information informing about body displacements and rotations are hypothesized to provide an animal with information about its movement in cases where external cues are unavailable or unreliable (Etienne et al. 1996).

Mittelstaedt and Mittelstaedt (1982) tested female gerbils, *Meriones unguiculatus*, in a circular arena where the females were placed with their pups in a nest at the edge. Then the pups were removed and placed into a hole on another side of the circum. The females, once they had found their pups, returned to the nest along a straight path. Although their outward routes were complicated, they continued to demonstrate path integration (finding the shortest route home) even in complete darkness, suggesting that path integration was possible based solely on inner signals generated in the animal body.

The evidence from passive displacement setups also supports the involvement of internal cues in completing path integration tasks. Thus, in an experiment with golden hamsters, *Mesocricetus auratus*, the animals had to walk along circuitous ways or were passively rotated in a circular arena before returning home. Their path integration abilities were then observed (Etienne et al. 1988). It was shown that the more complicated an outward route of a hamster had been, the poorer was the hamster's performance (greater errors in estimation of the homeward course). But their performance was affected significantly more when they were rotated passively. Passive rotation deprived the hamsters of true information about the change in their current position, so they obviously calculated their home direction as if they stood at the last place visited by active walk.

Similarly, gerbils tested in a two-leg outward journey, where they moved along one leg actively and were displaced passively along the other, failed to demonstrate compensation for passive displacement (Mittelstaedt and Mittelstaedt 1982). The results of this experiment may indicate that idiothetic path integration is only possible when animals perform an outward journey actively, and thus have an opportunity to analyze navigational information generated inside their bodies.

However, indications do exist in literature that some vertebrates are able to track passive displacement. For example, painted quails, *Excalfactoria chinensis*, forced to move along a corridor were found to compensate for angular deviation regardless of whether the movement was active or passive (Merkel and Fischer-Klein 1973; Merkel 1978). Additionally, although the abovementioned gerbils failed to compensate for passive-leg displacement, they had previously been found to compensate after walking along a straight path in a rotating arena (Mittelstaedt and Glasauer 1991).

Similar ability to account for passive displacement has also been found in rats. But path integration after passive displacement was eliminated after rats' vestibular

organs were lesioned (see Etienne et al. 1996). This leads to a suggestion that the vestibular apparatus of vertebrates can compensate for passive displacement when other body-generated signals are unavailable, obviously provided that sufficient acceleration of movement has been achieved – the so-called inertial navigation (Barlow 1964).

Although the evidence is contradictory and no statement is possible by this time, the involvement of the vestibular sense in path integration has been shown in some 3D setups. Insect organs responsible for interpreting gravitation differ from those found in vertebrates. Nevertheless, some experiments with ants may bring an insight into how sensing gravitation may contribute to the accuracy of path integration as a whole. Animals walking across the surface of the Earth move along courses that are curved in three dimensions because of the relief. Therefore, in order to calculate their position relative to a starting point they have to account for turns in the vertical plane as well. Desert ants, *Cataglyphis fortis*, were tested in a three-dimensional corridor, in which the first leg was forward-directed, and the second was turned orthogonally to the right (Grah et al. 2005). The second leg included a segment directed at some angles to the ground plane. The ground projection of the second leg (and thus the ant's real ground displacement to the right) was equal to that in a similar two-dimensional setup, but the actual corridor was longer due to its three-dimensional configuration. After training to reach the feeding site at the end of the corridor, experimental ants were tested for finding the beeline path back to their nest (point of departure). In the second trial, the corridor was placed horizontally on the ground (literally stretched on the ground), causing thus greater actual displacement of the ants to the right. It is, therefore, easy to note that the directions from the feeding site to the nest in the first and the second trials were significantly different. The question was how the ants measured their linear displacement. Did they count steps as they walked, or they were able to interpret their displacement in the three-dimensional space and compensate for the vertical component? The results showed that the ants were able to incorporate the information about their vertical displacement into their path integration system. The resulting homing azimuths differed between the two trials, and correctly pointed towards the nest in both cases. Additionally, the ants were tested on the ground (two-dimensional test), where the second (turning to the right) leg of the corridor was equal in length to the projection of its counterpart in the three-dimensional trial. The resulting homing vectors from the feeding site did not differ significantly from those obtained in the three-dimensional trial, corroborating thus the evidence that path integration (at least in ants) is a three-dimensional process, and that the vestibular sense must play some role along with other perception systems involved. Although the exact mechanism of how the ants interpret the vertical component of their movement is not known, these results suggest that the input from the sense of gravitation may be incorporated into the path integration system of insects (Grah et al. 2005; see also Wohlgenuth et al. 2002).

Theoretically, this may be the case in vertebrates as well. Indeed, a set of studies support this assumption. Among classical experiments on vertebrates are those including path integration in rats. For example, rats with lesions of vestibular

organs were shown to be unable to complete simple navigation tasks on a circular arena (Wallace et al. 2002). The task was to find the food location inside a uniform circular arena, after which the rats returned to their hidden nest to eat the food. Their returns were investigated under two conditions – illuminated and dark. When the arena was illuminated, both normal and vestibular-lesioned individuals returned successfully, apparently with the help of visual cues. The dark trials with no landmarks visible, on the contrary, required true idiothetic dead reckoning in order to return successfully. Under this latter condition, only intact individuals were found to be able to locate their nests. The vestibular-lesioned rats were also unable to utilize path integration and navigate during further illuminated tasks in novel environments.

In another set of experiments, rats had to find a feeder in complete darkness inside a circular area the floor of which had the shape of a low cone (Moghaddam et al. 1996). Search tracks of rats were juxtaposed with the shortest routes from the starting point to the feeder. The results showed that the length of the paths the rats moved along while searching the food was inversely proportional to the height of the cone. The self-evident interpretation of the results suggests that higher cones favored higher vestibular “resolution” and thus allowed more accurate measurements of displacement during searches. This, in turn, appeared to allow better calculation of the straight return route.

Combined, these experiments demonstrate that at least some vertebrates actively use the vertical displacement component for path integration. Therefore, we have some evidence that corroborates the involvement of the vestibular sense in dead reckoning. Similarly, it can be suggested that three-dimensional path integration may play a minor role in vertebrates that inhabit vast relatively flat territories and actively move for long distances (as some hoofed mammals), since there is evidence that some mammals use step counting or other signals generated in the body during movement to calculate their linear displacement. This imposes some restriction on the possibility to employ vestibular navigation observed in ants, which seem to use optic flow to measure their actual ground displacement. But two-dimensional path integration may be sufficient in case of these mammals, in view of the much larger horizontal displacement and minor influence of relief across the territories they inhabit. Nevertheless, the suggestion still needs testing on different groups of vertebrates. Further research should probably incorporate studies taking into account the life history and locomotion of any particular group. This also stimulates investigation of the hypothesized use of other sources of body-generated information by animals, which is supposed to finally provide an empirical platform for formulation of some firmer theory on the idiothetic mechanism being discussed.

Some mathematical models dedicated to explain what functions the animal path integration system might use for calculating and updating the animal’s position relative to some starting point have been approached (for review, see Maurer and Seguinot 1995).

The first mathematical model of path integration was invented by Jander (1957). Based on experiments with ants, Jander supposed that path integration could be achieved by integrating all the directions an animal has walked in,

weighted by the corresponding times of travel for each direction. In the underlying experiment, ants were trained to locate a goal by following a straight route in the presence of two lights that blinked on an alternating basis. While homing they were presented with just one unblinking light. As a result, the ants chose the homing direction depending on the timing of blinking and angles between the body axis and the lights they had been exposed to during the outward journey, as if they didn't notice that the outward journey had been straight. Analysis of their homing directions demonstrated that ants "integrated" all the angles between their body and the instant light (one of the two that was shining at a particular moment they had traveled) weighted by the corresponding times. It seems that they hadn't noticed that there had been two lights. Therefore, when one light was turned off and the other turned on, the ants appeared to perceive it as a corresponding change in their movement direction in respect to the "single" light instead of admitting the existence of two lights. As a result, ants behaved as if they had followed a curved route. So, their homing direction seemed to be generated by integration of all the "directions" weighted by the timing of traveling in each direction, which was actually the timing of blinking. Calculated in such a way, we can expect a direction to be obtained that is the geometrical average of vector summation, where the length of the vectors is measured in walking time. Based on these and other observations, Jander invented the following equation to describe the process of path integration:

$$\alpha_r = \frac{1}{t_z - t_N} \int_{t_N}^{t_z} \alpha_i dt \quad (2.1)$$

where α_r is the resulting straight path vector direction, and t_N and t_z are times at the beginning and the end of the journey respectively.

The model was valuable as the first explanation of the process of path integration in mathematical terms. Nonetheless, in spite of its simplicity, the model seems to have flaws that cast a shadow of doubt on whether it describes the actual process accurately. First of all, the equation doesn't include any errors animals are naturally supposed to make. But even in view of this fact, there is inconsistency in that simulations show that the equation does not calculate the resulting vector direction accurately. So there is a hidden error in it that hardly corresponds to the actual errors animals use to make. Another serious defect of the hypothesis is that vector lengths are calculated by time instead of distance. This means that in order to fit the equation the animal must move at a constant speed, which is far from being the case in reality.

Mittelstaedt (1985) supposed that while Jander's hypothesis worked more or less properly on simpler outward journeys, calculation of more complicated routes with detours and especially loops would cause significant errors. Instead, Mittelstaedt (1962; see also Mittelstaedt and Mittelstaedt 1973) proposed another model that gave geometrically correct solutions – the so-called "bicomponent model" which, unlike Jander's, was based on the assumption that animals prima-

rily use external (geocentric) references. The model stated that calculation of an animal's position is performed in the central nervous system of the animal and employs exocentric (Cartesian) coordinates, though the author didn't exclude the possible role of an egocentric (body-centered) polar coordinate system (Mittelstaedt 1983). In this hypothesis, the movement of an animal is decomposed on its trigonometric components:

$$\tan \beta_{\text{res}} = \frac{\int v_i \sin \beta_i dt}{\int v_i \cos \beta_i dt} \quad (2.2)$$

where β_{res} is the direction of the final vector, v_i is the movement speed during the i th time interval, and β_i is the direction of the movement during the i th time interval.

As can be deduced from the equation, movement is decomposed into two components where, in terms of Cartesian coordinates, the x and y components are represented through integrated cosines and sines, respectively. If then the resulting vectors obtained from allothetic and idiothetic sources are added by vector summation, an animal is able to deduce another vector that defines the final bearing, which is more "balanced." Theoretically, there are no barriers to preclude addition of the third coordinate to the model to navigate in the three-dimensional space based on this scheme.

It is easy to note that Mittelstaedt's model returns a geometrically accurate resultant vector. Nevertheless, the hypothesis, like Jander's, doesn't consider errors actually made by animals and can, therefore, also serve as an approximate simplified reflection of the actual process. Unfortunately, at the time the two models were designed there was no clear understanding about the types of errors animals might make while navigating by path integration. The concept of systematic and spontaneous errors was just emerging (see Maurer and Seguinot 1995). Nevertheless, the Mittelstaedts recognized that using this model implies some spontaneous errors that accumulate as a path becomes longer and more complicated (Mittelstaedt and Mittelstaedt 1973).

Benhamou et al. (1990) developed yet another model that was also based on trigonometric decomposition solutions, but came closer to the study of errors (the noise in path integration). Unlike the Mittelstaedt model, this was based on the animal's internal (egocentric) reference. The model proposes that the source of errors made by animals is not computation itself, but the process of measurement, i.e., the animals measure their movement (both rotation and linear displacement) inaccurately. This inaccuracy, according to the hypothesis, might be characterized by normal distribution with zero as the mean, and therefore is not some specific error animals make on a regular basis, but a kind of noise (imprecision) that randomly distorts the results of final computation. The equations describing the calculation process are as follows:

$$D'_{i+1} = (D_i'^2 + P_{i+1}'^2 - 2D_i'P_{i+1}' \cos(\omega_i' - \alpha_i'))^{1/2} \quad (2.3)$$

for updating the distance from the animal's current position to the starting point, and

$$\omega'_{i+1} = \arctan \frac{\sin(\omega'_i - \alpha'_i)}{\cos(\omega'_i - \alpha'_i) - \frac{P'_{i+1}}{D'_i}} + k\pi \quad (2.4)$$

for estimation of the direction towards the starting point. If movement is split into discrete segments intermitted by points where measurements are performed, the variables in the equation are as follows: P_i is the length of the i th segment of the route; P_{i+1} stands for the distance between the points i and $i+1$; D_i means the distance between the i th point of the outward journey and the start; D_{i+1} is, correspondingly, the distance between the point following the i th one and the start; α is the angular (directional) difference between the successive segments; ω stands for the angle between animal's sagittal axis (the direction of its current movement) and the homing vector; and, finally, $k = 0$ if the denominator of the equation is positive, and $k = 1$ if it is negative. The stroke assigned to the variables in the equations (e.g., like P' instead of P) means that the variable is with an inherent error (noise) that appears as a result of imprecise measurement by an animal, i.e., it is the animal's representation of the variable.

In order to further develop their model and investigate errors (noise), the authors performed some simulations based on the following hypothetical properties of the process. First of all, it should be recalled that animals are potentially able to use two main sources of navigational information, namely the idiothetic (body-generated) and allothetic (external cues). In addition, path integration is supposed to be possible in two coordinate systems, egocentric (body-centered polar coordinates) and geocentric (Cartesian) coordinates centered at some stable external point of origin. Based on this theory, Benhamou and his team suggested that noise should affect measurements of both distance and angular deviation (change in direction). Estimation of distances most probably is performed idiothetically. Measurements of angular deviation are possible through both idiothetic and allothetic (such as external compasses) cues. Further, the authors suggest the following properties of errors: (1) the standard deviation of the error in measuring the length of a segment of route will increase proportionally to the increase in the square root of the segment length, (2) the scatter in idiothetic estimation of a direction change will be proportional to the value of the change, and (3) the scatter in allothetic estimation of a change in direction will be constant. Simulations based on these presumptions, with different values of variables, have led the authors to the following predictions:

1. Errors in estimation of length produce relatively little effect on egocentric spatial coding (memory for spatial relationships), and the accuracy of it remains high.
2. Errors in idiothetic measurements of directional changes considerably affect the accuracy of egocentric spatial coding.
3. Errors in allothetic measurements of directional changes impose little effect, and the accuracy of egocentric spatial coding remains high.

4. Angular and distance errors influence the accuracy of spatial coding independently (a combination of both types of noise produced a variance roughly equal to the sum of their variances, but not their product, the latter being likely to appear if the two types of errors depend on each other).

The model of Benhamou and his team was innovative in that it incorporated the noise (random errors) in the system of path integration. Moreover, analysis of the differential effect of random noise on different parts of the path integration process is definitely a merit of the model. The fact that rodents, for instance, do not measure linear displacement accurately (Etienne et al. 1988) can be explained based on the predictions of the model, since the simulations have shown that errors in distance estimation should have little effect on the overall accuracy of path integration.

But although the hypothesis is in accord with some experimental evidence, it has an appreciable drawback, as it doesn't consider the systematic errors many animals have been found to make. Moreover, the occurrence of these regular errors, itself, suggests that the noise (error) distribution may differ from normal, which undermines potential reliability of the model (Maurer and Seguinot 1995).

Müller and Wehner (1988) took a closer look at the problem of systematic errors during path integration. They also studied desert ants, and noted that the ants made errors while estimating their homing vector, and that the errors were largely constant (predictable). Indeed, analysis of path integration errors in animals pertaining to different phyla suggests that the process of path integration may function based on one common algorithm, irrespective of what group a certain animal belongs to.

Figure 2.9 schematically shows vectors leading towards the starting point, calculated by different animals. It can easily be seen from the picture that all the represented groups make similar errors that only differ in size. Müller and Wehner supposed that common mistakes in homing vector calculation might reflect an inherent path integration algorithm error, rather than random noise.

The authors speculate that trigonometric solutions in calculation may impose much heavier demands on the animal memory (system of computation), and arithmetic approaches appear more likely to have been preferred by the evolutionary

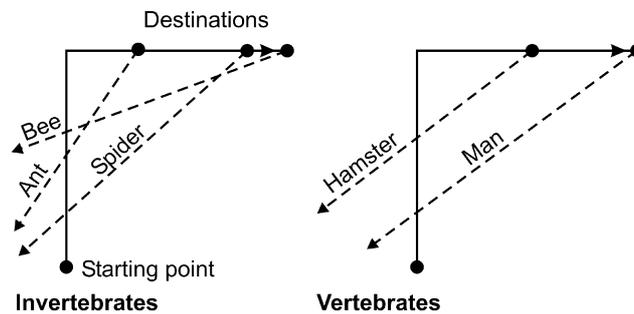


Fig. 2.9 Homing vector calculation errors during path integration by different animals (adapted from Maurer and Seguinot 1995)

process. Animals were supposed to update their position on a regular basis after covering some fixed distance. The fact that the path is discretized into steps of equal length, and position updating is performed after covering another step, implies that we can take 1 for the length of one step, which somewhat simplifies the equations used for the calculation.

Therefore, the final model is based on the following equations:

$$l_{n+1} = l_n + 1 - \frac{\delta}{90^\circ} \quad (2.5)$$

and

$$\varphi_{n+1} = \varphi_n + k \frac{(180^\circ + \delta)(180^\circ - \delta)}{l_n} \quad (2.6)$$

for estimation of current distance and direction to a starting point, respectively. A path is discretized into n steps of equal length 1; δ stands for the angle between the directions of steps n and $n + 1$ (the angular deviation of the next step in relation to the previous one); φ means the compass direction from the start to the animal; l means the shortest (straight) distance between the start and the animal. The constant k was introduced to fit the model into the observed behavior of ants (for desert ants $k = 4.009 \times 10^{-5} \text{ deg}^{-2}$). In other words, the experimental ants made errors in estimating their homeward directions, and these errors were relatively constant (systematic) and predictable. The constant k corrects (2.6) so that the final result of calculation is not the proper course to the starting point, but deviates from the true course by the angle the ants use to deviate in real experiments.

What is interesting in the model of Müller and Wehner is that it is remarkably precise in predicting the actual navigational behavior of ants, i.e., the deviations ants actually make from the true homeward course match those calculated based on the model. In addition, the model has been shown to properly describe the behavior of some spiders and bees. Unfortunately, its application to vertebrates still has to be tested, since few studies have touched the question. Seguinot et al. (1993) have found that the model works well on golden hamsters, *Mesocricetus auratus*. Hamsters navigating under infrared light in a two- or three-segmented outward journey task returned results predicted by the model. However, in cases where the outward journey included initial loops returning the animals back to the starting point, the hamsters did not show predictable behavior any more. Results of several other experiments and computer models also suggest that this model works well only in simpler tasks, and that more complicated geometry of outward journeys causes its failure.

Moreover, there are some unresolved puzzles that are inconsistent with the existing mathematical models and suggest that path integration may be a much more

complicated process. Results of the following experiment demonstrate it. When a desert ant returning from a foraging trip is just about to enter its nest and is passively displaced at this moment, it starts searching and moves along a spiral route with ever-expanding coils. The behavior has largely remained unexplained. Further, if this ant moving along the spiral is displaced once more, it continues its movement as if it didn't notice the second displacement, i.e., continues movement from the imaginary point on the "previous" spiral it was taken from (see Wehner and Srinivasan 1981; Wehner and Wehner 1986; Müller and Wehner 1994). In general, switching from path integration to landmark navigation (like beaconing) in the vicinity of a goal might somewhat explain the behavior. From this point of view, an animal begins merely to systematically search the goal visually. This, in turn, may indicate that animals possess a navigation system based on interactions of different cues (allothetic and idiothetic), depending on what cue is more appropriate or available in a given moment. Moreover, golden hamsters have recently been shown to rely on stable external cues for updating their path integrator (idiothetic) information (Etienne et al. 2004). Therefore, the idiothetic and allothetic systems of route-based navigation may cooperate by calibrating each other, which improves the accuracy of path integration by compensating for errors (particularly those of idiothetic nature).

Nevertheless, the model of Müller and Wehner, as well as the other ones indicated, seem to offer a fruitful field for future investigation. Extensive testing of the models on different vertebrates is needed. Then, compared with the existing evidence on invertebrates it may bring some new insights into the question of general applicability of the models for path integration by animals in whole, and vertebrates in particular.

Unfortunately, few studies have been carried out to test all the mathematical models of path integration described above in application to vertebrates, and this topic remains for future challenges.

On the neural level, path integration, as well as vertebrate navigation in whole, has so far mostly been studied on mammals. And there are two main factors that have influenced the choice of study object in this respect. First of all, a variety of mammals, especially rodents, have always been classical study objects in many biological disciplines, due to the ease of rearing them in captivity. They also are excellent objects for navigation studies, since their prominent cognitive abilities are well known. The second factor is that the mammalian limbic system is best developed among vertebrates, and its relation to animal cognitive abilities has been established and is being extensively studied nowadays.

The fundamental beginnings of the neurophysiology of vertebrate navigation can be traced back to the time when Tolman (1948) published his now classic paper, and formed his hypothesis stating that vertebrate navigation is grounded on the phenomenon he called "cognitive maps." The definition of the cognitive map has already been presented in the above sections, but briefly the general principle is that animals keep in memory the spatial relationships among the objects and places of the surrounding world, and this memory is responsible for providing information

on where the animal is presently located in space, or where it should move in order to reach a specific intended goal inside the area concerned. Later, many objections were raised to Tolman's initial hypothesis (for references see in Benhamou 1996; Harrison and Schunn 2003; Foo et al. 2005), and even now it remains debated and controversial (Jacobs and Schenk 2003).

O'Keefe and Nadel (1978) were the first to place the hypothesis of cognitive maps on a solid theoretical ground. Based on the evidence accumulated by that time, they linked the hypothesis with the function of the hippocampus. Later, it was revealed that not only the hippocampus but also the whole limbic system of vertebrates participates in the process of spatial learning by vertebrates, and therefore contributes to animal navigational abilities.

Up to now, there is no general consensus on what structures form the limbic system. Nevertheless, some parts of the vertebrate brain are most often referred to as components of the limbic system. Those usually include hippocampus, amygdala, hypothalamus, mammillary body, orbitofrontal cortex, nucleus accumbens, and parahippocampal, fornicate, and cingulated gyri.

The main functions of the limbic system are centered around emotions and memory formation and processing. The latter function (memory) is closely related to navigation and spatial cognition. Therefore, vertebrate navigation mechanisms are thought to reside in different parts of the limbic system. And this especially applies to mammals due to their highly developed limbic structures. Structures homologous to the components of the mammalian limbic system are found in all major groups of vertebrates (O'Keefe and Nadel 1978), but their exact functions still are not understood as well as those of mammals. In particular, the avian hippocampus has been shown to be highly homologous to the mammalian, with apparently the same role in navigation (Macphail 2002; Gagliardo et al. 1999, 2002).

There are two main research approaches that have provided evidence in support of the involvement of the hippocampus and the associated limbic structures in spatial learning and navigation – brain lesions and neuronal activity recordings. Lesions of a brain compartment disrupt its function. If a lesioned animal is then tested for completing spatial tasks, its behavior can be compared with that of control (intact) conspecifics. If significant differences in navigation performances between the two groups are observed, it suggests that the lesioned part of the brain may play some role in navigation.

There is ample evidence for the crucial role of the hippocampus in navigation in both birds and mammals. Rats with damaged or amputated hippocampus demonstrate impaired path integration and spatial learning abilities (Moser and Moser 1998; Gilbert et al. 1998; Cimadevilla et al. 2001; Wishaw et al. 2001; Mumby et al. 2002; Ergorul and Eichenbaum 2004). The majority of these experiments included different laboratory trials testing spatial navigation performance in rats, where the behavior of intact and hippocampus-lesioned individuals was compared. As a general rule, individuals with damaged hippocampus demonstrated significantly poorer performance than intact rats. For example, when tested in a water maze where rats swam in an attempt to find an escape platform hidden by submersion in opaque water, individuals with intact hippocampus were found to speed up when they approached the platform

location and slow down as they passed over the place. This behavior was not observed in the hippocampus-lesioned individuals, which swam with roughly constant speed, which suggested that hippocampus-lesioned individuals had deficits in platform location recognition (for more details see Hollup et al. 2001).

Similar results have been obtained with birds. For instance, the importance of the hippocampus in spatial learning has been revealed in pigeons trained to find food by relying on the sun compass only. While intact individuals readily learned the task, hippocampus-lesioned birds were unable to locate the position of the bait (Bingman and Jones 1994). Relying on some other cues indicating the position of the food, however, didn't result in a difference between intact and lesioned birds, and therefore the results suggested the impairment of only the sun compass after damage to the hippocampus in pigeons. Nevertheless, inability by hippocampus-lesioned pigeons to learn landmark patterns has also been shown (Gagliardo et al. 1999). And although such results were not so evident in some other studies (see Wishaw et al. 1995), the important role of the hippocampus in vertebrate spatial navigation has been conclusively demonstrated in most of the studies carried out so far (for review see Good 2002).

Interestingly, hippocampal tissue transplanted in order to substitute the damaged regions in the hippocampus of initially hippocampus-lesioned zebra finches, *Taeniopygia guttata*, was found to reverse the lesion-induced spatial memory deficit effects (Patel et al. 1997). The hippocampal formation, which includes the hippocampus proper, the dentate gyrus, and the subiculum, is a complex structure distinctively compartmentalized and interconnected with other parts of the limbic system (O'Keefe and Nadel 1978; Bousquet et al. 1998; Wallace and Wishaw 2003). There is evidence of differential importance of various parts of the hippocampus for navigation. While studies say that navigation may be possible with a significant level of damage to hippocampal tissue (Broadbent et al. 2004), it is now evident that at least the dorsal part of the hippocampus must be preserved (Moser and Moser 1998).

Lesion experiments show that navigation is only possible when the hippocampus interacts with some other limbic compartments. Thus, lesions of fimbria-fornix, a bundle of axons connecting the hippocampus with the mammillary bodies and the septal nuclei, have been shown to profoundly affect navigation in rats (Wishaw and Maaswinkel 1998; Devan and White 1999), especially when only idiothetic cues are available (Wishaw and Gorny 1999). Interconnection of the hippocampus with the septal nuclei is particularly important because the nuclei are known to receive reciprocal connections from many parts of the brain (like hypothalamus, amygdala, cingulate gyrus, etc.), and therefore form one of the bridges maintaining the signal traffic between different parts of the limbic system. The connection with the mammillary bodies is crucial in view of the fact that they receive inputs from the semi-circular canals (vestibular information), and thus may be important for idiothetic path integration (Bassett and Taube 2001). Similar lesion studies have also shown the importance of function coordination between the hippocampus and thalamus (Warburton et al. 2001) and some other parts of the limbic system. This suggests that the hippocampus is involved in an integrated neural network, in which different

parts of the limbic system and other parts of the brain work in accord in order to allow the spatial navigation which we observe in vertebrates.

Some comparative anatomical and behavioral observations may also provide additional information. Thus, comparative analyses of the size of the avian hippocampus show that food-storing birds, in which accurate navigation and excellent memory is essential for proper food cache recovery, possess a larger hippocampus than non-food-storing species (Sherry and Duff 1996).

Another approach widely used today includes neuronal activity recording. Electric discharges (firing) in brain neurons serve as a conventional indicator of the involvement of the cells in certain mental processes. Recordings of the firing activity of single cells or cell assemblages residing in certain parts of the mammalian brain analyzed in the context of animal spatial performance constitute a method which gives us some insights into what happens inside the brain when an animal is performing a navigational task.

The initial suggestion by O'Keefe and Nadel (1978) that the hippocampus and the nearby structures are responsible for spatial performance, and may constitute a place where cognitive maps are stored, has been conclusively proved through cell activity recordings (for review, see Etienne and Jeffery 2004). The recordings show that the activity of some neural cells (the so-called "place cells") in the hippocampus and its nearby structures has a spatially regular character and corresponds to the animal's present position within its familiar area (O'Keefe and Dostrovsky 1971; Olton et al. 1978; Quirk et al. 1992; Wilson and McNaughton 1993; Jung and McNaughton 1993); the boundaries of the familiar area are used to "determine" the relative spatial distribution of the firing activity of the cells (O'Keefe and Burgess 1996). Therefore, we can suggest that at least mammals (and possibly other vertebrates) are able to determine their present position within the familiar area based on the location of cell firing patterns.

In order to navigate properly, in addition to positional information animals need to detect the direction of their movement. This function is believed to be accomplished by the so-called "head direction system" (Taube 1995, 1998; Taube et al. 1990a,b), which is composed of cells (the so-called "head direction cells") that fire depending on the direction of the head of an animal, independently of the place within an area at which the animal is currently located. Head direction cells have been found in different parts of the limbic system, including retrosplenial cortex, some of the thalamic nuclei, post-subiculum, striatum, dorsal tegmental nucleus, etc.

Therefore, place cells (PC) and head direction cells (HD) are believed to be responsible for the map and compass senses, respectively. As an animal moves, both PC and HD update their activity patterns, (Blair and Sharp 1995; Knierim et al. 1996; Taube et al. 1996; Sharp et al. 2001), thus constantly informing the animal about the newly acquired position and direction. In cooperation, these two systems are thought to provide the general basis for the neural mechanism of path integration.

The behavioral models of path integration discussed above in terms of computation obviously require animals to possess yet another ability, namely the ability to measure the distance traveled in a certain direction. There is some evidence that

terrestrial vertebrates (at least some mammals), unlike many arthropods, are able to measure the distance walked based solely on body-generated movement cues (Loomis et al. 1993; Seguinot et al. 1993, 1998). Proprioceptive signals and motor efference copies are probably among the most effective sources of positional displacement measurement in mammals, as passive transport during which these sources are “silent” has been shown to result in more significant mistakes in rodent and human navigation (Etienne et al. 1988; Bovee 1994; Mittelstaedt and Mittelstaedt 2001). Nevertheless, inertial signals may also play some role in path integration (Israel et al. 1997; Merfeld et al. 1999), and constitute a complementary mechanism providing some navigational information when cues generated by active movement are unavailable.

The neural mechanisms underlying linear displacement measurement are still unclear. Some studies indicate that measurement of the distance traveled is based on signals from both idiothetic (body-generated) cues and distances to visual landmarks (reviewed in Etienne and Jeffery 2004). What is known is that place cells of a moving animal respond by a correspondent spatial displacement of their activity pattern, and are likely to participate in distance measurement. O’Keefe et al. (1998) have also shown the existence of the so-called “speed cells” in the hippocampus proper, the firing rate of which is highly dependent on the speed of movement. Nevertheless, the exact mechanism of travel distance measurement remains to be discovered.

Therefore, path integration in vertebrates is a complex process. Its functioning is obviously dependent on coordinated interaction of many structures in the brain, primarily those relating to the limbic system. In addition to many detailed properties of path integration displayed by different vertebrates, there remain many general unanswered questions. It is unclear whether a path integrator exists as a separate brain entity (and where it is located), or whether path integration is accomplished in the hippocampus and this structure itself is the path integrator. How exactly are places and directions encoded in the brain? What is the nature of time–space associations when an animal analyzes its movement within an area? Answering these and many other questions is not only important for understanding the phenomenon of path integration, but is also expected to contribute to our knowledge of other higher order processes in the brain.

2.1.2 Group Navigation: The “Many Wrongs Principle”

Up to this point, we have been discussing orientation and navigation in vertebrates, focusing on the individual level. Some hypotheses and models attempting to describe the mechanisms defining the navigation abilities of individual animals have been successively highlighted. But it is common knowledge that many vertebrates migrate in groups (flocks, herds, shoals, etc.). Naturally, the synchronized migratory behavior of such groups raises the question of whether they share some common navigational strategies that keep them together during their sometimes prolonged travels.

Bergman and Donner (1964) were the first to suggest that group navigation may bring some advantages to animals by increasing the accuracy of their orientation. Later, Hamilton (1967) and Wallraff (1978) developed a theoretical basis for this assumption.

As has already been shown, individual navigation is characterized by marked impreciseness, that may be seen for instance in the dispersion of the individual bearings of many tested animals in almost all experimental setups based on circular statistics. Interpretation of any test results is mostly based on the mean directions of the bearings of a group of animals (a sample). Often individual scatter may be considerable in these tests, but this fact is omitted, since only mean (though significant) directions are taken into account. In many cases, similar experimental setups bring discrepancies in the results obtained by different researchers.

There are two main sources of such variability in individual orientation by animals. The external factors may include limited use of some orientation cues, like unavailability of some cues in certain geographical regions or at certain times of day. The internal cause is natural variability of cue interpretation by individual animals. The “many wrongs” hypothesis suggests that group navigation produces an effect when many inaccurate compasses combine to result in one more accurate one. The simplest graphic interpretation of the effect is shown on Fig. 2.10. In terms of statistics, the standard deviation of the mean (vector of flight) is a function of sample size. If a flock is taken as a random sample of a population, we can suggest that the accuracy of their orientation will increase in larger flocks.

Gathering in flocks, therefore, will bring navigational advantages for particular individuals. Provided that individuals differently interpret the same orientation cues (like different interpretation of wind drift or local values of the geomagnetic field parameters), group decision-making that involves some consensus among the members of a group, by itself, is theoretically expected to produce a more balanced cue “reading.” In reality, however, there might be more complex schemes.

Thus, while young individuals of many migrant species orient well, they often are unable to compensate (correct their route) for displacement – for instance, by winds.

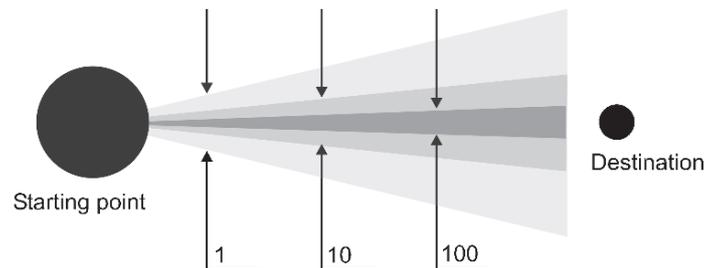


Fig. 2.10 A graphic interpretation of the “many wrongs” principle. Navigation precision (restricted by arrows) is expected to increase as the group size (1, 10, and 100 individuals) increases (adapted from Simons 2004)

Therefore, the actual number of individuals in a mixed-age group that participate in decision-making may narrow to only adult experienced ones. But the overall success of the whole group, as well as that of any particular individual member of it, in locating destination will not decrease. In extreme cases, one leader may lead a migrating group. In this situation, it is suggested that individual success increases as well, since younger individuals are led by an older experienced one (Simons 2004; for further indications of the role of social interactions, see Chernetsov et al. 2004).

Few studies have been carried out to test the hypothesis. And those are limited to a few experiments on pigeons and observations of the spring migration of skylarks, *Alauda arvensis*, where group orientation has actually been shown to be more accurate than individual (Rabol and Noer 1973; Tamm 1980; Burt and Guilford 1999). However, the effect was not observed in all cases (e.g., Keeton 1970).

Nevertheless, great potential for future investigations exists in the area. According to Simons (2004), there are several predictions that can be inferred based on the hypothesis. The first prediction is that within one species the directional variations among migrating groups are expected to be lower with increased mean flock size. Also, it is hypothesized that larger groups will deviate from the appropriate direction less than small ones. Therefore, species migrating in small groups are assumed either to have better navigation mechanisms, or to endure heavier losses of individuals during migrations. Perilous areas or regions where some orientation mechanisms are inefficient are supposed to cause greater flocking. In the case that wintering quarters and breeding areas differ in size, the flocks performing fall and spring migrations are presumed to differ correspondingly.

These and many other conjectures have to be tested before these early suggestions, supported by only a few experiments and observations, have a chance to become a theory. Miraculously, regardless of the half-century history of extensive investigation of vertebrate navigation, this area has remained poorly studied.

2.2 Navigation Strategies

In this section, we will try to summarize the main features and properties of navigation and orientation in vertebrates by shortly repeating some of the previously highlighted material, and adding a specific angle of analysis dedicated to explaining how current biology interprets navigation applied to certain most studied cases in the realm of vertebrate animals. There are several groups of vertebrates for which navigation has, for various reasons such as their prominent migratory behavior or their convenience as study objects, been investigated most thoroughly. Happily, these groups represent different environmental and migratory specifications, thus allowing us to trace potentially different navigational strategies. For example, pigeon homing is a good model for terrestrial short- and middle-range navigation, migration of sea turtles and albatrosses is characteristic of long-distance navigation in visually featureless stretches of the ocean, avian migration denotes similar terrestrial navigation over vast terrains, etc.

The “representativeness” of these systems provides us with a good basis for building a more generalized theory of animal navigation and its evolution, but this work still largely remains for future challenges.

2.2.1 Pigeon Homing

The amazing ability of pigeons to home from distant places has been known and used by people since many centuries ago. In fact, it is one of the oldest mailing systems in the world, which, however, has almost no application nowadays. But regardless of the long history of the practical application of pigeon homing, its mechanisms remain unclear even today. Indeed, detailed scientific investigation of the phenomenon started mainly in the twentieth century, and became most intensive in its second half when the growing experimental evidence produced many hypotheses dedicated to explaining animal navigational abilities. Pigeons as a relatively convenient study object have become one of the most extensively examined model systems. The tremendous number of experiments carried out on pigeons have resulted in much discrepancy in their interpretation, and produced one of the most debated issues in the realm of animal navigation. And the reason is clear. Pigeon homing encompasses more potential strategies to test than do other classical systems (e.g., long-distance migrations in birds and turtles), because it includes middle-range and short-range navigation with its specific orientation cues, while possibly retaining some basic strategies common to all birds, including long-distance migrants. Therefore, if the notion of loggerhead turtles possessing an odor map of half of the Atlantic Ocean, for instance, may not seem very plausible, this type of map in homing pigeons is at least possible, not to say that it has obtained some evidence during the last three decades. On the other hand, the use of different strategies other birds utilize (such as the geomagnetic field) has also been experimentally supported for pigeons. Therefore, the larger number of potential cues suggested to be used by homing pigeons complicates the question of the primary strategy pigeons employ to navigate during their homeward flights.

Therefore, although we cannot refine any unequivocal and generally accepted theory on pigeon homing strategies, the evidence accumulated to date allows some more or less theoretically and empirically substantiated speculation.

First of all, experimental evidence supports the ontogenetic development of a navigational map in pigeons. This means that inexperienced individuals are not capable of true navigation and possess only an innate magnetic compass and develop a sun compass. The use of these compasses is subject to preference, i.e., the sun compass may sometimes (in young individuals) dominate over the magnetic, but older pigeons seem to use the two on a complementary basis (discussed in previous sections). It has been demonstrated (Keeton and Gobert 1970) that inexperienced (untrained) pigeons that are not familiar with the experimental territory do not home normally unless the Sun is visible. By contrast, trained individuals seem to be able to home even under overcast conditions. Moreover, the sun compass

of pigeons has been shown to be well tuned to the changing speed of the Sun's movement across the sky. It is well known that visually the speed of the Sun's movement is different, say, in the morning and near noon. Pigeons clock-shifted by 4h and released during late morning and in the afternoon responded differentially by deviating from the true home direction by a predictable angle that depended on the time of release, which suggests that they may be able to detect the changes in the Sun's speed of movement during the day (Wiltschko et al. 2000).

A series of experiments on olfactory navigation has resulted in a conclusion that pigeons may possess olfactory maps; they need to develop and are able to use olfaction for homing only after sufficient "olfactory" experience with the territory is gained. Pigeons not able to sense the natural winds around their loft during their post-fledgling ontogeny demonstrate significantly poorer homing than birds allowed to smell natural odors (Gagliardo et al. 2001), which may indicate that they learn the pattern of odor distribution around their home loft and, thus, have probably formed a kind of olfactory map of their home territory (though this is only a hypothesis).

The development of any of the hypothesized navigational maps occurs as a young pigeon flies across the territory surrounding its home loft, or at least has some access to the cues that potentially can form the map (such as visual cues, odors, the geomagnetic field, etc.). It has been shown that there is a sensitive period of about 3 months after hatching during which young birds seem to learn and form their maps (Gagliardo et al. 2001). Acquisition of a map changes the orientation behavior of the bird, which, it is supposed, relies upon the map from then on. Manipulations with the pigeon sun compass show that clock-shifted pigeons differ in their orientation depending on age. Inexperienced young individuals orient predictably according to the position of the Sun and the degree of the experimental clock-shift. So do pigeons having a map of their home area, but released far beyond it. By contrast, experienced individuals released within the familiar territory deviate from the predicted "clock-shifted" direction, which can be interpreted as a conflict between their "clock-shifted" compass and the mental representation (map) of the area (Wallraff et al. 1999) or indications of other compass cues, e.g., the magnetic compass. In general, there is evidence that pigeon homing strategy alters (evolves) as the bird grows older, so while young, pigeons rely more on path integration and information provided by the magnetic compass. Later, they develop the sun compass, and finally the "map" sense of the familiar area. This map may be either olfactory or magnetic, or even both types may be used, with the extreme ability of most experienced individuals to orient homewards from sites well beyond the familiar area relying on the extrapolation of the learned regular pattern of the magnetic map (see Wiltschko and Wiltschko 1978b, 1985).

The exact nature of the familiar area map in pigeons is still unclear. Several hypotheses have been proposed. Some researchers suggest that an olfactory navigational map model would best describe the pigeon's homing behavior (e.g., Papi 1990b; Benvenuti et al. 1998; Wallraff 1990, 2001), while others dispute the hypothesis and propose that the navigational map may be based on the geomagnetic gradients as a dominant or supplementary cue (Wiltschko 1996). Also, some researchers suggest the use of landmarks as a basis for familiar area landmark map

formation in pigeons (Holland 2003). The latter hypothesis is not in conflict with the former two, since use of landmarks is considered a contributory cue, which becomes more and more relevant as a bird approaches the nearest vicinity of its home loft. Nowadays, navigation and the navigational map of pigeons is supposed to be based on a multifactor system proposed by Keeton (1974) and supported by most researchers. This hypothesis suggests that pigeons are able to use multiple cues for homing. If, for instance, olfactory information is not available during ontogeny, the landmark-based map of the familiar area may be supplemented by other cues (Wiltschko and Wiltschko 1985), such as magnetic. This hypothesis is in accordance with studies on the ontogeny of homing abilities. Thus, pigeons treated with $ZnSO_4$ solution, which deprives them of the olfactory sense for several days, seem to home differently, depending on whether they have been reared anosmic since hatching or made anosmic just before experimental release. In the latter case, birds showed significantly worse homing (Schmid and Schlund 1993). Application of xylocain (another anesthetic) in a similar study produced the same results (Papi et al. 1989). Interestingly, the initial orientation of individuals with short-term anosmia was good; they knew the homeward direction, but were unable to complete the whole journey. The best explanation of these results is probably that the map component of birds that had been reared anosmic was supplemented by other than odor cues, and they were able to use this while homing. In contrast, pigeons reared with free access to natural winds might have formed a map heavily relying on olfaction and, therefore, not functional during the olfaction impairment experiments.

Therefore, it is supposed that homing in pigeons includes both map and compass components. The birds are assumed to collect the relevant navigational information needed for true navigation wherever and whenever is possible (Wallraff 1996). But theoretically we can divide this information into three types: (1) information collected at the home loft site, (2) information gathered during an outward journey, and (3) features detected at the release site (or at the site from which a pigeon starts returning home). And although the exact process of homing navigation is still unclear, some evidence already obtained allows an outline of some of the main features of pigeon homing.

Most data suggest that pigeons use a combination of a gradient (grid) map, such as magnetic or/and probably olfactory, and a mosaic map based on landscape features, infrasound (Hagstrum 2000), etc. The use of a gradient map is supported by evidence that pigeons are able to home successfully from distant unfamiliar areas (Keeton 1973). Moreover, pigeons do not need to have access to navigational information during their transportation to release sites. Irregular rotation (Matthews 1951; Keeton 1974), magnetic field distortion (Kiepenheuer 1978b), or a combination of these treatments with olfactory sense deprivation (Wallraff 1980) during transportation of pigeons to release sites does not seem to affect their homing. Full anesthesia (Walcott and Schmidt-Koenig 1973) during transportation doesn't result in impaired homing either. These studies have clearly demonstrated that orientation at a release site may be independent of the information available en route. So pigeons appear to be able to determine their homeward course based solely on information obtained at a release site. Whatever compass mechanism pigeons use, it will

not be sufficient to tell them in which direction their home is, unless they know where they have been displaced. Since proper homeward orientation is possible without en-route information, mosaic maps are unlikely to be a primary facility here, since they are formed by remembering spatial relationship between real objects. Instead, a grid map may apply, since it is suggested that this type of map is based on a mental representation of the direction and degree of parameter change, and thus involves extrapolation that potentially can give one's relative position even well beyond the familiar area. Nevertheless, grid maps are less precise on smaller areas (close to the home loft). So, mosaic maps appear to be more important closer to home. It was shown, for example, that pigeons released within their familiar area and allowed to preview the landscape for several minutes immediately before release homed faster (Biro et al. 2002, 2003; Burt et al. 1997), suggesting that within a familiar area they may rely more heavily on visual landmarks than on environmental gradients.

Another set of evidence supporting the use of mosaic maps (landmarks and possibly odors) comes from GPS tracking of pigeon homing routes, which reveals that within their familiar area pigeons prefer their individual routes. When released at a new site off the preferred homing paths, they tend to fly towards these paths and then follow them while homing. Sometimes, these preferred routes may be far from straight (bee-line), and theoretically it may seem irrational to follow them (Biro et al. 2004); nevertheless, pigeons seem to prefer familiar routes as obviously more reliable indicators of the homeward course. In addition, analysis of 216 GPS-monitored pigeon tracks up to 50km long in Italy revealed their significant convergence to highways and railroads (Lipp et al. 2004; see also Bonadonna et al. 2000). This feature of pigeon homing behavior provides substantial evidence strengthening the hypothesis of the use of landmarks.

As has already been mentioned above, a debate is going on nowadays between the adherents of olfactory navigation hypothesis (reviewed in Wallraff 2004) and those who deny exclusiveness (or dominance) of the olfactory sense of pigeons in homing and formation of their navigational map. There is no need to discuss the hypothesis of olfactory navigation here, since it has largely been detailed in the previous chapter. Nevertheless, in the context of all the above material concerning pigeon homing, it should be mentioned that navigation by pigeons is unlikely to be based on completely different mechanisms from those observed in many other bird species and thought to be common to birds overall. Hans Wallraff, one of the biggest proponents of the hypothesis of olfactory navigation, mentions in his review (Wallraff 2004) that in view of what experimental evidence says, pigeon homing can be considered as a model of short-range navigation and homing for all birds. The idea is interesting in that short-range navigation has been studied in only a few bird species, and more studies would probably have revealed some parallels between different species. But continuing this idea further, we have to admit that, for instance, magnetic navigation has been proved clearly for many long-distance migrants among birds and turtles. In view of the existing evidence, therefore, we can speculate that the role of olfaction in pigeon homing and models of pigeon homing may indeed serve for building models of avian short-range navigation.

The discrepancy in navigation research between results obtained on pigeons and those for long-distance migrants leads to the idea that migratory birds may encounter different navigational problems during different stages of their long journey, and the final stage (when they arrive at a destination area) may well involve mechanisms similar to those pigeons use for homing. Occlusion of the sense of olfaction impairs homing, but has a far smaller effect on initial orientation at release sites. Decreased homing success in this case can probably be explained by worse navigational abilities in olfaction-occluded pigeons on further stages of a homing flight, due to which the birds are unable to complete their way back successfully, regardless of the initially proper course. Therefore mosaic maps based on odors and landmarks cannot be excluded from future consideration, and a kind of distance hierarchy may be supposed in bird navigation, where navigation over long distances is provided by, say, magnetic or/and celestial mechanisms, while during mid- and short-range navigation odors and landmark cues become dominating. Moreover, this idea has already been proposed for long-distance migration in sea turtles (Sims 2003; Lohmann et al. 1999). Nonetheless, this question remains open today and requires more detailed investigation.

2.2.2 *Navigation in Sea Turtles*

As has already been discussed, long-distance navigation imposes somewhat different challenges on migrating animals. The features which might be attributed to mosaic maps (such as landmarks) seem to become less important. This is supposed to happen due to the scarcity of these features (e.g., in oceanic migrants), or as a result of the impracticability of exclusive reliance on them (as in long-distance bird migrants). The vast stretches of oceans are almost featureless. By contrast, terrestrial terrains contain many landmarks (coastlines, highways, lakes, city lights, etc.), but the huge amount of land features to memorize during long-distance migration, and their irregular distribution, make their relevance become limited as the distance of migration increases. First-time migrants traveling alone and being unaware of the en-route distribution of these features demonstrate that long-distance migration may employ some other mechanisms. And one of the most tempting models proposed so far has been the use of grid maps with large-scale gradients of certain environmental variables.

Further, long-distance navigation seems to include several components; those specific to short- and middle-range navigation when an animal approaches its destination, and particular ones designed for navigation over long distances.

Sea turtles constitute an excellent model for navigation over vast stretches of oceans. Long-distance migrations seem to be quite common among sea turtles. In addition to the turtles from Florida beaches and Brazilian green turtles already mentioned, Kemp's ridley turtles, *Lepidochelys kempi*, are known to cover up to thousands of kilometers, gathering from the Caribbean, Gulf of Mexico, and some parts of the Atlantic Ocean at their nesting sites on a small beach in Mexico (Carr 1963).

Loggerheads nesting in Japan appear to cross the Pacific Ocean to reach California and, afterwards, return to their natal beaches to breed (Bowen et al. 1995).

Loggerhead and leatherback sea turtles nesting on Florida beaches and green turtles from the Brazilian coast are among the best-studied populations in this respect. The life history of these species was briefly touched on in the previous chapter, so there is no need to repeat it here, and we will concentrate directly on what is known about the mechanisms which allow turtles to navigate along their tremendous migratory routes.

Sea turtle hatchlings almost always emerge from their underground nests at night (Mrosovsky 1968; Witherington et al. 1990). As they appear, the first challenge they encounter is to crawl to the water edge. They must do this as quickly as possible in order to avoid many terrestrial predators. So they start crawling in just a few seconds after emergence and move along a straight line directly to the sea (Lohmann and Lohmann 1996b). This is their first navigational task, and they use the bright seaward horizon to indicate the direction to the sea (Limpus 1971; Lohmann and Lohmann 1994b) and dark silhouettes of vegetation to sign the reverse course (Salmon et al. 1992). The landward horizon is always dimmer than the seaward.

Such quick orientation (right after emergence from nests) has raised a question of whether this behavior is innate or the seaward direction is acquired upon appearing from underground. To address this question, turtles from the east coast of Central America were transferred to the west coast. The experimental individuals didn't crawl in the eastward direction typical of their natal beaches and headed properly for the sea in their new location. This experiment supported the notion of quick direction acquisition after emergence, and excluded the likelihood of the directional preference being inherited. The use of visual cues seems to be critical at this moment, because hatchlings with covered eyes (devoid of vision) are unable to locate the seaward direction (Carr and Ogren 1960). It is these early findings, supported by the fact that hatchlings prefer brighter light to dimmer light, which have finally resulted in the hypothesis that the seaward horizon plays the most important role in sea finding by turtle hatchlings (Mrosovsky and Shettleworth 1968) at this initial stage of their migration.

However, this behavior may be more complex in nature. Ground slope has been shown to play some role in experiments where hatchlings were tested to compare the roles of illumination and elevation. The hatchlings in the experiment oriented mainly by illumination cues (moved towards brighter parts), but once devoid of any light cues they used slope and moved down the slope (Salmon et al. 1992). Provided with gradient light conditions, they tended to move towards the brightest part, but if dark silhouettes simulating the naturally occurring grasses and dunes on the landward part of the beach were presented they moved away from them, irrespective of light gradient.

Therefore, the system may work based on the following scheme: turtles move towards the lowest illuminated horizon, but if the ground surface is a plane (with equal elevations in all directions) they turn to the side with the most illuminated horizon (Lohmann and Lohmann 1996b). Beach grasses and sand dunes on the

landward part of the beach which appear as dark silhouettes at night may be important indicators of the direction opposite to the ocean for the turtle hatchlings.

Apparently, during this initial stage, hatchlings calibrate their magnetic compass. It has been shown that hatchlings initially exposed to light stimulus that appeared in the magnetic east oriented eastwards if placed in darkness. Similarly, those exposed to light from the magnetic west oriented westwards. When in complete darkness the experimental magnetic field was reversed, both groups responded by turning their orientation to the opposite direction (Lohmann and Lohmann 1994b).

Early investigators suggested that crawling toward water itself might be important for the subsequent orientation of green sea turtle hatchlings in the ocean (Frick 1976). However, this idea is not supported in more recent studies on leatherback and green sea turtles. Experiments have revealed no difference in oceanic orientation between individuals with and without crawling experience. Once in the water, the hatchlings seem to rely on a completely different system of navigation, the main orientation cues of which seems to be the direction of the sea waves (Lohmann et al. 1995). Experiments with hatchlings placed in special tanks where the direction of wave propagation was artificially controlled showed that hatchlings oriented roughly perpendicular to the wave crest, and their behavior didn't depend on the configuration of other cues (Lohmann et al. 1990). Under conditions when no waves were present, hatchlings either oriented randomly or moved in a circular manner (Salmon and Lohmann 1989).

Using wave propagation direction is an efficient strategy to get off the natal bay towards the open sea. Subsequently (in the case of Florida) turtles will meet the currents of the North Atlantic gyre that are warm, rich in food, and thus favorable for further growth and development of the young.

Hatchlings orienting in approaching waves have been shown to perceive the direction of the waves without the visual sense. Turtles appear to be able to detect wave propagation direction even when swimming underwater and in the night. Visible light seems not to be necessary (Lohmann et al. 1990; Wyneken et al. 1990). One hypothesis trying to explain this ability says that underwater detection of the direction of wave propagation is possible in view of the fact that moving waves create rotation of subsurface water masses so that pelagic objects placed within describe a circular trajectory. So, if a turtle hatchling is moving in a direction opposite to the direction of wave propagation it will experience a sequence of accelerations – upwards, then backwards, downwards, and finally forwards, as shown on Fig. 2.11. Reverse movement by the hatchling will change this sequence – upwards, forwards, downwards, and then backwards (Lohmann et al. 1995; Lohmann and Lohmann 1996b). Similarly, an orthogonal heading of a turtle can be extrapolated. This hypothesis has been tested by rotating hatchlings hanging in the air. Since the swimming behavior of the hatchlings is known to be triggered as their ventral surface detaches from the ground (Carr 1963), rotational movements in the air are suitable for simulation of the turtle's movement in approaching sea waves. Hatchlings respond to rotation by turning their orientation depending on direction of rotation exactly in the way predicted by the hypothesis (Lohmann et al. 1995).

Therefore, the available pool of experimental data suggests that the initial orientation of turtle hatchlings in the water is primarily based on the direction of wave

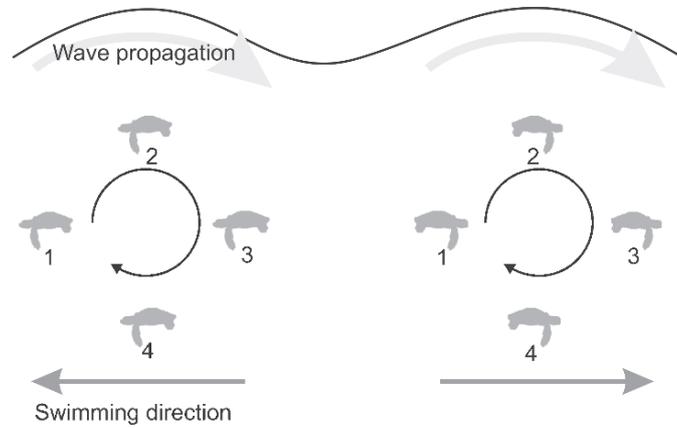


Fig. 2.11 Underwater detection of wave propagation direction (see explanations in the text) by hatchling sea turtles (adapted from Lohmann et al. 1995)

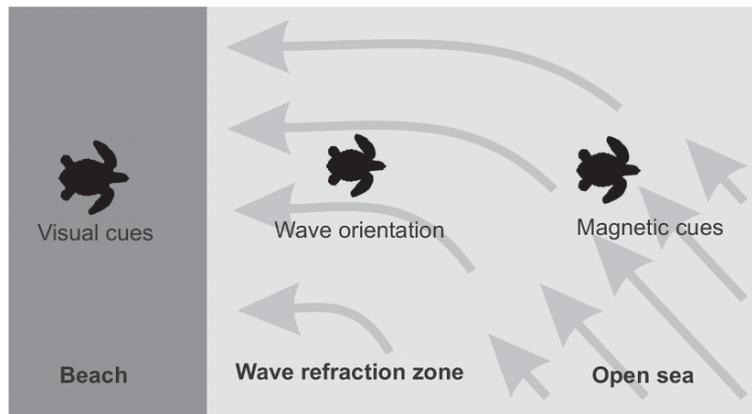


Fig. 2.12 Diagram illustrating the main initial stages of sea turtle hatchling orientation (adapted from Lohmann and Lohmann 1996b)

propagation. No other cues have been found to participate. However, this strategy can only be useful up to some distance from the shore where wave refraction bends the waves to propagate towards the shore (in a direction perpendicular to the shoreline) and the wave propagation direction serves as a reliable indicator of the seaward direction. Further, in offshore areas, hatchlings appear to maintain their seaward course regardless of the fact that wave propagation doesn't coincide with their selected course farther out to sea (Fig. 2.12). Studies have revealed that hatchlings are able to orient in approaching waves only for a short period, after which they obviously change the cues employed (Lohmann and Lohmann 1996b).

Just as in the case of magnetic compass calibration during the beach crawling stage, magnetic directional preferences have been shown to establish themselves during the initial orientation in shallow waters. In experiments with manipulated magnetic fields, individuals that hadn't had crawling experience oriented in the water predictably according to the alignment of the magnetic field applied. When no waves were present, the hatchlings maintained their seaward course in a normal magnetic field and reversed it after field reversal (Light et al. 1993). However, although tested without crawling experience, the hatchlings were allowed to swim towards a light for an hour before the testing procedure. Therefore, the position of the light source (was placed at the east side) might have calibrated their magnetic compass.

To date, the geomagnetic field is considered as one of the most evident guides sea turtles use during further stages of their migration. In the case of turtles from the Florida coast, the migratory route extends for tens of thousands of kilometers encompassing the so-called North Atlantic gyre, and lasting several years, after which they return to Florida as adults to breed. Although experiments on adult individuals are scarce, we have some evidence obtained on the young suggesting that turtles are sensitive to the magnetic field inclination (Lohmann and Lohmann 1994a) and intensity (Lohmann and Lohmann 1996a). It is suggested that these features facilitate orientation while turtles move in the vast and featureless ocean, and may participate in the formation of the geomagnetic grid map, as turtles are known to respond to regional magnetic fields by heading in directions that keep them within their migratory route (Lohmann et al. 2001; Lohmann and Lohmann 2006).

Hatchlings exposed to different inclination angles encountered along their route were shown to respond with the changes in orientation they would normally carry out after reaching the corresponding locations, and were disoriented when subjected to inclination angles they would not normally encounter on their route (Lohmann and Lohmann 1994a). Therefore, inclination can potentially provide at least one coordinate most probably responsible for determining latitude. The intensity of the geomagnetic field may provide the second coordinate and form a bicoordinate map. In the case of Florida turtles, measuring latitude by inclination seems even more likely in view of the south–north direction of the beaches the turtles breed on; such a location makes the coastline direction almost coincide with the direction of the steepest inclination gradient of the region. Some researchers assume that turtles' high sensitivity to inclination of the geomagnetic field lines is a possible explanation of the females' ability to return to the area they hatched at (Lohmann and Lohmann 1994a), which has been proved by means of mitochondrial DNA analyses (Bowen et al. 1993, 1994, 1995). Complete replications of the Earth's magnetic field (inclination and intensity) characteristic of specific points along the turtles' migratory route around the North Atlantic gyre also caused the animals to change their orientation direction predictably. Manipulations with the fields have suggested that turtles may possess a magnetic map of their migratory route (Lohmann et al. 2001). What is particularly interesting about the putative magnetic map of sea turtles is the fact that hatchlings respond predictably to magnetic

site simulations just described, which suggests that the map may be inherited. This, if true, would be another principal discrepancy between long-distance navigation in birds and sea turtles. Nevertheless, the suggestion needs further testing.

Another experiment has provided yet more support for the hypothesis of magnetic maps in turtles. Juvenile green turtles of several years of age captured at their feeding sites near Florida beaches were subjected to two magnetic conditions (Lohmann et al. 2004). One of these reproduced the parameters of the geomagnetic field occurring naturally 337 km to the north, and the other simulating the field at 337 km to the south of the capture site. Turtles exposed to the first magnetic condition oriented roughly southwards, and those exposed to the second field directed northwards. As can easily be seen, the juveniles responded so that they would swim to the site of capture in either case had they been actually displaced to the simulated sites, which provides yet stronger evidence that they use a kind of magnetic map for navigation (see also Lohmann et al. 2001). However, how these maps could be organized, or whether they are based solely on magnetic cues or magnetic cues providing only some partial positional information, remains unclear.

Radio tracking studies also provide some support to the hypothesis of magnetic navigation in sea turtles. Some turtles of the North Atlantic gyre have been found to maintain remarkably straight courses to distant destinations, even when moving orthogonally to water currents (Lohmann et al. 1999). In addition, turtles displaced from their nesting beaches with attached magnets have been shown to return significantly less effectively and along more complicated routes than those displaced and released without any magnetic treatment (Luschi et al. 2007). Moreover, the magnetically treated individuals were found not to notice off-course displacement by water currents.

Nevertheless, several other cues may guide sea turtles as well. First of all, Earth's magnetic field seems not to be an exclusive basis for navigation in turtles. Green turtles subjected to distorted magnetic fields, and therefore devoid of magnetic guidance, remained able to follow their usual migratory route of about 2,000 km in length with trajectories similar to those by undisturbed individuals (Papi et al. 2000). This suggests that some turtles devoid of magnetic cues may still remain capable of finding their way. However, finding the vast Brazilian coast is a priori a much easier task than locating the tiny Ascension Island during the reverse migration. Moreover, the migratory route of the turtles from Ascension Island to the Brazilian coast studied in this experiment largely overlaps with the general direction of the South Equatorial current at the northern boundaries of the South Atlantic gyre, which may, in theory, also guide them. Therefore, the results of this study cannot be treated as conclusive.

In the context of these results, some other studies indicate the presence of a multifactor navigation system in turtles. Thus, distorted magnetic fields affected loggerhead sea turtle juveniles only if visual cues were unavailable (Avens and Lohmann 2003). Juveniles were still able to orient properly in a distorted external magnetic field if visual cues were available. Only disruption of both cues disoriented the tested animals. This suggests, first of all, that turtles may rely on a multiple cue-based orientation system. In addition, the use of some kind of celestial

compass in natural conditions can also be suggested. Therefore, the exact nature of turtles' long-distance navigation system remains unclear.

Odors, just as in case of pigeons, have also been proposed to contribute to sea turtle navigation. Green turtle females displaced up to several tens of kilometers away from Ascension Island returned to the island with different success depending on the place of release – upwind or downwind. Returns from upwind releases were significantly poorer (Hays et al. 2003). This suggests that turtles from downwind releases might have used odors emanating from the island to guide them in their search. But apparently olfactory navigation is useful only at shorter distances, and it is hardly the primary cue employed during long transoceanic migrations. As a whole, the results of this study are rather inconclusive, as there are a number of other explanations possible. For example, the downwind release site is part of the turtles' migratory route, and thus may represent a familiar area for them, whereas the upwind site is probably an area where the animals never go. In addition, there is a suggestion that the upwind release area is located within a magnetic anomaly.

Some researchers also suggest that currents may play an important navigational role as well (Luschi et al. 2003). The question is whether turtles really migrate, or passively drift with major currents. Nonetheless, following currents by turtles is more an evolutionary adaptation forcing turtles to keep within warm environments rich in food. No navigational guidance by currents has yet been documented. On the contrary, as the North Atlantic gyre approaches the shores of Portugal the currents divide into two major branches – the northern one that veers north and passes near the British Isles, and the southern branch heading for the equator. Those rare individuals that are swept by the northern branch die soon because of the fast lowering of water temperature (Carr 1987). A similar danger emerges in the southernmost part of the route, where turtles risk being taken out of their normal range by the currents of the South Atlantic system (Lohmann and Lohmann 1996b). Therefore, the water current may even be a dangerous guide in some cases. Nevertheless, one of the most important roles of currents may be revealed in the huge energy savings turtles make by following major streams passively. Passive displacement instead of active migration is intuitively evident, since without, say, the North Atlantic gyre the tremendous circum-Atlantic migrations would have probably never existed.

2.2.3 Navigation in Migratory Birds

Birds are probably the most intensively studied group among vertebrates with regard to navigation. Obviously, it's due to the impressive phenomenon of their seasonal mass migrations. Bird migrations are worldwide, often clearly noticeable, and include huge numbers of individuals and species. A view of hundreds of birds flying in accord towards some mysterious place to breed or to winter captivates almost any observer – no matter whether it is a bird student or a layperson. Therefore, it's clear why birds have been among the first animals that made scientists

reason about the mechanisms that guide their flight to specific yet distant sites and allow them to return home without mistakes.

Naturally, such a large number of species involved, each with specific ecology, evolutionary origin, and migratory biology, have produced different strategies to navigate, depending in each particular case on the character of migration, local conditions, availability of orientation cues, etc. Therefore, it's not easy to describe the navigational strategies birds employ in a uniform way. Nevertheless, apart from specific features, some general characteristics obviously do exist.

As has already been described, birds use multiple orientation cues including the Earth's magnetic field, the Sun, star constellations, polarized light in the sky, as well as site-specific landmark features. Some of the orientation mechanisms based on these cues are innate. Those are mainly the compass mechanisms (like magnetic), which birds seem to possess from birth. Compass mechanisms give a bird the direction in which to fly during its first migration, but do not provide a bird with the capability of true navigation. True navigation (knowledge of one's position relative to other objects and the ability to set proper courses to different destinations) is thought to be possible only when a migrant has a map and a compass. Unlike the magnetic compass, maps are thought not to be inherited in birds (but see Fransson et al. 2001). Maps seem to develop with migratory experience, in the form of learned spatial relationships between different objects and sites a bird has encountered on its way. Knowing (at least approximately) distances from one object to another is also beneficial, and increases the preciseness of the use of maps. The best-substantiated maps used by birds during long-distance migrations are the magnetic map and that based on prominent landmarks (like sea shores, rivers, etc.).

Comparative analyses of the migratory routes of conspecific adults and first-time migrating young individuals (Perdeck 1958; Moore 1984; Hake et al. 2003) have suggested that young birds employ a strategy of orientation that is based on compass mechanisms, while experienced adults make major corrections to their route that are consistent with the use of a map. It has been shown that young inexperienced honey buzzards, *Pernis apivorus*, fly more directly from one stop-over to the next, but their overall directional scatter among different segments of the route is significantly larger than that in adults, thus causing the young to cover a longer overall distance during migration. Adults fly in a more sophisticated way, but by correcting their compass directions they make the entire route much shorter (Hake et al. 2003), which indicates that they may employ a map.

The use by adult birds of positional as well as directional information is also supported by findings that adult birds are able to compensate for wind displacement. Side winds make flying birds veer (passively) from their original course. If only a compass orientation mechanism were employed, a bird would be able to maintain its original course without noting this positional displacement. Adult ospreys, *Pandion haliaetus*, and honey buzzards have been found to be able to detect their displacement driven by winds and correct the compass course. Young birds appear not to notice the wind-caused change in position and only maintain the innate compass course (Thorup et al. 2003). A similar difference in this respect has recently been found between young and adult white-crowned sparrows, *Zonotrichia*

leucophrys (Thorup et al. 2007). An increased rate of en-route course re-determination mistakes has also been documented in young birds of many passerine species (Herbert 1970; Ralph 1978; McLaren 1981), while adults have been found to re-determine their wind-caused displacement significantly better (Moore 1990).

But within adults there may be different strategies of compensation for wind drift, depending on species and particular routes and wind configuration. Many arctic migrants have been found to follow the winds, probably in order to save energy, and compensate for displacement only on the final stages of their migration in cases where wind carries them astray (Green et al. 2004), indicating some variability in strategies. In the case of migrants employing passive wind drift, some tradeoff between energy savings provided by following major wind currents and increased route length caused by the same reason may take place. But this variation in strategies only strengthens the idea of true navigation in birds.

Another series of experiments also supports the idea that birds are able to determine their global position. Experienced dark-eyed juncos, *Junco hyemalis*, held before autumn migration close to their wintering range, failed to fatten and demonstrate migratory restlessness – events that usually take place before the start of their migration in nature. By contrast, birds displaced north of their winter quarters did show the typical signs of the upcoming migration (Ketterson and Nolan 1987). In this experiment, some birds were allowed to see local landmarks, while others were not. All the birds failed to show pre-migratory behavior and physiological changes if kept during summer near their wintering range, indicating that the birds were able to interpret their global position regardless of the visual surroundings. In a similar experiment with thrush nightingales, *Luscinia luscinia*, which migrate to their winter quarters from Scandinavia to the south parts of Africa, birds subjected to an artificial magnetic field resembling the geomagnetic field parameters at northern Egypt showed extensive refueling (gained in weight). Northern Egypt is their usual stopover site, where nightingales stay for some time to replenish their fat deposits before crossing the vast and foodless Sahara desert. In contrast, control birds held in the ambient (Scandinavian) magnetic field didn't show such rapid refueling (Fransson et al. 2001). Interestingly, the birds used in this experiment were juveniles making their first migration. As in the case with sea turtle hatchlings, this suggests that birds may inherit their map, or at least some prototype (frame) of it. The possibility that they may inherit the map partially (i.e., some principal part of map-like information) should not be neglected. Nevertheless, this assumption is not in agreement with many other studies, some of which have already been mentioned. A particular case apropos in this context is a recent study on European robins (Kullberg et al. 2007) from Sweden which winter in southern Spain. In this study, first-time young migrants were also tested for fuel deposition dynamics changes after magnetic treatment. As a result, magnetically treated birds caught during late onset of their autumn migration demonstrated lower fat deposition than their untreated counterparts. In contrast, robins captured during early onset of the migration demonstrated low fuel deposition irrespective of treatment. As can easily be seen, these results contrast with those obtained on nightingales and juncos. And although all three experiments have revealed some influence of magnetic cues on fuel deposition dynamics in

migratory songbirds, speculations on the nature of this influence should be made with care, as such a dependence may be species-specific, or may hide a completely different mechanism that cannot be explained in terms of the putative pre-programmed map-like navigational information in migratory birds.

Therefore, based on these and many other investigations, we can conclude that the map-and-compass model of long-distance navigation is most likely to reflect the actual process of navigation in migratory birds. The existence of navigational maps in birds has obtained much evidence, and the magnetic map that develops as a bird obtains some migratory experience is among the most substantiated candidates so far.

There are two main hypotheses on how young birds might use their innate compasses (Akesson et al. 1995). The clock-and-compass hypothesis suggests that young individuals follow a pre-programmed (inherited) sequence of steps consisting of flying in a fixed direction during a certain time, then changing direction and moving along another straight piece of the way, and so on (Berthold 1991a,b). It is suggested that this model works well on shorter distances, but longer migration based on this mechanism is assumed to be imprecise, since directional and positional errors that accumulate during the route are obviously a function of its length. Wind-drift displacement unnoticed by inexperienced migrants may be an example of the causes of these errors.

On the other hand, the goal area navigation hypothesis proposed by Rabol (1978, 1985) supposes that the whole migratory route may be an inherited program in birds.

Although the latter hypothesis appears not to be supported by experimental evidence already discussed (although no study has completely disproved it), the former one, the clock-and-compass model, is also not devoid of problems. For instance, migratory white-crowned sparrows, *Zonotrichia leucophrys*, breeding in northern Canada were (both young and adults) displaced for 100–1,000 km to the east of their breeding grounds and tested in cages and free flight releases for the autumn migratory bearings (Akesson et al. 2005). Instead of the expected flying in their seasonally appropriate migratory direction southeast, both young and adult individuals began flying in a direction leading back to their breeding sites. The results of this study show that there may be a more complex navigational system in young birds, which in this case allowed them to compensate for the eastward displacement. If the birds used a compass in the way predicted by the clock-and-compass hypothesis, they would probably fly in two different directions, the young moving in their expected southeast direction, and the adults south-southeast, compensating thus for the longitudinal displacement. The model of genetically pre-programmed migration of the young appears not to reconcile with these results as well.

However, other studies have brought completely different results. In one such study (Mouritsen 1998b), predictions of a mathematical model of the clock-and-compass mechanism were compared with actual distribution of ringing recoveries of young pied flycatchers migrating for the first time towards their wintering quarters. The results showed a significant correlation, thus implying that young migrants may indeed employ the clock-and-compass program from one stopover to another without taking benefit of true navigation. Subsequent experimental testing of these

calculations (Mouritsen and Larsen 1998) included displacement of young first-time migrant pied flycatchers due south and due west with the control group released from their natural site in Denmark. As a result, all three groups headed in the same direction; no directional compensation for displacement was evident. This means that young pied flycatchers, as well as probably many other birds, may use a simple inherited clock-and-compass program which tells them in which direction they should fly from one stopover to another one along their first fall migration route. Although this model may seem self-evident based on the fact that true navigation by inexperienced bird migrants has not been demonstrated, not all researchers agree with these results. A similar modeling approach carried out by Kasper Thorup and his co-workers didn't produce such strong correlation between theoretical predictions and actual ringing recoveries data (Thorup et al. 2000). However, in this study a slightly different mathematical model was employed, and the question still remains open (for debate, also see Mouritsen 2000).

Therefore at this time, unequivocal conclusions on the exact nature of the mechanisms regulating the use of compasses by migratory birds (particularly by the young) should obviously be avoided. This topic incorporates huge potential for future investigation.

Nevertheless, experiments in extreme conditions where the importance of some cues varies provide an appreciable basis for speculations on what compasses are used by birds. The use of magnetic, stellar, or topographical features for orientation may be traced by comparing migratory routes of birds with those calculated theoretically based on known spatial and temporal distribution of these cues. In this way, it has been shown that the position of the Sun in combination with the putative bird internal clock may play a significant role in orientation at high northern latitudes where the use of magnetic cues is militated by the steep angles of inclination of the geomagnetic field gradually approaching vertical field conditions towards the north magnetic pole and the rapid longitudinal changes in its parameters. Tracking the routes of some Arctic waders, such as *Phalaropus fulicarius* and *Calidris melanotos* (Alerstam and Gudmundsson 1999; see also Alerstam et al. 2001), migrating between Siberia and North America across the Arctic Ocean was designed to compare the trajectories with the four predicted (theoretically calculated) schemes: (1) migration along geographical loxodromes, (2) sun compass routes, (3) magnetic loxodromes, and (4) magnetoclinic routes. The results reveal that during the migration the birds gradually change the direction of their flight, and this change is consistent with the use of sun compass routes. Moving eastwards at high latitudes obviously causes a rapid clock shift effect, with the predictable course change by the birds.

As stated above, the use of the magnetic compass is significantly impaired close to the magnetic poles, since the inclination is steep and leading to the vertical field towards the pole. Birds exposed to a vertical magnetic field when celestial cues are unavailable fail to orient in any consistent direction (Akesson et al. 2001b; Sandberg and Petersson 1996). Nevertheless, the bird inclination compass seems to be very sensitive. Young white-crowned sparrows have been found to be able to orient consistently when inclination deviates less than 3° from the vertical

field (Akesson et al. 2001b). Therefore, the avian magnetic compass may, nevertheless, be useful even at high latitudes. In an experiment providing additional support for this idea and conducted at high northern latitudes, it was possible to elicit predictable changes in migratory orientation of young white-crowned sparrows subjected to deflected magnetic fields (Akesson et al. 2002).

However, pooled evidence is not so strong during such experiments. Often birds behave in ways difficult to explain and totally unexpected. In some cases, phototaxis to the Sun or other vague factors were suggested to affect the birds whose behavior was atypical (Akesson et al. 1995; Muheim and Akesson 2002).

Based on all this evidence, the navigational system of birds is proposed to function based on a rather complex interaction of several compass mechanisms, predominantly magnetic and celestial ones, depending on availability of the cues and local environmental conditions (Muheim et al. 2003; Akesson et al. 2005).

In addition to the high latitude exposure, crossing the magnetic equator by transequatorial migrants constitutes another type of extreme conditions, where the value of one cue, namely the inclination of the geomagnetic field lines, changes dramatically, imposing a great challenge on birds relying on it. Nevertheless, at least some birds have been shown to handle the problem. Garden warblers and bobolinks (and possibly many other species) “reverse” their inclination compass when subjected to a horizontally aligned magnetic field (Wiltschko and Wiltschko 1992; Beason 1992). It is suggested that this feature allows transequatorial migrants to use the geomagnetic inclination compass even when they cross the magnetic equator of the Earth.

Still, the best way to test the comparative use of different compass system by birds is to subject them to artificial conditions where sensory inputs from different potential compass cues are contradictory – the so-called “cue conflict” experimental setups. A review of the results of such studies reveals some regular patterns. The main cue-conflict experiments have concentrated around manipulations with magnetic field parameters, position of the Sun (often easily “changed” with the help of mirrors), and patterns of skylight polarization (achieved with the help of polarizing filters).

Three main types of setup have been employed. The first has included exposure of birds to cue-conflict conditions during the premigratory period. In these cases, birds were tested for orientation responses afterwards, at the time of migration. In the second type of experiment, birds were subjected to conflicting conditions and tested in orientation funnels right at the time of migration. And finally, birds exposed to an artificial “cue-conflict” environment during migration were subsequently tested for orientation under natural conditions (without conflicting inputs).

Pooled results from numerous studies designed as described above have revealed that during the premigratory stage both young and adult birds mostly rely upon celestial cues that are used to correct magnetic information (calibrate the magnetic compass). The pattern of skylight polarization is also used to calibrate the magnetic compass at this time. The mechanism seems to change at the time of migration, when priority is given to magnetic stimuli, which, in turn, recalibrate celestial cues. However, these data are not so uniform, and several studies suggest orientation similar to that of premigratory period.

The pattern of skylight polarization, in cases where it is available, has been shown to be of primary importance during either premigratory or migratory periods. This cue appears to function as a universal compass calibration in birds, and serves to calibrate both magnetic and celestial compasses. Here, it should be mentioned that, as far as migratory birds are concerned, the pattern of polarization of the sky above the horizon has been shown to be most important at the time of sunset, and possibly sunrise (for a more detailed review, see Muheim et al. 2006a,b).

Initially, the idea of magnetic compass calibration by sunset/sunrise cues came to William Cochran in the mid 1970s, but due to unexpected reasons his work of 1986 was never published. Much later, Cochran and his team (Cochran et al. 2004) published another work that included his early results and new studies. In these experiments, Swainson's and grey-cheeked thrushes, *Catharus ustulatus* and *C. minimus* respectively, were subjected to eastward-directed magnetic fields during twilights, then released and followed for over 1,000 km. It was revealed that the birds didn't fly in their normal northward direction, but instead headed for the west. However, on the subsequent night they resumed their normal northward migratory headings. Later, Muheim et al. (2006a) also showed a similar effect of twilight cues on the migratory orientation of savannah sparrows in caged experiments. Therefore, although evidence is still scarce, we have some preliminary information indicating that twilight cues may calibrate other bird compasses.

It is interesting to admit that several studies have found different responses of birds in relation to planes of symmetry in which a cue is manipulated. For example, pied flycatchers have been found to recalibrate their magnetic compass only if the magnetic field was shifted clockwise in relation to the celestial cues. Counterclockwise shift resulted in disorientation (Prinz and Wiltschko 1992). The results suggest a more complex process of interaction of different compass systems in nature, perhaps due to lateralization of sensory input in the bird brain or some other reasons. These findings are, for example, in accordance with later studies that support lateralization of magnetic cues interpretation by birds. Thus, in view of light dependence of the bird magnetoreception, European robins were allowed to orient in a magnetic field with either left or right eyes capped. Only those that used the right eye showed a significant consistent response to magnetic stimuli (Wiltschko et al. 2002a).

Some researchers hypothesize that this feature, indeed, may be connected with the light-dependent nature of bird magnetoreception. In view of the evidence suggesting the importance of sky polarization during twilight, it can be assumed that such asymmetry may be an adaptation of the visually mediated magnetic sense to the spectral gradient appearing in the evening sky. Therefore, it is predicted that responses of birds placed in cue-conflict conditions should differ (be opposite) in the Northern and Southern hemispheres. Unfortunately, evidence from the Southern hemisphere is scarce, and mainly suggests the dominance of the magnetic field over celestial cues in either case (Wiltschko et al. 1998b, 2001) of the rotation plane. The problem remains for future studies (for details, see Muheim et al. 2006b).

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