Avian Magnetoreception Navigation Systems: A Biophysical Marvel

J. Romero – 20806791

Professor Brenda Yasie Lee

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Abstract:

Migratory species of birds can navigate using the earth's weak magnetic field. This is believed to be made possible by two biophysical magnetoreception systems. One of which, uses the radical pair mechanism and occurs in the short-wavelength cones of the retina; utilizing light-induced oxidation of a cryptochrome, followed by a further light independent oxidation of the resulting species in the presence of a weak magnetic field. The latter part of this process being the crucial step in the radical pair mechanism since it is sensitive to the physical orientation, relative to the magnetic field vector lines, because of its electron-spin characteristics. The second occurs via a small deposit of iron-rich structures found in the beak by which information is electro-physiologically transmitted through the ophthalmic nerve. The navigational framework by which birds interpret these senses is still poorly understood; however, current literature suggests the use of both magnetoreception systems, polarity independence, magnetic field intensity sensitivity, and a navigation framework that utilizes inclination with respect to the local magnetic field.

Introduction

Birds are not the only species to exhibit magnetoreception. Indeed, many other organisms can sense the earths weak magnetic field (~10 mT) and utilize that sense for long-distance navigation. Other magneto-receptive organisms include but are not limited to; invertebrate species such as crustaceans, reptilian species as with sea turtles, certain insects and even some bacteria. Notably, it has been proposed that, though these other organisms are capable of magnetoreception, they often use the sense as a secondary cue for navigation (preferring non-magnetic cues if available) due to the complicated physical nature specific magnetoreception mechanisms that may make the information provided difficult to interpret in real time [1].

Avian migration is one of the most robust and intensive applications of sensory magnetoreception. Migratory species of birds are believed to navigate using at least two receptors. Thus, two separate hypotheses exist for the magnetoreception sense. Both senses have been explored to a limited extent. Further, their nexus; that is, a framework to unify the electrophysiological data assumed to be provided by the two independent receptor systems, is all the more poorly understood [2].

The first mechanism for sensory magnetoreception discussed in this review is the chemical process that occurs in the avian retina. This process, termed the radical pair mechanism [3], provides directional information in the form of an ‘inclination compass’ that can infer orientation information from sensory data based on the relative angle of inclination from the local magnetic field lines. This directional information provides some picture of what is ‘poleward’ or ‘equatorward’ but is not specific to either the North or South geomagnetic poles [4]. The radical pair model proposes the light-activated degeneracy of a flavoprotein that specifically reacts in presence of light above a specific frequency threshold, a cryptochrome. The light-dependant degeneracy of the cryptochrome serves only as the prerequisite for the further reoxidation of the resultant chemical species. The ratio between the two resulting spin states, singlet and triplet, depends on the alignment with the local magnetic field [5]. This ratio is believed to be the active indicator of magnetic field information; however, the neurological analysis of this indicator is a mostly unexplored topic and will not be discussed here.

The second, but equally as important, form of sensory magnetoreception that will be discussed is the magnetite-based sensor in the beaks of migratory birds. Though iron-rich structures have been definitively found in the beak, the exact composition is still poorly understood[2], [6], [7]. Research suggests that the receptors are sensitive to the intensity of the magnetic field and, thus, serve a different purpose than the photoreceptive counterpart [2].

Behavioural experiments suggest that migratory birds employ both receptor systems to generate and update their cognitive navigational map [5], [8]. Theories on the framework that enables the simple cues from these receptor systems to be leveraged for directional and spatial bearing information is a subject matter that has not been commonly explored by researchers (Only briefly discussed in review [2]); likely due to the fact that the receptor systems themselves have not been defined with reasonable uniformity among researchers and, thus, they are the preferred subject for inquiry. To enable a navigational framework discussion, a few assumptions will be outlined prior. The framework then serves as a snapshot of what may occur in the brains of migratory bird species, given current state of research as presented in this review.

Chemical Magnetoreception in the Avian Retina

The first clue that avian magnetoreception may occur in the eyes may have come from early observations of songbird species during twilight hours, at roughly dusk and dawn. Early observers might have noticed that birds exhibit a higher ‘migratory readiness’ during these periods. A recent ornithological study set out to examine garden-warblers’ (long-range migrants) compass calibration behaviour during the twilight periods. The study used Emlen funnels to record ‘jumps’, ‘flushes’, ‘cage crawling’, and crucially ‘head scanning’ which was defined as turns of the bird’s head from torso axis with an angle of greater than 60°. Though the avian light-dependant magnetoreception mechanism was not discussed in this particular study, the results showed that ‘head scanning’ saw a rough maximum around sunset, that is, the point at which the sun was at 0° with the horizon ± 5° (Figure 1).This finding is supportive of a system that is, at least partially, dependant on light because the highest level of directionally-linked calibration activity (‘head scanning’) occurred during the periods where the sun’s rays were at the largest angle of incidence with the vertical eyeline of the retina. It is reasonable to ask, then, if birds actively calibrate; meaning they update their cognitive navigational map, during these periods [9]. This area of the subject matter is, for the most part, unexplored because the retinal receptor is not fully understood; though, given the current research findings regarding chemical magnetoreception (summarized below), a study to cross examine this ‘head scanning’ behaviour with the effects of full spectrum light (sunlight) on successfully vectored migratory flight legs could help further describe the navigational framework applied by birds.

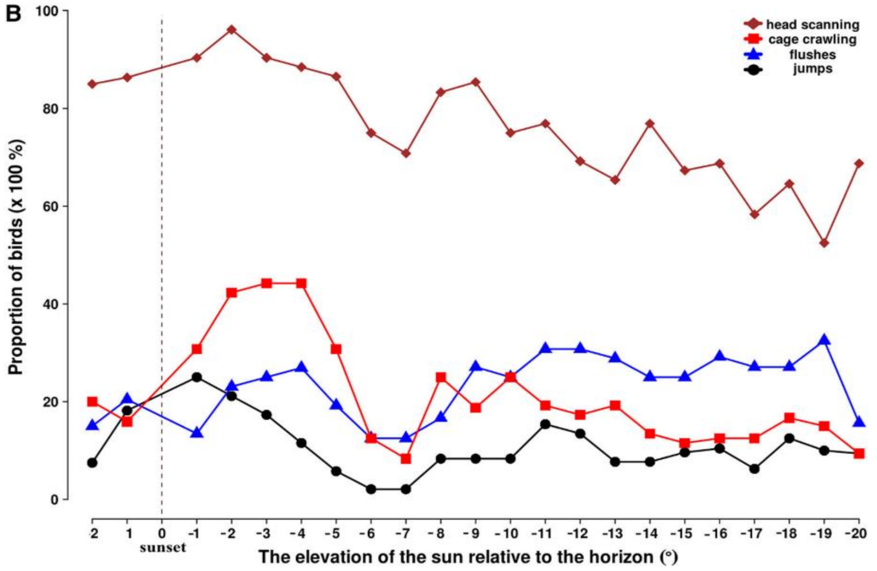

Figure 1: 'Migratory Readiness' Activity with respect to the sun's position relative to the horizon. [9]

a. Light-dependence and light-independence

From a physical viewpoint, if the avian 'compass' magnetoreceptor were to be located in the retina, then there must exist a biochemical species that is both reactive to directional orientation with respect to the local magnetic field lines, as well as, responsive to the light intensity level incident on the retina.

The radical pair process has been suggested as the driving mechanism behind the retinal magnetoreceptor[3], [10]. This process begins with Rhodopsin, a well understood photoreceptive protein which relies on a chromophore that undergoes a structural change when an incident photon is absorbed. A 2013 study examined the light-dependence of the flavin adenine dinucleotide reduction-oxidation cycle. The article aptly describes some crucial background knowledge for the experiment, taken directly: "The light-absorbing cofactor of cryptochrome is flavin adenine dinucleotide (FAD), which undergoes a redox cycle. In the dark, it exists in the oxidized, resting form FAD_{ox}; photoreduction by UV and blue light (up to 500nm) triggers the transfer of an electron from a nearby tryptophan (Trp), forming the radical pair FADH•/Trp•. The semiquinone FADH• can be directly re-oxidized in a reaction not requiring light. However, in the presence of light (UV to 570nm green) it can be further photo-reduced to its fully reduced form, $FADH^-$, which is then re-oxidized in a light-independent reaction to FAD_{ox}. During re-oxidation, a second radical pair is generated, involving FADH• and a yet unidentified radical, possibly O_2^-•" (figure 2). Thus, since the FAD reduction-oxidation cycle has a light-dependently formed (flavin photoreduction) and light-independently formed radical pairs (flavin re-oxidation), the experiment by Wiltschko et al. set out to determine which of these was the crucially magneto-sensitive radical pair [5].

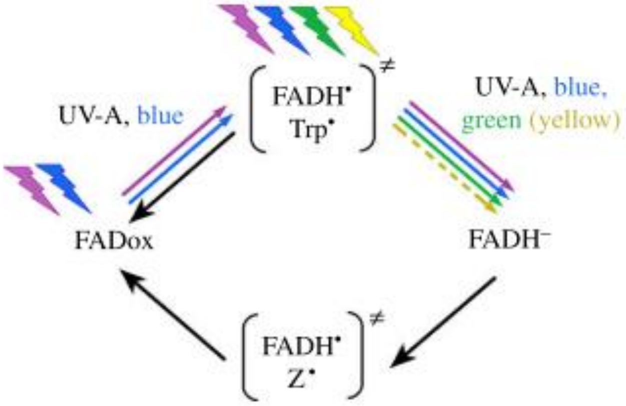

Figure 2: The Cryptochrome Redox Cycle – Radical pairs given in parentheses, coloured arrows show photo-reduction via respective wavelengths, black arrows show light-independent reactions. The 'Z' species is a radical generate during re-oxidation but not yet definitively identified.[5]

Using European robins during a period of induced, premature, spring migratory activity; the birds were tested individually using the standard funnel-shaped cages lined with thermo-paper to be imprinted on by the test birds' claws. This allowed the recording of the scratches left as they exhibited orientational migratory activity and tended to align themselves with the earth's magnetic field vector. Light emitting diodes of 502nm turquoise, a wavelength where the full redox cycle can occur, and 565nm green light, a wavelength believed to induce the second step of photo-reduction from the semiquinone to the fully reduced form only, was used and the light intensity level was carefully measured and controlled. The geomagnetic field was compensated, for some trials using Helmholtz coils. The critical tests featured the alternation of the artificially compensated geomagnetic field and lighting-system-power with a frequency of 1Hz. In order to isolate the retinal receptor mechanism, the upper beaks were anaesthetized. As seen in figure 5, the critical tests, where the light was powered on for 300ms and the geomagnetic field was compensated during the 700ms dark interval, showed no significant difference from the control. Hence, it was concluded that, though light is required to trigger the initial tryptophan reduction, the radical pair generated during the light-independent re-oxidation of fully reduced $FADH^-$ and the corresponding triplet/singlet ratio provides the basis for orientational bearing in birds [5].

a. Identifying and understanding the cryptochrome

The search for the specific biochemical species responsible for retinal magnetoreception played an important part in understanding the mechanics of this phenomenon. An *in vivo* study [11] preceding the experiment described above presents strong evidence in support of Cryptochrome CRY1A as the biochemical species to undergo light-induced oxidation (Figure 3). Cryptochrome 1A has previously been found in the outer segments of the of the violet cones of chicken retinae and in the UV cones of European robins, this small discrepancy in the location of CRY1A is notable since most of the research on avian magnetoreception understandably assumes little to no variation between migratory species. The experiment utilized immunofluorescent antiserum directed against the C-terminus of the CRY1A cryptochrome to label the crucially activated form in the excised eyes of chickens. The first portion of the experiment sought to validate previous research by examining adjustments in light wavelengths and exposure times as controls, generating a convincing picture when compared to the violet immunolabeled opsin (figure 4). Since magnetoreception is not the only purpose of the CRY1A cryptochrome, due its involvement in the regulation of circadian rhythm, the second portion sought to explore how the CRY1A may undergo confirmational changes at the C-terminus where and when the antiserum binds. The expanded experimental set included pre-treatments in daylights and darkness (30 minutes) as independent variables and light treatments in darkness, full spectrum sunlight, UV, blue, turquoise, green, yellow, and red as controlled variables. Leveraging the findings from these, researchers concluded that the Cry1a cryptochrome can still be postulated as the receptor molecule responsible for magnetic orientation; however, the FADH•/Trp• radical pair may not be the crucial magneto-sensitive species. This result undoubtably prompted the research described in part (a) that disassembled the redox cycle and identified the key magnetically responsive portion of the process [11]. To determine the exact magneto-sensitive confirmational nature of the Cry1a receptor molecule, further research is required. A study involving X-ray crystallography seems like the logical next step in understanding this versatile cryptochrome.

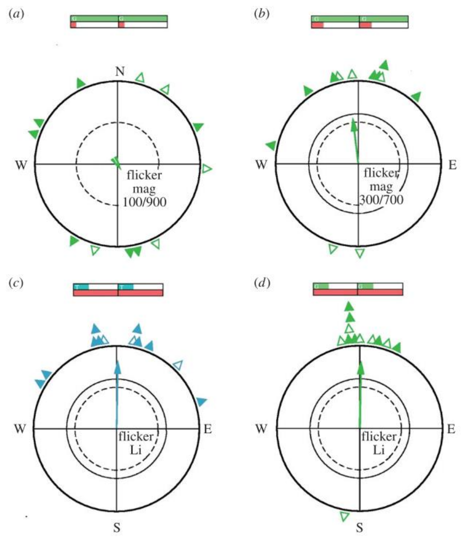

Figure 3: Testing the required duration of the presence of the geomagnetic field under continuous green light (above) – (a) The geomagnetic field present for 100ms and compensated for 900ms, (b) The geomagnetic field present 300ms and 700ms compensated. Testing the flickering light in a constant magnetic field (below) – (c) under flickering turquoise light, (d) under flickering green light. The filled triangles mark the unimodal mean headings of individual birds and the open triangles mark the preferred end of an axis of individual birds. The arrows represent the grand mean vector drawn proportional to the radius of the circle. [5]

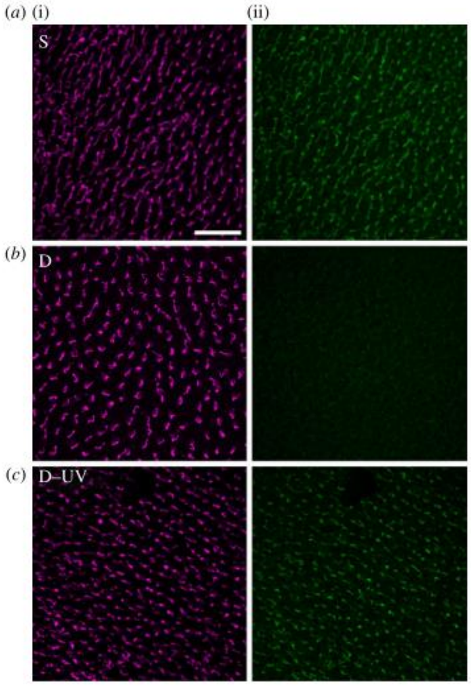

Figure 4: Immunofluorescence labelling of chicken retinae for violet opsin marking violet cones, control, (left side, i) and for green for CRY1A (right side, ii), responding. The images in each row show the same patch of retina – (a) pre-treatment in 30 minutes of sunlight, (b) pre-treatment in 30 minutes of darkness, (c) 30 minute pre-treatment in darkness and 5 minute treatment in 373nm light. The scale bar in (i, a) represents 50µm which applies to all panels.[11]

b. The Radical Pair Mechanism

Though the specific identity and properties of the bio-receptor molecule responsible for the magnetic field responsiveness has only recently began to uncover itself; the physical mechanism by which magnetoreception is made possible at the molecular scale has been commonly identified since the late 20th century and further outlined by ritz et al. in 2000 [10]. As depicted in (Figure 9); with the benefit of a simplified model owing to its chronological precedence with respect to the specific cryptochrome descriptions above, when the initial cryptochrome is oxidized (and further re-oxidized), the effects of a magnetic field on the electron-spin characteristics of the radical pair species control the ratio of singlet and triplet conversion which is believed to be visualised by the colour cones colour or light cones of avian retinae. The details of this latter process, by which the chemical difference of the singlet and triplet product yields are leveraged for sensory information is yet significantly unexplored. However, biochemist perspectives point toward an orderly array of photopigments oriented in various directions, but this is conditional on a spherical arrangement of receptors in the eyes. Thus, the radical pair process would generate characteristic patterns for activation which could, presumably, be recognized and transmitted into sensory information to be processed in the optic tectum [2], [10].

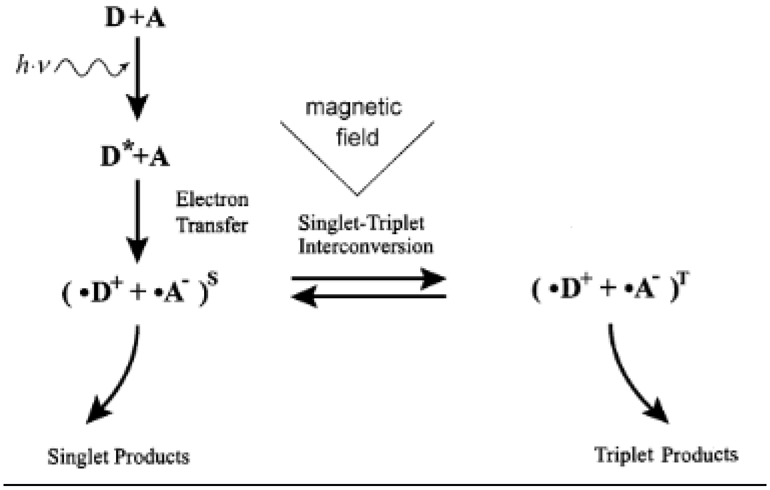

Figure 5: Simplified Schema of radical pair mechanism. The donor, D, represents the electron donor (a tryptophan); the singlet radical pair is shown in brackets on the left; at the centre is represented the singlet-triplet conversion which can only happen when correctly aligned with a sufficiently strong magnetic field; The triplet radical pair product, shown on the right, is the key product for magnetoreception.[10]

Given these biophysical explanations of avian chemical magnetoreception, an analogy can be drawn about the nature of the retinal magnetoreceptor with respect to light. The avian magnetoreceptor is 'powered' by full spectrum sunlight, in most cases, but 'functions' by way of the electron-spin characteristics of a light-independent reoxidation process. Hence, the suggestion that bird's calibrate their navigation using geomagnetic cues during twilight periods seems likely to have greater significance than stellar cues which are cues given by the directional orientation with respect to sunset and sunrise [9].

Magneto Reception Via the Iron-rich structures in the Avian Beak

Though it is not overly common, there are a few key examples of magnetic material in living organisms, that is, iron-based structures that are produced by biological means. An interesting example of this phenomena can be found in water-born bacteria, *Aquaspirilum magnetotacticum*, that exhibit magnetotactic motion whereby they orient and navigate along geomagnetic field lines. This is enabled by the presence of magnetosomes which are intracytoplasmic, membrane-bound particles of Magnetite, Fe_3O_4. These small parcels of magnetite are arranged in a single linear chain that is within the single-magnetic domain size range of 40-50nm, each has its own permanent magnetic moment. The small, single-domain magnetite links form a long enough chain, a magnetosome chain, to physically limit the bacteria's orientational freedom, and thus; the bacterial colony is perpetually oriented along the magnetic field lines (Figure 6) [12].

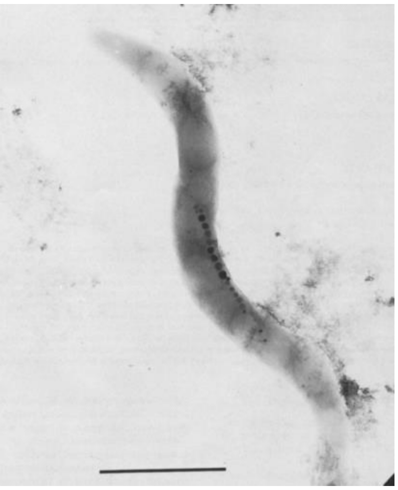

Figure 6: Electron micrograph of A. magnetacticum. Scale bar is 1.0µm [12]

a. Single-Domain vs. Paramagnetic crystals

It is possible, then, for birds to employ some manifestation of this single-domain magnetosome in the iron-rich structures that have been postulated to be in the upper beak of birds. The postulation stems from an early study that used a SQUID magnetometer to discover a small (1mm by 2mm) section of the upper beak that was permanently magnetic and had a mirror counterpart on the other half of a vertically severed pigeon head [13]. Notably, the same experiment also examined the subject tissue with light and electron microscopes and found the tissue contains nerve fibres and is richly supplied with clusters of electron-opaque structures of an appropriate length and length-to-width ratio that would support a single-domain magnetite-based hypothesis (approx. 0.08 to 0.15 µm and 4:1). Later, two experiments by Beason and Semm supported this postulation of magnetite single-domains forming a basis for a magnetoreceptor located in the bird beak. The first used small electrolyte-based sensor methodology to record variations in single cell electric potentials in various branches of the trigeminal nerves of bobolinks when subjected to an artificial manipulation of the external magnetic field. The experiment concluded that the magnetoreception system is complex and must involve more than one receptor as supported by a measurable response to magnetic manipulation in the absence of light [14]. The second, also involving bobolinks, was a behavioural experiment in which 14 birds were placed indoors, in a circular funnel, during the hours of migratory readiness, then treated and tested for a control, a magnetized, and a nerve-blocked condition. The mean modal direction (nearest 10°) was measured and revealed that a strong magnetic pulse can re-magnetize the mean direction, and that a lidocaine numbed ophthalmic nerve will abolish this effect [15]. The re-magnetization result supports the single-domain magnetite hypothesis since small magnetite particles with a stable magnetic moment, like the observed in magnetotactic bacteria, would result in the observed behavioural reorientation vector (mean) shifting as it did [16]. A sub-hypothesis, wherein even smaller superparamagnetic magnetite crystals are responsible for the magnetite based hypothesis, was discussed in a later experiment using migratory silvereyes [17]. The primary support for the superparamagnetic magnetite, which would be found in the upper skin of the beak as opposed to the inner nasal cavity nerves as for the single-domain counterpart sub-hypothesis, is that the re-magnetization by strong pulse is not permanent. A later experiment, similar to Beason and Semm (1996), used circular funnel cages lined with typewriter correction paper so that the test birds, Australian Silvereyes, would leave scratches in the coating on the paper, which was removed, subdivided into 24 sections, and scratches tallied for each section. The experiment employed Helmholtz coils to induce a stronger biasing field (approx. 20x earth's magnetic field intensity) to ensure a reliable reorientation behaviour as well as a 0.5T magnetic pulse meant to potentially re-magnetize the single-domains to point perpendicular to their previous alignment. The test group that was treated with the strong pulse in the presence of an artificial field and exhibited clear disorientation one day after treatment. This supports the both sub-hypotheses for the magnetite size, single-domain (chain) and paramagnetic crystals, however; the disorientation was only observed for a week after treatment before returning to their normal migratory direction. This does not support the single-domain hypotheses since a single-domain magnetite parcel, with a stable magnetic moment, should remain permanently as stable when forcefully reoriented by a strong magnetic pulse [8]. Thus, the second sub-hypothesis, involving superparamagnetic crystals leads further research.

b. The Iron Dendrite

Besides the confirmation of these superparamagnetic magnetite nanocrystals, the question of whether the location of magnetite based magnetoreception lie in the nasal cavity trigeminal nerves or the upper skin of beak had not been laid to rest. The previous experiment by Wiltchko, Munro, Ford and Wiltshko had used local anesthetic to numb subdermal nerves of the upper beaks of migratory silvereyes [17]. This was done by gently rubbing a cotton swab soaked with 2% Xylocaine solution on the along the mucous skin at the inner edges of the upper mandible. The intention was to numb only a superficial layer in the upper beak. However, because of the proximity to the nasal cavity region, an argument that other, interior, sections of the beak may have also been temporarily paralyzed does exist. A consecutive study was undertaken to shed light on this question by isolating and removing the dermal lining on the beak and staining it with Prussian Blue for histological and x-ray analysis. The Prussian Blue stain test was designed to highlight any magnetite material (iron [III] oxides) during the histological study. In preparation for the experiment, perfusion fixation was done to avoid a false positive resulting from other, non-magneto-sensitive structures iron in blood (ex. hemoglobin in erythrocytes). The results of the histological study show clear evidence of small, iron-rich bullets (diameter 1 μm), clustered around the dendrites identified.

Additionally, the experiment tested 4 different species of birds with varying migration capabilities which included homing pigeons to represent trained homers, chickens for extreme residents, European Robins for short distance migrants, and Garden Warblers for long distance migrants. The variation in species was done to assert the generally postulated hypothesis that the delicate iron-containing dendrites in the dermal lining of the upper beak was not specific to homing pigeons. The histological results supported this assertion as all four species exhibited the iron-rich dendrites (Figure 7).

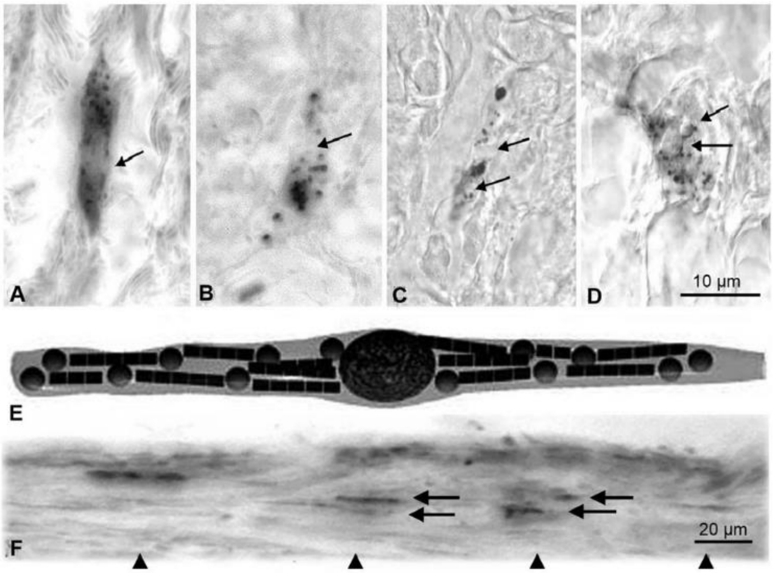

Figure 7: Prussian blue stained dendrites in the inner lining of the upper beak of various bird species. – A) Homing Pigeon, B) Garden Warbler, C) European Robin, D) Domestic Chicken. Arrows point to vesicles. E) General semi-schematic drawing of an iron containing dendrite. D) Axon bundle with several iron containing dendrites. Note: The dendrites are aligned in a distinct architecture: Parallel dendrites lie closely attached to each other as represented by the arrows. The dendritic groups keep a regular distance from each other.[6]

Notably, the homing pigeons seemed to have the most dense and defined cluster of iron parcels and the clusters observed for chickens were significantly less so. The significance of this observation is obvious since homing pigeons would presumably require a reliable magnetometer-function magnetoreceptor, in addition to the compass function of the retinal magnetoreceptor, to provide an adequate cognitive map complete enough to allow navigation to an arbitrary home location. Furthermore, x-ray analysis (micro-SXRF) of the adjacent unstained dendrites confirmed the iron parcel-like contents of the dendrites. As Well, a micro-XANES analysis of the iron-rich parcels revealed that the composition does not match the magnetite or maghemite control samples; consequently, it is suggested that the iron inside the biological material cannot be composed of magnetite exclusively [6].

Falkenberg’s (et al., 2010) experimental results supported the iron-based magnetometer hypothesis and gave the field a few new points to be used as footholds in further research: (I) The terminal region of the dendrites (length of 20-30 µm) contains 10-15 iron rich ‘bullets’ with a rough diameter of about 1µm, as well as, one clear cut vesicle in the middle, believed to be covered by an iron crust. (II) In any migratory, or previously migratory, species of bird, these ‘iron-dendrites’ are typically aligned along axon bundles from front to back (See Figure 7). (III) The pattern, that is the dendrite arrangement observed, was close together in parallel but uniformly separated longitudinally (see Figure 8). (IV) Future research must be especially prudent to discern between the iron-rich parcels in the dendrites and other locations where iron concentrations could be found like scattered or clotted erythrocytes that may remain after perfusion fixation, granular tissue that may accumulate iron, melanin which can be found in the stratum corneum of the cuticle surrounding the beak, or by accidental contamination which will can never be fully dismissed.

Figure 8: A Chain of dendrites identifies by Prussian Blue staining reconstructed from different focal planes. Arrowheads mark the dendrites.[6]

The presented research findings may elicit confidence in a somewhat simplistic outline of the avian magnetometer in the upper beak. Early experiments by Beason and Semm (1987 and 1996) proposed non-behavioural evidence that the trigeminal and ophthalmic nerves should serve as the electrophysiological pathway for magneto-sensory information in birds. Further experiments supported the sub-hypothesis that the magnetometer-like sense was localized to the dermal lining in the upper beaks of birds [17]. The re-magnetizable orientation of those same behavioural experiments pointed narrowly to a magnetite (or other iron [III] oxides) based receptor, which was supported by the PB staining histological experiments done by Falkenberg et al. The temporary nature of the observed behaviours after the reorientation of the magnetic materials in the avian beak suggest that the crucial magnetite in the beak are not paramagnetic single-domains as was previously suggested [8]. All of these factors point to an ‘iron dendrite’ that contains enough superparamagnetic material to experience a force in response to movement about the geomagnetic field, finely sensitive to intensity, that is transmitted and processed by the a bird’s neurological system. However, this outline is far from complete and does not describe many key factors (ex. iron containing dendrite’s mechanosensitive properties in magnetic field) that are necessary to understand this magnetoreceptor model. Furthermore, a 2012 immunohistochemical study by Treiber et al., explored the same area, particularly as outlined by [7], and concluded that the iron clusters in question were not magneto-sensitive iron-oxides but instead merely macrophages [18]. Therefore, the search for the avian magnetometer continues, and an exhaustive model is unlikely to arise for many decades.

Theories on a Navigational framework

Throughout this review, evidence has been provided to illustrate the extremely complex biophysical nature of the 2-factor navigational magnetoreceptor system. In order to enable concrete discussion about a possible framework for the navigational orientation using these systems, two assumptions must be made. This is due to the lack of universal agreement about the exact composition, functional process and conclusional evidence that would be needed to definitively describe the receptors in an exhaustive model.

a. Assumptions

i) The avian 'compass', which is the directional orientation with respect to the bird as the central vertical axis, is functionally derived from the chemical magnetoreception (radical pair) mechanism that occurs in the short-wavelength cones in the retina of both presently migratory and not-presently migratory birds. Though research suggests that the threshold frequencies ranges for correct confirmation and activation of the CRY1A cryptochrome can vary by species [11], the variation can be ignored since, in almost all cases, the bird will be migrating by day and, thus, navigating with access to full spectrum natural light. Aside from this discrepancy, birds can be assumed to update their directional 'compass' by turning their head through various angles and interpreting the altered optical view, which is transmitted from the retina through the ophthalmic nerve and processed in the optic tectum of the bird's brain [19].

ii) The avian 'magnetometer', which is the magnetoreceptor system that is capable of finely measuring the intensity of the relatively weak geomagnetic field for a particular 3-dimensional polar orientation (with the bird's brain as the central origin), is functionally derived from the iron-based mechanism in the dermal lining of the avian beak. For this assumption to hold, we must deny the suggestion that the iron-rich structures previously found in the dendrite nerves on the dermal lining of bird beaks are not functionally involved in magnetoreception, but instead are macrophages, and all of the evidence that supports this claim and contradicts the 'iron dendrite' hypothesis aforementioned [18].

b. Framework

The navigational framework for migratory navigation, excluding factors that do not employ the use of the geomagnetic field, is then a 2-factor system. The first is the 'compass' system that functions with respect to inclination of the magnetic field lines as opposed to polarity. It is presumed that, when scanning their environment, birds can sense (with reasonable certainty) the direction of geomagnetic field lines. By leveraging this vector, they can distinguish between 'poleward' and 'equatorward' (see figure 9). For long distance migrants, specifically in situations where cross equatorial travel is required, the ability to reorient with respect to the other pole is believed to be a learned skill since there are no significant magnetic cues that differentiate between the north and south poles. The second is the ‘magnetometer’ factor that functions by utilizing the intensity-sensitive magnetometer sense from the beak with experience. This means that a bird must remember the magnetic field strength from their home or hatch place, as well as other locations, and compare any location where it may thereafter find itself. Since magnetic field intensity increases as one travels poleward, when a bird finds itself in an area where the magnetic field intensity is higher than that of their home, they might infer that they are closer to the pole (see figure 10). It’s worth noting that the bird may only be able to detect the peak strength of the magnetic field when their beak is pointed toward the geomagnetic field lines which is a vector that can only be detected using the retinal magnetoreceptor [2]. Thus, through some combination of these two factors, various species of birds can geolocate with impressive precision. In extreme cases, such as with homing pigeons, this geolocation is precise enough to allow for point-to-home navigation, an ability to which humans require 20th century technology to do effectively in aviation.

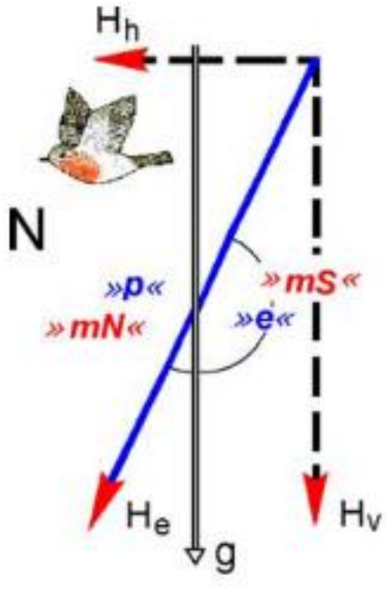

Figure 9: The Inclination Compass – Vertical section through the geomagnetic field (both). H_e – magnetic field vector, g – gravitational force vector, angle p – the crucial reference point for inclination compass functionality.[2]

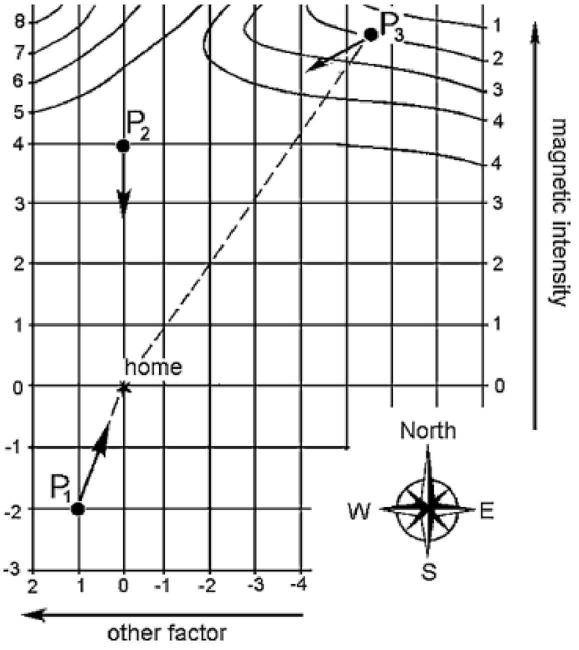

Figure 10: Schema of navigational 'map' with magnetic intensity given in relative units. Home marks the starting point for the exploratory journey a homing pigeon may take (dashed line), the P vectors mark the starting points for flight legs on a return journey.[2]

Conclusions

This review has sought to explain the complicated nature of the biophysical two factor reception system that enables migratory navigation in birds. Birds have had this capability for all of human history and, since the discovery of the seasonal migration patterns exhibited by birds, many have wondered how birds ‘instinctively’ know how to orient and navigate to warmer climates in winter months and plentiful areas for breeding in the spring and summer months. The research and discussions presented above provide a general picture the research to this point. The long-standing nature of this question means that this picture is constructed from key points scattered across decades. As well, the conclusions derived from behavioural, histological, or otherwise experiments do not always concur. Indeed, this area of study, that is both receptor mechanisms as described above, are far from being uniformly accepted. Both receptor systems are often fundamentally called into question by comparable research, making the field particularly dynamic.

The retinal magnetoreceptor is a particularly resilient hypothesis, the focus on this area has shifted from understanding the two halves of the flavin redox cycle and radical pair mechanisms to understanding the CRY1A cryptochrome from a biophysics perspective. Since the CRY1A cryptochrome is does not serve only one purpose, understanding the complex confirmations required to serve the magnetoreception mechanism is a crucial next step in understanding the receptor. Modern biochemical analysis methodology should serve as an appropriate progression for researchers but given the lack of concrete monetary motivators for an exhaustive model, the field will likely progress sluggishly.

The iron-based hypothesis is one that has come under special scrutiny. There exists reasonable evidence to suggest that the iron rich structures in the dermal lining of the beak are not paramagnetic crystals, but instead simply macrophages. However, this conclusion does not provide a counterhypothesis to explain the bird’s responses to a magnetic field in the absence of light, or the strong magnetic pulse experiments that cause temporary re-orientation of the magnetic mean vector in Emlen funnel experiments.

As well, a third hypothesis has recently emerged but lacks enough supporting evidence to be included in this review (for preliminary research, see [20]).

Thus, magnetoreception and its role in migratory navigation is a question that remains mostly unresolved. Since birds exhibit the most robust and extensive application of magnetoreception, it will continue to the be the primary area for researchers. In the years to come, we can expect future experiments that make use of modern experiment methodologies to provide a better understanding of the radical pair mechanism and the corresponding cryptochrome, as well as, proving or disproving the iron-based hypothesis conclusively.

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