



Physics of animal navigation

Miguel A. F. Sanjuan^a

Nonlinear Dynamics, Chaos and Complex Systems Group, Departamento de Física, Universidad Rey Juan Carlos, Tulipán s/n, Móstoles, 28933 Madrid, Spain

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Abstract Animal navigation is a fascinating research field where scientists have been attempting to answer some key and basic questions explaining the mechanisms behind it. Interestingly, most of the scientific explanations for the orientation and navigation of numerous animals derive from ideas in physics. Accordingly, the main purpose of this Special Issue is to provide a general overview of this field and show, mostly to the physics community, the enormous interest of this interdisciplinary field and all its possible connections to diverse physics disciplines. It would be delightful if this could stimulate future research collaborations among physicists in this interdisciplinary research area.

1 Introduction

At some point in our lives, we have all been fascinated by how migratory animals can find their way back after having traveled a great distance from a starting place. For many years, scientists tried to answer such relevant questions by explaining the key reasons behind animal navigation. It goes without saying that the field of animal navigation is a large and complicated area of research, involving many disciplines in principle. Unsurprisingly, ideas from physics strongly contribute to scientific explanations for how various animals find their orientation and navigate. The mechanisms are of a very diverse nature. On the one hand, we have magnetoreception in animals, especially birds, and the effects derived from the Earth's magnetic field. Nevertheless, there are other mechanisms that include infrasound, ultrasound, as well as echolocation, as in the case of bats. Likewise, light and visual systems are extremely important for insect vision and bird navigation. Another topic of special importance is celestial navigation, by which certain birds and insects find their orientation using a solar compass by detecting the pattern of polarized light in the sky. In recent years, it has been found that other mechanisms derived from quantum physics such as the hypothesis of quantum entanglement in the cryptochrome may have some relevance for navigation, especially for birds. Also, in the field of fluid mechanics, it seems that turbulent flows in the atmosphere and oceans also play a relevant role. We can even find thermal effects within

the scope of thermodynamics, where thermal boundaries have been found, as well as energetic and efficient movements or infrared radiation that affect animal navigation. Finally, hypotheses have also been raised about possible effects due to gravitational variations. In short, we can find that different disciplines of physics play a relevant role in animal navigation, such as electromagnetism (including geomagnetism and magnetoreception), acoustics (ultrasound, echolocation, and infrasound), optics (light and visual systems), astronomy (celestial navigation), quantum physics (quantum entanglement and the cryptochrome hypothesis), fluid mechanics (turbulent flows and turbulent atmosphere), thermodynamics (thermal limits), and gravity (gravitational variation).

In his recent, stunning book *Incredible Journeys* [1], David Barrie leads us on an exciting adventure into the advances in the science behind animal navigation, whereby in a collective effort and on different fronts, inspirations, and ideas, scientists are trying to unravel how animals as diverse as butterflies, birds, insects, crustaceans, fish, reptiles, and even people find their way. Although most of the mechanisms of animal navigation are founded in principles and ideas from physics, I believe all this remains rather unknown to the physics community. After having decided on the subject, I was very excited to learn the recent news about the discovery of a long-lost letter from Albert Einstein addressed to Prof. Karl von Frisch, 1973 (Nobel Prize in Physiology or Medicine) on this subject that was published by a group of Australian researchers [2]. In this unknown letter, Einstein discusses the possibility of finding a

^a e-mail: miguel.sanjuan@urjc.es (corresponding author)

link between physics and biology, writing “It is thinkable that the investigation of the behaviour of migratory birds and carrier pigeons may someday lead to the understanding of some physical process which is not yet known.”

It would be good to reflect on the fact that, especially in recent years, there has been a lot of talk about the value of interdisciplinary research in science, yet few researchers have pursued this ideal. Considering the current importance of cross- or interdisciplinary research using physics principles, this constitutes one of the main motivations for this Special Issue, to contribute to the knowledge of this interdisciplinary field among physicists. Consequently, the main aim of this Special Issue on Physics of Animal Navigation is an attempt to explore this fascinating interdisciplinary field of research by bringing together scientists from different disciplines and providing a general overview of the state of the art of the role that physics plays in animal navigation.

2 Animal navigation and physics

The connections among the different aspects of animal navigation and physics are certainly not new. One relevant point is to determine how animals orient themselves using the Earth’s magnetic field. A discussion of the physics behind such magnetoreception in animals was presented by Sönke Johnsen and Kenneth J. Lohmann [3] in a paper published in *Physics Today* a few years ago, and in the review paper “The physics and neurobiology of magnetoreception” [4]. In these articles, the fact that various animals can detect the Earth’s magnetic field is described and discussed. They proposed three main mechanisms supporting the evidence for such use of the geomagnetic field: electromagnetic induction, ferrimagnetism, and chemical reactions involving pairs of radicals. However, they also indicate that there are still many open problems in relation to how all this occurs. In particular, they mention the case of electrosensitive marine fish in which, although they can sense the Earth’s field through electromagnetic induction, there is still no direct evidence about the true nature of their magnetoreception. Despite recent advances in this field, and regarding the other two mechanisms, magnetoreceptors have not been identified with certainty in any animal, and many important issues remain unknown.

In a very appealing review article [5] published in *Nature*, Henrik Mouritsen considers “Long-distance navigation and magnetoreception in migratory animals.” In this article, he discusses in an elementary way the mechanisms used by animals for orientation and navigation, with a particular focus on long-distance migrants and magnetoreception. Just as the title of the article indicates, it focuses on long-distance navigation and defends the existence of three phases in this process, as well as the need for an integration of multiscale

and multisensory signals in the brain to enable long-distance navigation. He argues that the relevant mechanisms for long-distance navigation must be different from those that might be useful on short scales, be it in time or space. The three phases are: (1) a long-distance phase, (2) a narrowing-in or homing phase, and (3) a pinpointing-the-goal phase, which he considers essential to achieve a holistic understanding of animal navigation. Like other authors referred to above, he points out that, despite substantial advances in our understanding of long-distance animal navigation and magnetoreception during the past two decades, many unanswered questions still remain. He concludes by raising a series of important mechanistic questions related to long-distance animal navigation that should be resolved in the next future. In short, all this points to interesting future collaborative efforts that could be included in interdisciplinary research projects.

In his recent article “Unravelling the enigma of bird magnetoreception” [6], published in the News & Views section of *Nature*, Eric J. Warrant comments on new significant research carried out by Xu et al. also published in *Nature* [7]. The discussion focuses on the mystery of magnetoreception, that is, how animals perceive the Earth’s magnetic field and how they use it to determine their spatial orientation and ultimately navigate. As mentioned above, and despite the many scientific advances around this interesting problem, many problems remain open, among which it is worth mentioning where the magnetoreceptors are located. In migratory birds, the prime candidates are cryptochromes, which are magnetically sensitive proteins found in the retina. Still, it is not clear that these proteins actually possess the magnetic sensitivity and physical properties needed to detect Earth’s extremely weak magnetic field. Notwithstanding, the leading candidate for enabling cryptochrome-based magnetoreception in vertebrates is the CRY4 protein found only in birds, fish, and amphibians, which are types of animals with well-documented magnetically guided behaviors. Precisely, the work of Xu and his colleagues shows that a version of cryptochrome CRY4 (nicknamed ErCRY4) in the migrating European robin has a crucial property needed to detect the Earth’s magnetic field, specifically the ability to form radical pairs with high magnetic sensitivity. In fact, some scientists believe that CRY4 acts like a tiny compass needle. In addition, and surprisingly, they suggest that quantum physics would explain its operation, which is why the idea of a quantum “compass” has come to be talked about.

So far, we have mentioned several studies on the applications of certain areas of physics in relation to animal navigation. Nevertheless, and as it pointed out earlier, other disciplines are also involved. Acoustics is one of these, as discussed in the article “The physics of bat echolocation: signal processing techniques” [8] by Mark Denny published in the *American Journal of Physics*. This is a good new example where principles of physics are applied to develop the signal processing techniques underlying bat echolocation, as well as discussing calculation and simulation methods.

Fluid mechanics is another field that has something to say in this context, and in the paper “Turbulence explains the accelerations of an eagle in natural flight” [9], Laurent and his coworkers analyze the role of turbulence in the motion of an eagle. They conclude that their research reinforces the need for greater knowledge on turbulence to understand eagle movements and behaviors, with possible implications for other flying and swimming creatures.

In the interesting article “From dung beetles to seals, these animals navigate the stars” [10], Fiona McMullan describes various aspects of the effects of celestial mechanics and astronomical cues, where besides various examples of animal navigation by starlight, the case of dung beetles in South Africa that keep their treasure rolling in a straight line at night by orienteering with the Milky Way is mentioned.

Finally, in “The emergent physics of animal locomotion” [11] published in *Physics Today*, Simon Sonberg explains the physiological systems that are involved in enabling movement in animals and other organisms. Albeit not strictly related to animal navigation, the author tries to illustrate the physics related with the science of movement, neuromechanics, and exploring the ways animals move and interact with the environment.

In a word, the role that physics plays in understanding animal navigation, movement, or locomotion shows that there is a lot of room for interdisciplinary research on numerous open research problems that are far from being understood.

3 New developments contained in this Special Issue

After a broad overview of this captivating field of endeavor, this Special Issue offers an opportunity to publish a few articles on the topic to present new ideas and results, broad reviews, as well as a discussion on what we already know, as well as an example related to the physics of locomotion.

In the review paper “Animal navigation: how animals use environmental factors to find their way” [12], Roswitha Wiltschko and Wolfgang Wiltschko provide an excellent review on the different environmental factors affecting animal navigation. The review focuses mainly on the different ways that animals use the geomagnetic field of the Earth, as well as various astronomical cues to obtain compass information. In particular, they describe the magnetic compass, the solar compass, and the stars compass, using which these animals build maps with which to navigate in different circumstances. The authors describe in detail numerous experiments, especially with birds, but also refer to many other animals, providing a rich overview of the field. Besides magnetic and celestial factors, they briefly mention other factors such as gravity, infrasound, and odor. In any case, they clearly emphasize that the nature of the factors used to understand true navigation still

constitutes a largely open question. The navigation of migratory birds reveals the potential use of multiple sensory cues such as the stars, Sun, geomagnetic field, and polarized light for orientation.

In the article “Who’s calling: proof of concept for using laser doppler vibrometry to identify callers within african elephant vocalization episodes” [13], Caitlin E. O’Connell-Rodwell and colleagues propose a novel use of laser Doppler vibrometry (LDV) for elephant field bioacoustics and behavioral ecology, allowing the determination of which animal initiates and responds within a vocalization bout. The use of LDV in elephant communication studies would provide opportunities to ask more questions about elephant vocal and seismic communication, individual caller identity, and leadership structure, both in captivity and in the wild. Lastly, this method could be employed in other vocal communication studies of social animals where it may be difficult to discern the caller. Because some marine mammals have been found to vocalize at the surface in social contexts, this method could be a valuable tool to noninvasively record these surface vocalizations and provide more information about the social lives of these animals. While this tool has potential for the indicated application, further studies are needed to demonstrate its full value in a field context with large groups of elephants in the wild. Finally, LDV technology could inform studies focused on the physics of signal propagation of coordinated signals within group-living animals.

In “Compass in the ear: can animals sense magnetic fields with hair cells?” [14], Kirill Kavokin discusses the possibility of performing magnetoreception in vertebrates with chains of magnetite nanocrystals, also called magnetosomes, attached to the hair cells of the inner ear. To this end, he applies statistical mechanics to analyze the fluctuations of stereocilia bundles. Correlation functions of the fluctuations of the bundle position and of the number of open mechanoreceptor channels are derived. The sensitivity threshold of the hair cell to the applied forces is calculated. Its comparison with the torque exerted by the magnetosome in the geomagnetic field suggests that a compass magnetoreceptor can be realized with about 100 specifically adapted hair cells. By contrast, no viable magnetic map receptor is possible within this system. Despite much work on magnetic effects, the physiology of magnetoreception remains largely a mystery. Theoretically, three classes of possible magnetoreceptors have been proposed: those based on biogenic magnetite or other ferromagnetic or ferrimagnetic substances; photochemical, based on electron spin coherence in radical pair reactions in the eye; and those that use electromagnetic induction in conductive loops formed by semicircular canals in the inner ear. The author develops a consistent theory of the static response and fluctuations in the mechanoreceptor cells of the inner ear, based on the statistical mechanics of their hair bundles. In particular, the theory makes it possible to calculate the sensitivity threshold of a hair cell to the force applied to its bundle of stereocilia, in the regime when the position of the bundle is not fixed. Through theoretical reasoning, the possibility of

magnetoreception with hair cells with attached magnetosomes is evaluated. As a result, it is found that a magnetoreceptor for compass orientation by the geomagnetic field can, in principle, be realized in this way, with certain adaptations of the hair cells involved. On the other hand, the requirements for the magnetoreceptor that would provide geopositioning by measuring the intensity of the local magnetic field are far too stringent to be realized using hair cells and magnetosomes.

In the article “Over 50 years of behavioral evidence for magnetic sense in animals—What has been learned?” [15], William T. Schneider, Richard A. Holland, and Oliver Lindecke discuss magnetoreception as a key element in the sensory repertoire of many organisms. This is precisely, as previously noted, one of the most well-studied mechanisms, and one that plays a relevant role in animal navigation. Although the first data to demonstrate a magnetic compass in songbirds through behavioral measures were presented decades ago, behavioral studies remain the main source of information for learning about magnetic senses. However, the behavioral evidence is scattered, with sometimes conflicting results. In part, this is a consequence of the wide spectrum of methods used by multiple research groups when studying different model organisms. This has limited researchers’ ability to pin down exactly how and why animals use signals from the Earth’s magnetic field. The authors discuss how a variety of methods can be used to test such behavior, ranging from field observations to laboratory manipulations to test for a magnetic sense in animals. Therefore, they discuss the main limitations of behavioral evidence that tells us how animals perceive the magnetic field and argue that behavior must go hand in hand with other fields to advance our understanding of magnetic sense. In addition, the article raises key questions about magnetoreception, critically discussing some common assumptions about magnetoreception, citing relevant experiments, as well as including a very rich list of references.

In the article “Gravitation and bird navigation” [16], Valerii Kanevskiy discusses the gravity vector hypothesis to explain how long-distance bird navigation homing could be related to a new direction in navigation technology, i.e., gravitational navigation, which uses the Earth’s gravitational field as the most stable geophysical factor. The gravity vector hypothesis states that birds have an innate mechanism to remember the gravity vector at their home location and perceive the gravity vector along their flight path. According to the physical model of this hypothesis, to return home from an unknown location, the bird tends to reduce the mismatch between the gravity vector at their home and at the point of the flight path. The biological interpretation of this hypothesis uses biomolecules with gyroscopic properties to memorize the direction of the gravity vector at the origin location and the vestibular apparatus to fix the direction of the gravity vector at the points along the flight path. This hypothesis explains the influence of Earth’s gravity anomalies and the Moon’s gravitational field on the orientation behavior of birds. The unique properties of the pigeon

gravimeter are shown. The gravity vector hypothesis is of interest to fundamental physics: the gravitational and magnetic navigation hypotheses can be brought together using a unified field theory that declares the unity of the nature of the gravitational and magnetic fields. Among the conclusions of this hypothesis, one could establish that the constancy of the spatiotemporal characteristics of the terrestrial gravitational field over millions of years could be the main criterion used by natural biological evolution when choosing gravity for bionavigation. On the other hand, it establishes that distant migratory birds make long-distance flights at high altitudes, possibly to reduce the influence of strong gravitational anomalies. The amazing sensitivity of the pigeon gravimeter and its ability to detect small changes in gravity in the context of significant inertial forces may be of interest to applied physics to create nanoscale biophysical gravity sensors. Finally, the specific reaction of birds to gravitational, magnetic, and electromagnetic fields may be of interest to fundamental physics to study the origin of these fields.

Finally, in “Actuating mechanical arms coupled to an array of FitzHugh–Nagumo neuron circuits” [17], Isidore Komofor Ngongiah and coworkers aim to mimic the motion of myriapods by using an array of mechanical arms coupled to an array of FitzHugh–Nagumo (FN) neuron circuits. The mathematical analysis of the model equations state that, for different ranges of parameters, the system may have three distinct states: nonexcitable, excitable, and oscillatory. The action potential for the different situations has consequences for the motions of the legs. This brings them to analyze the motion of myriapods without rotation, and that the velocities of the propagation of nerve impulses and that of the displacement of legs are quantitatively the same. This constitutes an example of the physics of locomotion linked to a neuromechanical model.

4 Conclusions and future perspectives

This Special Issue aims to offer a broad perspective on the physics of animal navigation, providing new contributions on this subject, as well as interesting review articles that contribute to spreading knowledge on this research area. The main content of this Special Issue on the physics of animal navigation includes topics related to the effects of the Earth’s magnetic field and magnetoreception, gravitational effects, examples of the physics of locomotion, as well as an interesting discussion on advances in magnetoreception. As mentioned above on several occasions, fortunately this is a field where many interesting questions remain to be explored. Therefore, one of the main objectives of this Special Issue is to stimulate and inspire new research to be carried out in this interdisciplinary field of research where physics has much to contribute.

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