

THE HORIZONTAL MAGNETIC DANCE OF THE HONEYBEE IS COMPATIBLE WITH A SINGLE-DOMAIN FERROMAGNETIC MAGNETORECEPTOR

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(Received February 16th, 1981)

(Revision received May 1st, 1981)

Although honeybees are able to sense the geomagnetic field, very little is known about the method in which they are able to detect it. The recent discovery of biochemically precipitated magnetite (Fe_3O_4) in bees, however, suggests the possibility that they might use a simple compass organelle for magnetoreception. If so, their orientation accuracy ought to be related to the accuracy of the compass, e.g. it should be poor in weak background fields and enhanced in strong fields. When dancing to the magnetic directions on a horizontal honeycomb, bees clearly show this type of alignment behavior. A least-squares fit between the expected alignment of a compass and this horizontal dance data is consistent with this hypothesis, and implies that the receptors have magnetic moments of 5×10^{-13} emu, or magnetite volumes near 10^{-15} cm³. Additional considerations suggest that these crystals are slightly sub-spherical and single-domain in size, held symmetrically in their receptors, and have a magnetic orientation energy of approximately to 6 kT in the geomagnetic field. A model of a magnetite-based magnetoreceptor consistent with these constraints is discussed.

1. Introduction

Although the behavior and the orientation of a variety of animals is known to be influenced by the geomagnetic field (e.g., Keeton, 1972; Wiltschko and Wiltschko, 1972; Walcott and Green, 1974; Blakemore, 1975; Bookman, 1977; Emlen et al., 1976; Walcott, 1978; Quinn, 1980), very little is known about the manner in which various organisms are able to detect it. Prior to the work of Gould et al. (1978) and Yorke (1979), most theoretical analysis and speculation about this transduction mechanism dealt with various types of electrical induction (e.g., Kalmijn, 1974; Jungerman and Rosenblum, 1980) or on paramagnetic interactions (e.g., Leask, 1977). However, the discovery that many organisms have the biochemical ability to synthesize the ferromagnetic mineral magnetite (Fe_3O_4 —

Chitons, Lowenstam, 1962; honeybees, Gould et al., 1978; pigeons, Walcott et al., 1979; bacteria, Frankel et al., 1979; and dolphins, Zoeger et al., 1980) suggests that a new type of discrete, compass-like organelle could be involved in magnetoreception (Kirschvink and Gould, 1981). It is therefore legitimate to ask whether the published behavioral data on terrestrial animals is consistent with such a ferromagnetic receptor, and if so, what further predictions concerning the size or configuration of these as yet hypothetical organelles can be made.

One strategy for this consistency check would be to examine the orientation accuracy of a magnetically sensitive animal as a function of the strength of the background magnetic field. If placed in a zero-field environment, a magnetic compass would exhibit no net alignment and an animal relying upon it would display completely random orientations. On the other hand, if the compass was placed in an overly strong field it would closely track the magnetic direction with only

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a minor amount of thermally produced deviation; an organism relying upon it would then display its maximum orientation. As will be discussed in section 2 below, the simplest ferromagnetic hypothesis implies that the shape of this accuracy vs. field-strength curve should be similar to that of a compass (which is given by the Langevin function), and the best fit of this curve to the data should yield an estimate of the size of the hypothetical organelles involved. Note that this analysis alone would not yield an estimate of the number of organelles in the sensory array.

Of all terrestrial animals known to be sensitive to the geomagnetic field, the honeybee, *Apis mellifera*, is by far the best studied. Four separate magnetically influenced behavioral effects are known (Gould, 1980), of which the horizontal dance (Lindauer and Martin, 1972; Martin and Lindauer, 1977; Brines, 1978; Gould et al., 1980) is particularly suitable for the analysis outlined here. This experiment and the published data from it for the German honeybee, *A. mellifera carnica*, will be discussed further in sections 3 and 4 below. These data fit the ferromagnetic hypotheses reasonably well and lead to further constraints on the probable configuration of magnetite-based compass magnetoreceptors in the bee.

2. Alignment of a compass organelle in a varying magnetic field

Magnetite particles like those precipitated by most organisms examined to date are sub-microscopic in size, ranging from less than 300 Å to a maximum of about 2000 Å in diameter. For ferromagnetic crystals in this size range the magnetic energy of orientation greatly exceeds that of gravity, and viscous forces from the surrounding medium will overpower any inertial effects during movement of the animal (Yorke, 1979; Kirschvink and Gould, 1981). If one of these magnetite crystals was held in place such that it could rotate freely, it would align itself such that its

magnetic moment, μ , was close to that of the ambient magnetic field, B . This alignment would not be perfect, however, because the particle will be bombarded thermally and yield a type of Brownian motion. Therefore, the vector direction of μ will randomly wander around the direction of B with a probability density given by the Boltzmann distribution, $\exp(\mu B \cos\theta/kT)$, where θ is the angle between μ and B , k is Boltzmann's constant, and T is the absolute temperature.

Although the speed of this thermal wandering is a function of the crystal size, shape, and medium viscosity (Yorke, 1979; Kirschvink and Gould, 1981), its average alignment is not and can be readily found as follows. The projection of μ upon the direction of B is given by $\mu \cos\theta$, and so the average alignment is simply $\cos\theta$ averaged over the Boltzmann distribution, or

$$\begin{aligned} \langle \cos\theta \rangle &= \frac{\int_{\text{surface of sphere}} \cos\theta e^{\mu B \cos\theta/kT} d\Omega}{\int_{\text{surface of sphere}} e^{\mu B \cos\theta/kT} d\Omega} \\ &= \coth(\mu B/kT) - kT/\mu B \\ &= L(\mu B/kT) \end{aligned} \quad (1)$$

This is the definition of the Langevin function, L . Figure 1 shows the shape of this curve for different values of the ratio $(\mu B/kT)$. In weak fields or with small magnetic moments ($\mu B/kT \ll 1$) the average alignment is poor and well approximated by $\mu B/3kT$; stronger fields or larger moments ($\mu B/kT \gg 1$) produce an asymptotic convergence towards 1, which is given approximately by $1 - (kT/\mu B)$.

Organisms which depend upon one or more of these ferromagnetic compass grains for magnetic orientation should also show a similar accuracy function; their net alignment should be poor in weak fields when all of

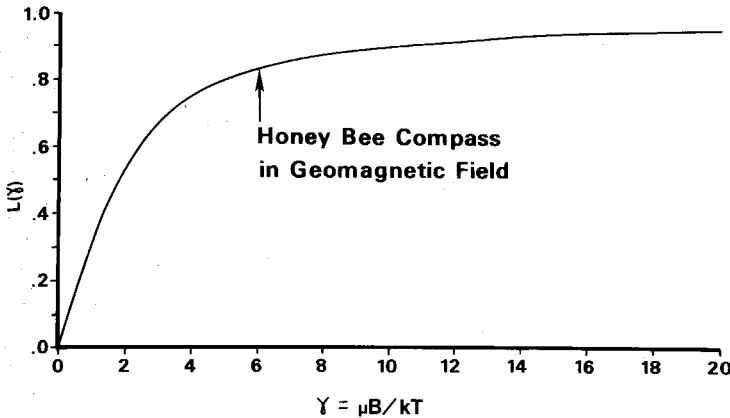


Fig. 1. Langevin function (Eqn. [1]) plotted as a function of $\mu B/kT$, the ratio of the magnetic to thermal energies. The arrow corresponds to the inferred moment of the honeybee receptor found by the least-squares analysis in the earth's 0.5 G field at honeybee temperature (310K).

their compasses are randomly aligned, and it should asymptotically approach some maximum alignment value in progressively stronger fields. As of now, the manner in which this Langevin response would be translated to the nervous system is unknown; the simplest initial approach, however, is to assume that it is a linear function. In turn, this implies that a neurologic array averaging over the response of many independent compass receptors would show a similar response, except that the overall accuracy should improve roughly as the square-root of the number of independent receptors (Yorke, 1979). Note that the shape of the Langevin function is specified essentially by the product μB because kT is a constant inside the honeybee. If the magnitude of the external field is experimentally varied and monitored, the orientation data ought to reveal the average size of μ and hence the volume of magnetite in each compass organelle. These data for the honeybee are analyzed next.

3. The magnetic dance of the honeybee on a horizontal comb

Honeybee workers normally perform their waggle-dance on sheets of wax honeycomb which hang vertically from the ceiling of their

hive. Gravity is their normal orientation reference; the angle between vertical and the direction in which they dance tells their fellow workers the angle between the sun and the

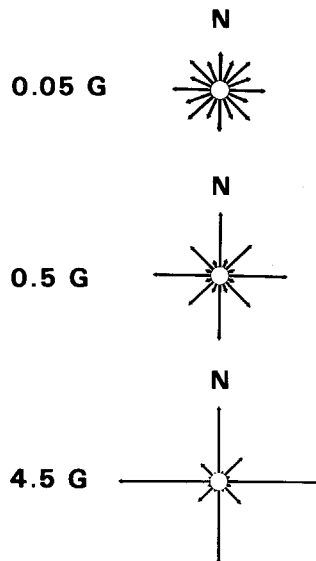


Fig. 2. Examples of the horizontal magnetically orientated dance of the honeybee (from Lindauer and Martin, 1972, and Martin and Lindauer, 1977). The length of the 16 arrows in each rose diagram represents the relative fraction of bees which danced to within $\pm 11.25^\circ$ of it. Magnetic north is indicated by the N at the top of each figure. Strong fields enhance the 8-point orientation, while weak fields diminish it. Data for this experiment are listed in Table 1. (N.B.: 1 Gauss (G) = $1 \text{ emu/cm}^3 = 10^{-4} \text{ T}$).

food source from which the dancer has most recently returned (von Frisch, 1967). If the hive is tilted on its side, the bees can be forced to live and work on horizontal sheets of honeycomb without their normal gravity reference. Under these conditions and in the absence of other cues dances are less frequent and disoriented. After 2 or 3 weeks, however, the bee dances are orientated preferentially to the 8 cardinal points of the magnetic compass (N, NE, E, . . .). As shown in Fig. 2, strong background magnetic fields enhance this orientation whereas weak fields reduce it. Individual bees do not always choose the same direction, but may vary in their selection from dance to dance. This 8-point orientation pattern has been observed in other insects when presented with a directional cue such as polarized light (von Frisch, 1967) and may be a characteristic of the insect nervous system; in any case, the alignment of these patterns with the local magnetic field direction suggests that magnetism is an orientation cue and that magnetoreceptors of some sort must exist. These horizontal dances are totally useless to the bees, however, because they cannot convey the location of any food source. Note also that honeybees, like many birds, seem to detect only the axial direction of the magnetic field and do not separate north from south.

In laboratory practice, the direction of each dance is determined by either videotaping it under red light (to which bees are blind) and measuring the orientation later on a TV monitor (Gould et al., 1980), or by using diffuse, unpolarized light and manually aligning a grid/protractor assembly to the dance direction at the hive (Martin and Lindauer, 1977). This measuring process probably contributes some small degree of inaccuracy to the experimentally observed dance alignment. As a consequence, even in relatively strong background fields one would not expect to find perfect octamodal alignment of the dance. Other noise-generating factors probably exist as well, such as the battering of the dancers by fellow workers in a crowded hive.

These factors are important to consider in the data analysis presented next.

4. Analysis of horizontal dance data

Although several authors have published results for this horizontal dance experiment, most of the available data comes from the German honeybee, *A. mellifera carnica*. Lindauer and Martin (1972) and Martin and Lindauer (1977) have done this experiment on the German bee a variety of times in six different background fields; consequently their data are most suitable for this analysis and have been compiled in Table 1. The data consist of rose diagrams like those shown in Fig. 2, along with the total number of dances counted and the percent of dances oriented to within $\pm 11.25^\circ$ of each of the eight principal compass directions (N, NE, E, . . .). By summing these percentages, the total number of dances in all cardinal and non-cardinal directions for each experiment can be found as shown in Table 1. These total dance numbers can then be combined for duplicate experiments which were performed in the same background fields, thereby giving the sums shown in columns 4 and 5 of Table 1.

From these raw data, it is necessary to compute next a measure of the average dance accuracy in each experiment for use in the least-squares analysis. The measure should have a theoretical range from 0 (no alignment) to 1 (perfect alignment) as does the Langevin function with which it will be compared. There is a simple, linear way to do this, given by:

$$D_i = \frac{(N_{\text{card}} - N_{\text{non-card}})}{N_{\text{total}}} \quad (2)$$

If there are equal numbers of dances in the cardinal and non-cardinal classes, the dances are essentially random and the alignment measure will be 0. On the other hand, if all dances lie along the cardinal points ($N_{\text{card}} =$

TABLE 1

Horizontal magnetic dance data of the German honeybee, compiled from Lindauer and Martin (1972) and Martin and Lindauer (1977)

Background magnetic field (B_i) in Gauss	% of dances along cardinal directions	% of dances not aligned	Total No. of dances along cardinal directions	Total No. of misaligned dances	Dance alignment ratio (D_i)
0.5 G	58.9	41.1	6 029	4 332	0.178
			$N = 10\ 541$		
0.5 G	84.3	15.7	20 739	3 862	0.672
	70.2	29.8	545	231	
	77.5	22.5	942	274	
			$\Sigma = 22\ 226$	4 367	
			$N = 26\ 593$		
1.2 G	86.1	13.9	6 917	1 117	0.722
			$N = 8\ 034$		
2.5 G	90.7	9.3	3 722	382	0.814
			$N = 4\ 140$		
3.5 G	88.3	11.7	4 443	589	0.794
	93.9	6.1	1 454	94	
			$\Sigma = 5\ 897$	683	
			$N = 6\ 570$		
4.5 G	94.6	5.4	9 767	557	0.822
	79.8	20.2	2 532	641	
			$\Sigma = 12\ 299$	1 198	
			$N = 13\ 497$		

LEAST-SQUARES ANALYSIS:

	c-value (in emu/erg)	x-value	Minimum sum of squares
Unweighted	12.12	0.8167	0.002876
weighted	11.83	0.8162	25.06184

N_{total}) the measure is 1. Although the behavior with respect to the N-S and E-W axes is slightly different than that along the NE-SW and NW-SE directions in Fig. 2, this definition of the accuracy measure seems to be a reasonable approximation to the actual complexity. Values for this alignment have been calculated for the combined data and are

given in column 6 (under D_i) of Table 1 and plotted as a function of the corresponding field strength in Fig. 3.

Finally, in order to estimate the size of the hypothetical compass organelles it is necessary to find the Langevin function of best least-squares fit to the data. However, as discussed in section 3 above there are reasons to

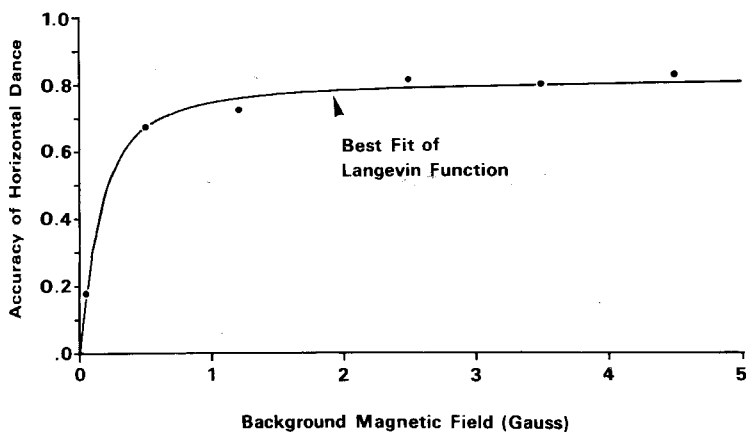


Fig. 3. Least-squares comparison between the honeybee horizontal dance and the Langevin function. The six dots are the average dance accuracies, D_i , in Table 1 plotted against the strength of the background field. The solid curve is the Langevin function of best least-squares fit.

suspect that the dance accuracy will not approach the maximum value of 1.0 asymptotically as does the Langevin function; instead it should approach some lower value characteristic of the errors generated by the whole magnetoreceptor-bee-observer system. It is therefore necessary to do a 2-parameter fit on the data, using the function $xL(cB)$, where x is a linear scaling factor less than 1 and $c = \mu/kT$. The value x represents the fraction of the observed behavior which is due to the compass receptor. Therefore we want values of x and c such that

$$S = \sum_i [xL(cB_i) - D_i]^2 \quad (3)$$

is a minimum, where B_i is the background magnetic field of the i th experiment and D_i is the corresponding dance alignment. Equation (3), however, gives unit weight to each of the six experiments in this data set. An alternate approach is to weight each experiment according to the number of dances involved, N_i , and minimize

$$S = \sum_i [xL(cB_i) - D_i]^2 N_i \quad (4)$$

instead. In both cases, c and x are independent so the minimum of S can be found by solving the two simultaneous equations,

$$\frac{\partial S}{\partial x} = 0 \quad \text{and} \quad \frac{\partial S}{\partial c} = 0. \quad (5)$$

Using S as given in Eqn. (4) these reduce to

$$x = \frac{\sum D_i L(cB_i) N_i}{\sum L^2(cB_i) N_i} \quad (6)$$

and

$$x = \frac{\sum D_i L'(cB_i) B_i N_i}{\sum L(cB_i) L'(cB_i) B_i N_i}, \quad (7)$$

where $L'(cB_i)$ is the first derivative of the Langevin function. Similar expressions are found if equation (3) is used for S , except that N_i does not appear. By equating (6) and (7), the value of c can be found using numerical iteration, and from this either (6) or (7) used to compute x . Results of this analysis for both the weighted and unweighted treatment are quite similar and are given at the bottom of Table 1. At the scale of Fig. 3, note that the weighted and unweighted Langevin functions of best fit cannot be resolved graphically, suggesting that there is no significant difference between the two methods. A further error analysis does not seem warranted at this point in view of the small sample size ($N = 6$) and the need for more experimental

data from low background fields between 0 and 1.5 G. These data are therefore consistent with the assumption made earlier of a linear transduction response. The best estimate of the magnetic moment of each hypothetical honeybee compass receptor is given by $\mu = ckT$, at the bee's body temperature of 310K, $kT = 4.28 \times 10^{-14}$ erg, so $\mu = 5 \times 10^{-13}$ emu. If the ferromagnetic material is magnetite, this would correspond to a crystal volume of about 10^{-15} cm³.

In the earth's roughly 0.5 G magnetic field, a magnetite grain with this moment has an energy product, μB , equal to about $6 kT$. As shown in Fig. 1, this value plots on the Langevin function just after it flattens out and begins the asymptotic approach towards 1.0. Consequently, the addition of more ferromagnetic material to the receptor could not improve the accuracy very much, whereas a slight reduction would reduce drastically the average thermal alignment. The honeybee seems to have struck an optimum balance between the inaccuracy of having too small a compass, and the waste of making it too big.

5. Results and discussion

It seems clear from Fig. 3 and the low least-squares residuals in Table 1 that the model of ferromagnetic-based magnetoreception outlined above is compatible with the horizontal dance behavior of the honeybee. Using this model, it is possible to estimate the size of the compass organelles involved, although their number and detailed anatomical configuration remain a mystery. The physical properties of magnetite, however, make possible a number of educated guesses as to this configuration. Along with the alternating-field demagnetization experiment of Gould et al. (1980) and the theoretical analysis of Yorke (1979) these properties can help to clarify further the probable physiology of a magnetite-based honeybee compass receptor.

The first such constraint is based on the known ferromagnetic stability properties of

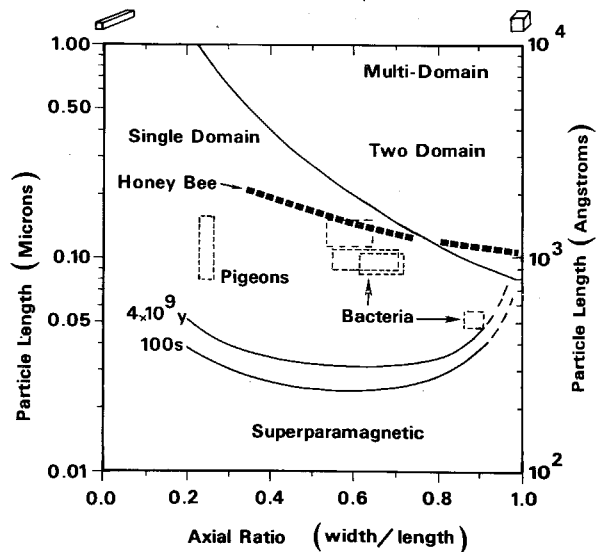


Fig. 4. Magnetic stability diagram for isolated rectangular parallelepipeds of magnetite (after Butler and Banerjee, 1975 and Kirschvink and Gould, 1981). Each point on this diagram represents a rectangular magnetite crystal of specified size and shape. Points which plot in the upper right area labeled multi-domain or two domain represent crystals with two or more differently magnetized sub-regions within them; their net external magnetism is consequently reduced. Crystals which plot in the single-domain field (central part of diagram) are those in which a single electron spin direction exists across their entire volume; they are magnetized fully to magnetite's saturation value of 480 emu/cm³. The particle shape constrains the magnetic remanence to lie permanently along its length unless forced to move by a strong magnetic pulse. Below the sharp transition zone bounded by the two lines labeled 4×10^9 years and 100 s, respectively, the remanence direction is no longer stable relative to the crystal and wanders freely in response to local fields and thermal agitation, giving rise to superparamagnetic behavior. Numerous bacterial and pigeon magnetite crystals which have been measured by electron microscopy all plot in the single-domain field as shown. The dashed line corresponds to those crystals which have the volume of magnetite estimated by least-squares for the honeybee compass receptor.

magnetite, which are summarized in Fig. 4 (after Kirschvink and Gould (1981), adapted from Butler and Banerjee (1975)). If a magnetite crystal is within the correct size and shape range, a stable electron spin structure will form spontaneously across its entire

volume and produce a uniform magnetization of 480 emu/cm^3 . Crystals of this size and shape are those which lie in the fields labeled single-domain or superparamagnetic in Fig. 4. In larger crystals the uniformly magnetized state is unstable and will break into two or more regions with different magnetic directions (multi-domain) and reduce the net magnetization of the crystal; consequently only the single-domain or superparamagnetic particles are likely to be used for magnetoreception. The volume of magnetite estimated earlier for the honeybee receptor corresponds to the dotted line on Fig. 4. If all of this material were in one crystal it could either be single-domain or multidomain, depending upon its shape. Therefore, the most probable configuration for this magnetoreceptor would be a single-domain crystal having a width/length ratio less than about 0.8 and a particle length slightly greater than 0.1 microns.

From this analysis alone, it is not possible to determine whether or not there are one or more discrete crystals involved in the compass structure. A chain of crystals could be held rigidly together like those in the magnetosome of magnetotactic bacteria (Balkwill et al., 1980) and yield the same alignment response as long as the total volume of magnetite is constant. A long chain or particle, however, will have a much greater surface area than an equant or spherical shape, and this in turn will drastically increase the viscous drag due to the surrounding medium (see Hong et al., 1972). Elongate particles will therefore have slower rotational diffusion speeds than more compact grains. Although the magnitude of the thermal wandering is the same for all shapes, the slower speed of an elongate particle implies that the bee would need to spend more time averaging over a grain's thermally wandering position in order to obtain the same directional information (Kirschvink and Gould, 1981). Natural selection ought to favor a more compact structure with a fast response time. Biogenic magnetite crystals of this appropriate size and shape

have been reported from magnetotactic bacteria by Blakemore (1975) and Towe and Moench (1981) as shown on Fig. 4. Note that these bacteria, however, need a larger total volume of magnetite in order to torque their entire cell into alignment with the geomagnetic field (Frankel and Blakemore, 1980); the magnetite in them is not free to move on its own.

The conclusion reached above that the honeybee compass receptors are of single-domain size disagrees with that of Gould et al. (1980). In that study, bees were selectively demagnetized in a strong oscillating magnetic field (2100 G, 60 Hz) produced by a large solenoid. Demagnetized bees were as highly oriented to the geomagnetic field as were normal (undemagnetized) bees. Strongly alternating fields ought to randomly flip the direction of the magnetic vector in any single-domain particle present, leaving half of them magnetized in their original direction and half antiparallel to it. If the polarity of these crystals were important to the function of the magnetoreceptor, half of the receptors should have been permanently confused by the demagnetization procedure and ought to have produced some behavioral effect. Therefore, Gould et al. (1980) prematurely concluded that the smaller, superparamagnetic crystals, of which bees have at least 10^8 (Kirschvink and Gould, 1981), were involved in the compass.

A more reasonable hypothesis would be to suggest that the polarity of the single-domain magnetite grains are not important to the function of the receptor; Kirschvink and Gould (1981) discuss several symmetrical configurations which could operate in this fashion. Such a model satisfies three important criteria: Firstly, it would be immune to alternating-field demagnetization in agreement with the results of Gould et al. (1980). Secondly, a symmetrical receptor would only allow an organism to determine the axial direction of the geomagnetic field; it could not use it to distinguish north from south. This agrees with numerous behavioral experi-

ments which show that honeybees and many birds are apparently unable to tell this difference (Wiltschko and Wiltschko, 1972; Walcott and Green, 1974; Martin and Lindauer, 1977). Finally, if the magnetic polarity of a single-domain crystal were important to its function, the crystal would have to be grown under carefully controlled conditions. The polarity in nature is determined by the local field direction at the time the particle grows in size across the superparamagnetic/single-domain transition shown on Fig. 4. All honeybee larvae and bird embryos are certainly not grown in the same orientation relative to the geomagnetic field, so from a developmental point of view it seems much simpler to make a symmetrical receptor. Although superparamagnetic crystals certainly exist in honeybees, their biologic function is as yet unknown.

A hypothetical magnetoreceptor which fits all of the constraints discussed above is sketched in Fig. 5 (adapted from the membrane-short model of Kirschvink and Gould, 1981). In this particular configuration, the slightly elongate single-domain magnetite crystal

would be azimuthally wrapped with an organic insulator such as myelin and allowed to rotate freely within a specially thickened membrane support structure as shown. Because magnetite has by far the lowest electrical resistivity of any known biological material (5×10^{-3} ohm-cm), it can passively depolarize a sensory nerve membrane. With the configuration shown, the angle of the crystal relative to the plane of the membrane governs the surface area of the magnetite electrically exposed to the medium, and hence it controls the size of the depolarization produced. The frequency at which this hypothetical organelle fires would tell the bee the position of the crystal, and three such isolated organelles with mutually perpendicular membranes would provide an estimate of the axial direction of the magnetic field. Note that this structure could not be used to determine north from south, nor could it be affected by alternating-field demagnetization; either reversing the ambient field direction or changing the magnetic polarity of the crystal would cause it to rotate 180° and produce an identical response. Using

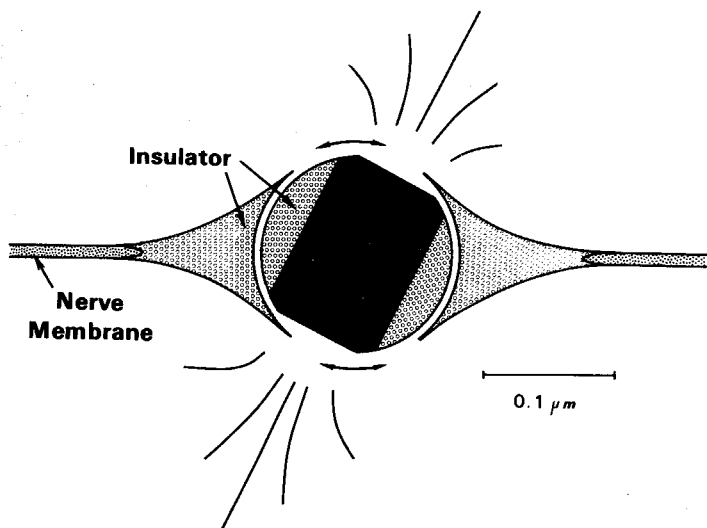


Fig. 5. Cross-section of the hypothetical honeybee compass magnetoreceptor. The magnetite crystal which is free to rotate into alignment in the geomagnetic field has been drawn with a length/width ratio of 0.7 as suggested in the text, with a total volume equal to that estimated from the least-squares fit. Organic insulation in this model surrounds the electrically conductive magnetite crystal, allowing the trans-membrane resistance to vary as a function of the angle between the crystal and the plane of the nerve membrane. This and other transduction models have been discussed by Kirschvink and Gould (1981).

the rotational time derivation of Frankel and Blakemore, (1980) with a medium viscosity of 0.1 P (10 times that of water) and the configuration of Fig. 5, one finds that it would take only about 30 ms for this organelle to realign itself — probably too short a time for the bee to notice.

Although this model as illustrated in Fig. 5 is consistent with the magnetically influenced behavior of the honeybee, structures similar to it have not as yet been found. Biochemically precipitated magnetite is present in the honeybee abdomen (Gould et al., 1978), but as yet there is no firm link between this material and the bee's ability to detect the geomagnetic field. An important factor to consider in the search for these compass organelles is that the SQUID magnetometers have a resolution on the order of 10^{-8} emu, whereas each of these crystals would have a magnetic moment of only 5.14×10^{-13} emu. Over 20 000 of these hypothetical structures could exist in the bee and remain undetected. However, Yorke (1979) and Kirschvink and Gould (1981) estimate that the bee would need at most a few hundred such organelles in order to adequately resolve the direction of the geomagnetic field against the background of thermal noise. The "needle in the haystack" analogy certainly applies to this search, and additional behavioral or neurological information will be necessary in order to find the receptors, if they exist. Note, however, that this argument does not apply to magnetite-based organelles if they are being used for *magnetointensity* reception. Yorke (in press) and Kirschvink and Gould (1981) have independently reached the conclusion that a neurologic array averaging over large numbers of organelles (10^7 – 10^8 , numbers detectable on the SQUID magnetometers) would be necessary to explain the sensitivity to weak geomagnetic intensity fluctuations displayed by many animals (Lindauer, 1976; Gould, 1980; Walcott, 1978; Keeton et al., 1974; Larkin and Sutherland, 1977). Although the optimum size of each of these intensity organelles would be much less than the com-

pass receptor considered here (Kirschvink, in prep.), they should still have single-domain properties and grain sizes close to that observed in pigeons.

In summary, the hypothesis that magnetite-based magnetoreceptors are responsible for the ability of honeybees to orientate to the geomagnetic field is consistent with their horizontal dance behavior. Other considerations imply that the receptors ought to have equant, slightly sub-spherical single-domain crystals which are held in place with 180° functional symmetry. Whether or not the paramagnetic or inductive strategies for magnetoreception are able to account for the horizontal dance of the honeybee is not yet clear. The recent analysis of Jungerman and Rosenblum (1980) makes the induction hypothesis unlikely because the 1–3 mm sized conducting loops required by their model do not seem to exist in the bee (see Dade, 1977). Neither induction or paramagnetic effects, however, seem capable of explaining the magnetic sensitivity of the bee to the weak geomagnetic fluctuations; this leaves ferromagnetism as the most likely candidate.

Acknowledgements

I thank Drs. John D. Morgan III, James L. Gould, and K.S. Deffeyes for helpful discussions and comments on this manuscript. This work was partially supported by NSF grants EAR78-03204, SPI79-14845, and BNS78-24754.

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