

Sensitivity and evolution of sea-turtle magnetoreception: observations, modelling and constraints from geomagnetic secular variation

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ABSTRACT

In a series of papers, Lohmann and Lohmann (1991, 1994a, 1994b, 1996) provide evidence for remarkable sensitivity of sea-turtles to the earth's magnetic field and suggest that it is used by these animals to determine global position and to navigate. In this paper, we emphasize that a consequence of these observations taken together is that sea-turtles should be able to accurately detect the full (vector) magnetic-field, and perhaps spatial gradients. In order to interpret these observations, we propose a simple model in which the turtle is considered as a small permanent magnet, on which the geomagnetic field exerts a torque. This torque varies as a function of turtle azimuth and field parameters which depend mainly on latitude. Although this simple model accounts for some of the observational evidence,

discrepancies might be due to a number of other factors, such as speed of magnetic field changes during experiments or lack of field homogeneity. Also, the earth's field has varied significantly over the last few centuries and some of the magnetic features observed today and suggested by the Lohmanns for use in sea-turtle navigation were very different or even not present two or three centuries ago. This would place constraints on the rate at which genetically inherited magnetic behavioural preferences can change with time. Alternately, it may imply that the experimental results need to be re-evaluated and complemented.

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Summary of experimental evidence

Lohmann's (1991) first paper describes the experimental procedure. Migratory hatchling sea turtles were removed from their nests in a sand beach hatchery in Florida at the time of birth and transported to a nearby laboratory, in which they were tested for swimming orientation when placed in a controlled magnetic field. Upon release in the water-filled container, all lights in the room were turned off except for a dim light suspended above water level on the east side of the device. This attempted to reproduce the dim glow of light along the seaward horizon encountered by hatchlings on their native beach, and was shown to play a role in calibrating the turtles magnetic compass (Lohmann and Lohmann, 1994a). In the first series of experiments (Lohmann, 1991) turtles were found to swim in a rather consistent direction, 42° to the east of magnetic north, after all lights had been turned off. When the horizontal magnetic field was reversed, they still swam 16° to the east of what they apparently felt to be magnetic north (Table 1). In a further series of experiments using better field control, Lohmann and Lohmann (1994a) showed that lack of training with light

led to random orientation. Weindler *et al.* (1996) have shown that, for some young bird migrants, two separate clues might also be jointly required to establish the distinctive population-specific migratory direction. These experiments suggest that the angular difference between reference light and horizontal magnetic direction is inherited. In the second paper (Lohmann and Lohmann, 1994a), a new experi-

ment with light to the west and field to the north was performed (Table 1). Unfortunately there was no experiment reported with light to the west and field to the south. Taken together, these observations would therefore argue that turtles can detect the direction of the earth's horizontal field with a standard deviation on the order of 25°, and are programmed to swim, based on this alone, in a NE direction.

Table 1 Some of the main results from the Lohmanns experiments used in this paper. Columns are: (i) Experiment (reference): gives the relevant paper—L stands for Lohmann and the publication date is given next; (ii) I (°): field inclination (in degrees); (iii) F (μT): field intensity (in microTesla) – horizontal field in first two papers, total field in last two; (iv) ϵ_δ (°): uncertainty in measurement of turtle azimuth (in degrees); (v) ϵ_F (μT): field gradient across experimental area (in μT); (vi) Δt (s): sampling interval of turtle swimming orientation (in seconds); (vii) δ (°): angle between turtle swimming direction and magnetic north (in degrees) – when light in W recalculated to be comparable to other cases; (viii) light: indicates from which direction dim light shines at onset of experiment; (ix) field: direction of field imposed by coils; (x) coils: system of coils used for field control

Experiment	I (°)	F (μT)	ϵ_δ (°)	ϵ_F (μT)	Δt (s)	δ (°)	light	field	coils
L1991	57	23–26	15	3	60	42	E	N	Rubens
id.	57	23–26	15	3	60	16	E	S	id.
LL1994a	57	23–26	2	3	30	70	E	N	Rubens
id.	57	23–26	2	3	30	65	E	S	id.
id.	57	23–26	2	3	30	51	W	N	id.
LL1994b	57	44–45	1.4	1	10	90	E	N	Merritt
id.	60	44–45	1.4	1	10	200	E	N	id.
LL1996	57	52	1.4	1	10	69	E	N	Merritt
id.	57	43	1.4	1	10	280	E	N	id.

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Lohmann and Lohmann (1994b) describe a third set of experiments in a constant total field of 44–45 μT . A new set of coils ensures that the vertical component of the field can be monitored. Two different sequences were conducted: one in which three successive field inclinations I of 15°, 57° and 75° were selected, another with I -values of 30°, 45° and 60°. There was apparently no orientated swimming response for 15 and 75°, little for 45°, but a significant response to the three other values. The most astonishing result is that the orientation for $I = 60^\circ$ is completely different from that for 57° (Table 1). A 3° change in inclination leads to a 110° change in swimming direction! It is unfortunate that these observations were not in the same set of experiments, and were not repeated. Being able to distinguish between 57° and 60° inclination and responding with completely different swimming orientation would allow turtles to head offshore north of the Florida coast and then, after crossing the Atlantic along the gyre, to head southward and avoid the deadly cold northern arm of the gyre. The Lohmanns also suggest that turtles use this sense to travel along isoclinic lines. Sensitivity of inclination is about 1° for 100 km displacement in latitude. Field heterogeneity due to coil geometry in the first experiments corresponded to inclination differences across the container of about 3°. So the various experiments may have a significant amount of cross-correlated response which should be elucidated further.

In their more recent work, Lohmann and Lohmann (1996) provide evidence that turtles are also sensitive to total field intensity. All other parameters being held constant, turtles swam with a mean angle of 69° in a field intensity of 52 μT but turned to 280° for a field intensity of only 43 μT (Table 1). The Lohmanns note that 'all or most locations have unique combinations of magnetic field intensity and field line inclination' and conclude that 'sea turtles possess the minimal sensory abilities necessary to approximate global position using a bicoordinate magnetic map'. Taken altogether, the successive experiments by the Lohmanns would demonstrate that turtles could in certain ranges of values be used to determine the total field vector (except for absolute polarity; only magnetic bacteria, salmon fry, bees and mole rats

apparently respond to absolute polarity of the field; other species with magnetoreception find the extreme value of the dip angle of the field and infer the magnetic North directional reference from this — Wiltshcko and Wiltshcko, 1995a). Sensitivities indicated by the experiments (Table 1) would be as low as 25° for D (standard deviation on the azimuth from six different sets of experiments, though not exactly with constant I and F), yet as high as 3° for I (from the experiments at $I = 57$ and 60°, which require confirmation) and a few μT on F .

A simple model of magnetoreception sensitivity

A model of magnetoreception linked to biomineralization (Kirshvink *et al.*, 1985; Lowenstam and Weiner, 1989) is necessary to provide a basis on which to interpret the experiments. In turn, such a model will be constrained by the experiments themselves. Because all major groups of the Chordates display magnetoreception, the receptors probably predate the evolutionary radiation of this phylum. Hence, the ultrastructure of magnetoreceptors isolated for instance in fish (Mann *et al.*, 1988; Walker *et al.*, 1997) should be similar in other groups. Single domain chains of magnetite enclosed within membrane-bound magnetosomes reside inside cells which are themselves connected to the ophthalmic branch of the trigeminal nerve (Semm and Beason, 1990). As is the case for magnetotactic bacteria, the crystal direction is found to be parallel to the magnetosome chain axis, increasing the net magnetic moment of the receptor (Mann *et al.*, 1988). The ferrimagnetic nature of the transducer was confirmed by Kirshvink and Kobayashi-Kirshvink (1991) in a series of experiments in which they reversed the compass of honey bees by subjecting them to a short magnetic pulse. Pulse-remagnetization experiments on birds have demonstrated subsequently that ferromagnetic materials are also involved in vertebrate magnetoreception (Wiltshcko *et al.*, 1994; Beason *et al.*, 1995; Wiltshcko and Wiltshcko, 1995b).

It can therefore be argued that turtles also possess magnetite-based magnetoreceptors which would be subjected to a magnetic torque in the geomagnetic field. For single-domain magne-

tites, this interaction is energetic enough to control directly the gating response of mechanically activated trans-membrane ion channels (Kirshvink, 1992), yielding depolarization of nerve membranes. For the purpose of this model, we can assume the simple case of a common response function for all such organelles, so that the whole animal can be considered as a small permanent magnet (with a position more or less fixed relative to the axis of their body). Turtles hence would detect a signal that they might wish to reduce or memorize and use as a guide. Let (m_t , D_t , I_t) be the magnetic moment and directional parameters of the turtle at some location and instant, and (F , D , I) be the spherical coordinates of the geomagnetic field at the same location and instant. Depending on how it swims, and how it feels and uses gravity at sea, the turtle might sense either the total torque Γ or only its horizontal or vertical components (Γ_H and Γ_V). Without much loss in generality, we assume that the turtle's magnet remains horizontal ($I_t = 0$; except when the turtle dives of course) and neglect magnetic declination ($D = 0$). D_t is simply the azimuth in which the turtle is heading. Then:

$$\Gamma = (\mu_0/4\pi) \cdot m_t F \cdot (1 - \cos^2(I) \cdot \cos^2(D_t))^{1/2}, \quad (1)$$

$$\begin{aligned} \text{abs}(\Gamma_V) \\ = (\mu_0/4\pi) \cdot m_t F \cdot \text{abs}(\cos(I) \cdot \sin(D_t)). \end{aligned} \quad (2)$$

The intensities of these torques are plotted in Fig. 1 as a function of inclination I and azimuth D_t . Note that the turtle cannot sustain equally fast changes in all parameters that control torque intensity. The turtle can quickly alter its course (D_t) but not I (unless it dives) and certainly not F . Both I and F are dominated by the geocentric axial dipole and will change on scales of a few percent per one hundred kilometres in latitude. At a given latitude (i.e. roughly inclination), the torque is of course minimized when the turtle swims to the north ($D_t = 0$; and more generally 'magnetic north' $D_t = D$): this is sensitive (with a pronounced minimum) near the equator and becomes much less so as one moves to higher latitudes.

This simple model can be used to interpret the experiments. Given proper prior information (such as light clues at birth), the turtles can function as

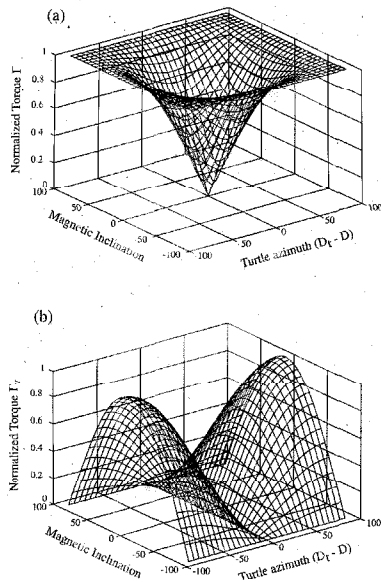


Fig. 1 Normalized intensity of the torque exerted by the geomagnetic field on a turtle (considered as a permanent magnet) as a function of turtle (magnet) azimuth D_t with respect to North and field inclination I (which depends principally on latitude). (a) total torque Γ , and (b) modulus of vertical component Γ_V of torque, both being normalized by $(\mu_0/4\pi) \cdot m_t F$ (see eqns (1) and (2) and text).

magnetic compasses. They can rapidly alter their azimuth and sense the torque when changing direction, then minimize the torque or compare it to a prerecorded threshold or level. It is more difficult to understand why they respond (as they seem to) to minute inclination changes. As latitude increases, Γ_V decreases and Γ_H increases (but is insensitive to azimuth). If there is a sharp sensitivity threshold in Γ_H , this could act as an additional latitude indicator which the turtle could respond to. The role of field intensity is only to enhance both response and sensitivity. Hence, F -related sensitivity should be better at higher latitudes and again there may be a threshold effect. But the drastic changes observed by Lohmann and Lohmann (1996) remain hard to understand (a 150° turn for a change of only 20% in field amplitude). This type of response may be related to apparent sensitivity of migrating animals to spatial gradients in the geomagnetic field, as has been suggested for homing pigeons (Gould, 1980) and migrating fin whales (Walker *et al.*, 1992).

Sensitivity to speed of magnetic changes

Mixed signals or experimental artefacts may have elicited atypical behaviour. In nature, turtles could not alter rapidly the intensity of the field, which requires swimming hundreds of kilometres. Yet, in the experiments, they are subjected to such changes very rapidly (on the order of seconds, though they are given 3mn for acclimation). We could surmise that the occurrence of fast field (hence torque) changes not encountered in nature would be felt as undesirable by the turtles, which could simply react by reversing their swimming direction. This might explain some of the experimental results, in which a 180° or so turn appears to be a common response. Also, particularly in the early sets of coils they use, field homogeneity in the experiments does not attain that found in the real environment. Swimming through spatial field gradients may have affected the turtle response. Rather simple additional experiments might allow these suggestions to be tested.

The effect of secular variation

The Lohmanns' experiments suggest that turtles possess the minimal sensory abilities necessary to approximate global position using a bicoordinate (F , I) magnetic map. Yet, the magnetic field changes with time. Observatory and ship-measurements have been compiled and integrated by Bloxham and Jackson (1992), who have produced field models spanning the last three centuries. Figure 2 shows the secular variation of iso-lines of I and F over the Atlantic Ocean from 1700 to 1990. We can follow the evolution of some of the key features felt by the Lohmanns to be relevant to turtle magnetic orientation. We outline in particular the field values on the eastern coast of Florida (F), at the 'Sargasso turn' on the eastern side of the Atlantic gyre (S), and near Ascension island (A).

The $45\mu\text{T}$ line in the Eastern Atlantic close to today's 'Sargasso turn' has shifted from 20°N to 40°N latitude, i.e. over 2000 km in 200 year. In contrast, the 'Florida' intensity of $49\mu\text{T}$ has shifted by about 1000 km. The non parallel bi-coordinate (I , F) system which is observed today in the south Atlantic, particularly near Ascension,

has shifted and did not exist 200 years ago, when isolines were almost parallel. In contrast, isolines formed a reasonable bicoordinate system in the North Atlantic until 1900, but they do not any more. Recalling the apparent sensitivity of turtles near 60° inclination, we note that the 60° isocline, near where the Gulf Stream now splits in two, has travelled 13° in the last 200 years. The southernmost location of the gyre has seen inclination changes from 35° to 15° in the last two centuries (recall the puzzling result of experiments that today there is no response of the turtles to 15° and 45° inclinations).

Conclusion

The experiments performed by the Lohmanns over the last decade have far-reaching implications. If confirmed, the directional sensitivity of turtles, particularly their rich spectrum of behaviour linked to particular values of geomagnetic field azimuth, inclination and intensity, must have been genetically inherited (the hatchling turtles never see their parents). Because the geomagnetic field changes quite fast with time, this provides an opportunity to compare the timescales of geomagnetic secular variation with those over which genetically imprinted information can evolve. Although the life expectancy of sea-turtles is difficult to measure, Rudloe (1979) states that they require something between 6 and 20 years to reach sexual maturity. Because the field has altered so much in the course of the last 300 years (Fig. 2), this means that genetically recorded geomagnetic field parameters must change significantly over the course of a few tens to a hundred generations.

On a longer timescale, the idea that changes in the geomagnetic field can provide a method to constrain the rate of genetically imprinted behavioural evolution would be quite important. During the last 2000 years, the field intensity in the north Atlantic has doubled. It was rather weak with complex geometry during the Laschamp (40 000 years ago) and Blake (215 000 years ago) events, and of course it went through a full reversal 780 000 years ago. Adaptations for maintaining migratory behaviour must be capable of handling fluctuations on these timescales. Although we are well aware of the difficulty and duration of the ex-

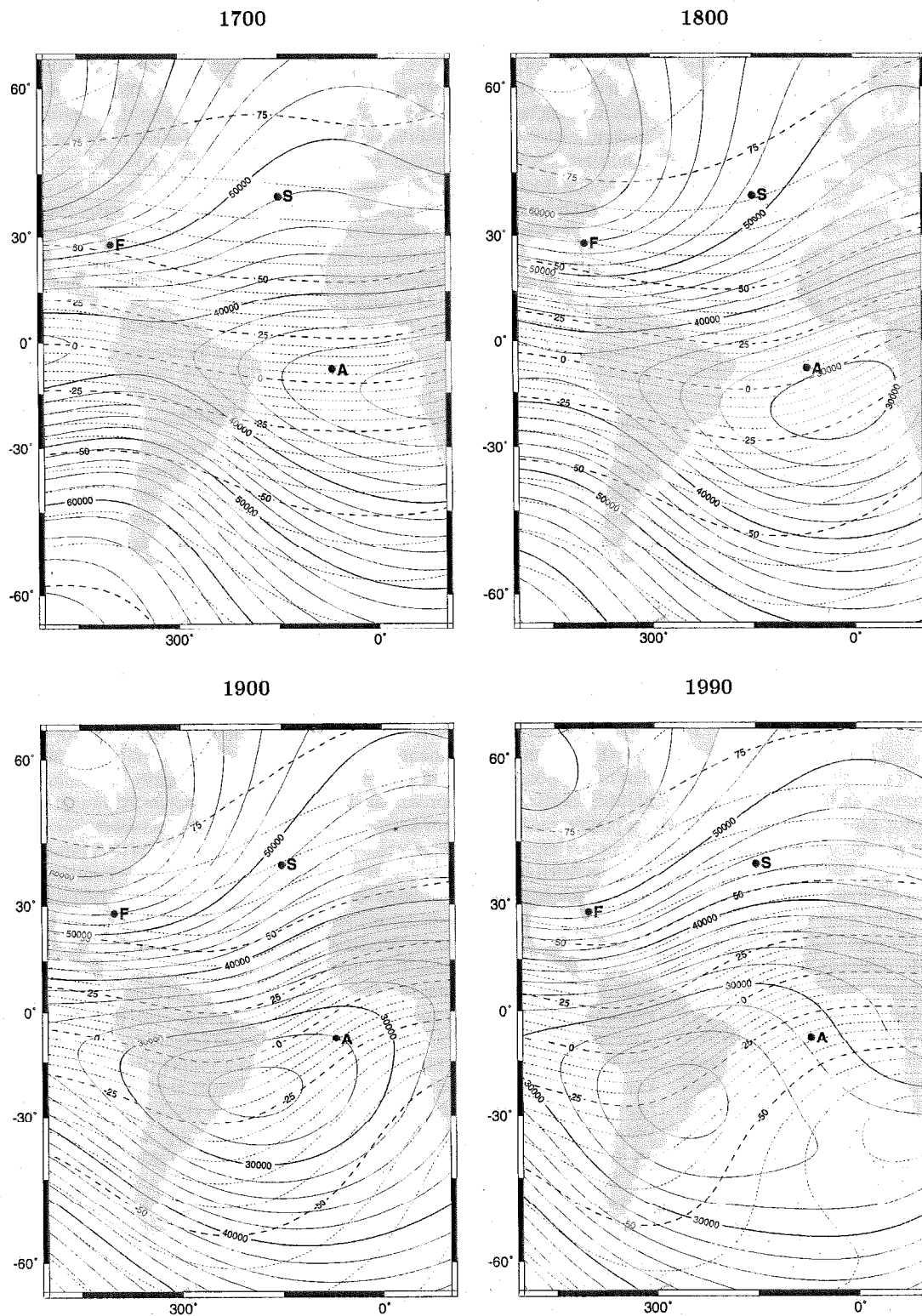


Fig. 2 Secular variation of the geomagnetic field since 1700 following the models of Bloxham and Jackson (1992). Lines of equal value of field intensity (F), i.e. isodynamics (full lines, values in nT) and inclination (I), i.e. isoclines (dashed lines, in degrees) shown for (a) 1700, (b) 1800, (c) 1900, and (d) 1990. These may form a bicoordinate system (Lohmann and Lohmann, 1996) used in sea-turtle navigation. Particular locations discussed in the text are the Florida Coast (F:28° N,80° W), ‘Sargasso turn’ (S:40° N,30° W) and Azores (A:8° S,14° W).

periments conducted by the Lohmanns, we believe that a number of the suggestions discussed above might be useful in planning further experiments for testing of these ideas: reaction to fast field changes, sensitivity experiments about thresholds (near 60° inclination or 50 μT intensity), experiments on cross-correlation and influence matrices between the various field components, and interpretation of observations in terms of simple magnetoreception models. Such experimental confirmations are needed before all consequences derived from the fascinating Lohmanns experiments can be accepted.

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