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Chapter 11

Particle-Size Considerations for Magnetite-Based Magnetoreceptors

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1. Introduction

The presence of a magnetic influence upon behavior now appears to be a fairly common trait among a wide variety of organisms, as outlined and discussed elsewhere in this volume. In a broad manner, these behavioral responses can be grouped into two categories, the first of which involves the use of a relatively insensitive "compass" to obtain directional (north/south) information, and a more sensitive system involved in the "map" sense of vertebrates and the time cue of insects.

1.1. Compass Organelles

Examples of the "compass" are numerous, and include the passive orientation of magnetotactic bacteria and algae (Blakemore, 1975; Lins de Barros *et al.*, 1981), the waggledance alignment of honeybees on horizontal honeycomb (Martin and Lindauer, 1977), the swimming preference of salmon fry and smolt (Quinn, 1980, 1982; Quinn *et al.*, 1981), elasmobranchs (Kalmijn, 1982), the stationary orientation of eels (Tesch, 1975, 1980), the orientation preferences of amphibians (salamanders and newts: Phillips, 1977; Phillips and Adler, 1978), and the cloudy-day backup compass of homing pigeons and migratory birds (Keeton, 1972; Wiltschko, 1972; Walcott and Green, 1974). Single-domain crystals of magnetite are clearly linked to the magnetotaxis of the magnetic bacteria (Frankel and

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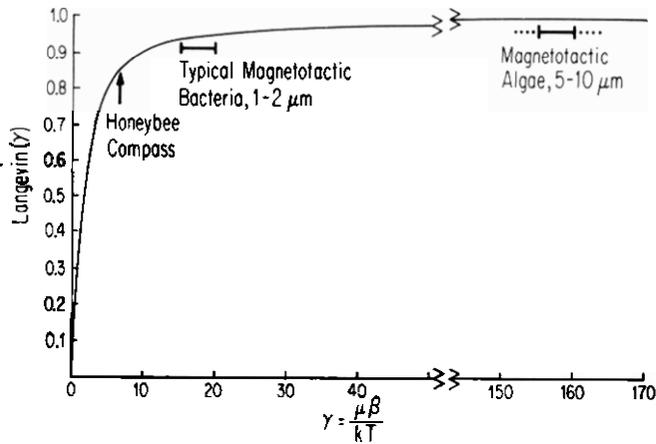


Figure 1. Alignment accuracy of bees, bacteria, and algae plotted as the Langevin function, versus the ratio of magnetic to thermal energies. The average alignment of these organisms (or the inferred organelles in bees) varies only slightly despite the large range of magnetic moments.

Blakemore, 1980) where individual cells possess stable ferromagnetic moments which are large enough to passively rotate the cells into a preferential alignment with the relatively weak ($50 \mu\text{T}$) geomagnetic field, despite the randomizing influence of Brownian motion. The critical physical requirement for passive compass systems of this sort to function is for the magnetic energy of orientation (μB or $\mu B \cos \theta$, where μ is the cellular moment, B the background flux density, and θ the angle between the μ and B vectors) to be significantly larger than the background thermal energy (kT , where k is Boltzmann's constant and T the absolute temperature). A freely wandering moment of this sort will have a dispersion about the applied field direction which is given by the Boltzmann distribution, $\exp(-\mu B/kT)$, which leads to an average alignment along the field direction given by the Langevin function, $L(\mu B/kT)$ or $\coth(\mu B/kT - kT/\mu B)$. This function is illustrated in Fig. 1, with γ representing the ratio $\mu B/kT$ as will be used throughout this chapter.

At room temperature and in the geomagnetic field, the values of the parameter γ which have been measured or inferred for the compass of bacteria, algae, and honeybee are shown in Fig. 1. Frankel *et al.* (1979) and Frankel and Blakemore (1980) directly determined the moment of a typical magnetotactic bacterium by measuring the magnetite volume of single-domain crystals aligned along the magnetosomes, and Kalmijn (1981) obtained a similar result by comparing their average swimming velocity in a variety of differing strength background fields to the Langevin function.

A similar swimming technique involving the radius of curvature when the field is reversed has also been applied to the magnetotactic algae by Lins de Barros *et al.* (1981) and implies cellular moments (and γ values) approximately 10 times larger than for the bacteria. In addition, a comparison between the accuracy of the honeybee magnetic compass response in various background fields and the Langevin function yields an estimate for their ferromagnetic compass moment corresponding to $\gamma = 6$ (Kirschvink, 1981). Despite this wide range of magnetic moments, the average alignment (given by the Langevin function) varies much less, from about 0.82 for the honeybee, 0.94 for the bacteria, and 0.99 for the algae. As can be seen in Fig. 1, a compass organelle smaller than that of the bees would be rather poorly aligned. The large moments for the bacteria and algae are apparently related to the need for greater torque ($\mu \times B$) to align their large cellular mass in the geomagnetic field with reasonable speed (Frankel and Blakemore, 1980; Lins de Barros *et al.*, 1981). A larger torque would be required for the magnetotactic algae, as they have diameters of $5-10 \mu\text{m}$ and far more surface area than a typical ($1-2 \mu\text{m}$) bacterium. Extending this argument to the smaller size of the honeybee compass suggests that there is relatively little additional organic material associated with the particle or chain of mag-

netic particles. In summary, the compass behavior of bacteria, algae, and honeybee is compatible with a ferromagnetic transduction mechanism.

1.2. The High-Resolution Magnetic Sense

Although the high-resolution magnetic sense has not been reported from as wide a variety of organisms as has the directional response mentioned above, the behavioral evidence for its existence is compelling and reproducible in many birds (discussed in this volume by Presti) and the honeybee (discussed by Towne and Gould). These behavioral results raise the difficult problem of understanding how organisms might perceive or be influenced by small perturbations in the background geomagnetic field (<1 part in 10^4). This problem is clearly more difficult than simply resolving the direction of the field.

Yorke (1981) and Kirschvink and Gould (1981) have independently analyzed this problem within the framework of the ferromagnetic hypothesis of magnetoreception. Both approaches are similar in that they assume that the high sensitivities are obtained by having the nervous system of the animals extract information from numerous magnetite-based receptors. In general, the quantity of magnetite located in organisms with this highly sensitive system is sufficient to allow either of these strategies to work. Yorke develops her strategy further elsewhere in this volume; in this chapter we consider some further implications of the variance hypothesis proposed by Kirschvink and Gould (1981) and suggest some behavioral experiments to test them. First, however, it seems worthwhile to examine the range of possible ways in which organisms might process information from the geomagnetic field into forms useful for bi- or multicoordinate navigation.

1.3. Magnetic Cues for a Navigational "Map" Sense

Navigational map systems proposed for animals range from the "familiar area map" discussed by Baker (1978) to bicoordinate grid maps involving two independent components (e.g., Quinn, 1982). A magnetic familiar area map could involve learning by the animal of a magnetic topography based on total magnetic field intensity, local gradients in total intensity, or functions of both. In these cases the problem of fixing a position in an unfamiliar area is reduced to the extrapolation of knowledge from the total intensity and gradients in the familiar area (Gould *et al.*, 1980). In the following section we shall focus our discussion on possible map systems.

Magnetic sensory components of the "map" could operate alone or in combination with one or more other senses. A variety of possible arrangements exist, each of which could form one component of a navigational "grid" system as outlined in Fig. 2. The simplest system would be one which operates alone, extracting information directly from the field as indicated in Fig. 2A. Without any additional directional cues, a system of this sort would only depend on a function of the total field strength. Because the intensity is a scalar quantity, it is the simplest geomagnetic parameter which is independent of the orientation of the animal. An array of magnetosensory organelles which could respond to a component of magnetic intensity could be exceedingly sensitive, as deduced by Yorke (1981) and Kirschvink and Gould (1981).

The next level would be to combine the magnetic and gravitational senses in some fashion, as appears to be the case with the magnetic compass in birds discussed above. A high-resolution component for the map sense could be formed by monitoring the spatial angle between "down" and the field direction, and integrating these small inclination differences over time (Fig. 2B). A map component of this sort would presumably be less

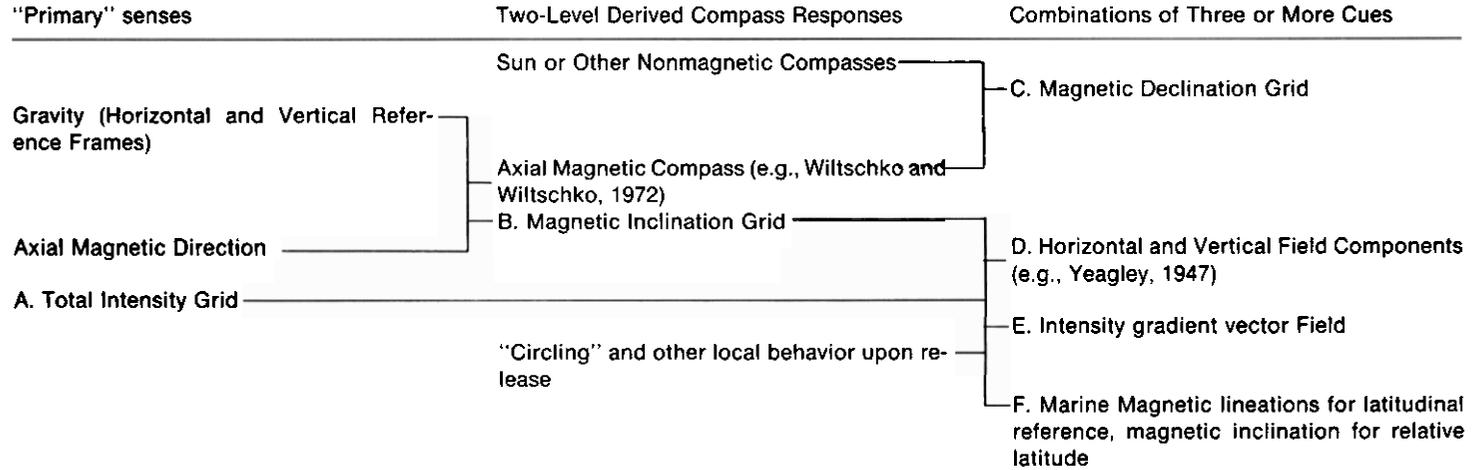


Figure 2. A possible hierarchy of geomagnetic-based cues for a navigational "map," based on bicoordinate grid systems.

sensitive than a pure intensity sense, as it must average out noise from both the magnetic and gravitational systems.

The next and probably least-sensitive level would combine three or more responses to form a map component. Two examples of this include the proposed use of the geomagnetic declination, or variations in the vertical or horizontal magnetic components as proposed by Yeagley (1947). The declination sense (Fig. 2C) would need the magnetic compass (gravity and axial magnetic direction) as well as an independent reference system like a sun or star compass. Although this composite system would be subject to noise from all of its component subsystems and would not work under cloud cover or for fish migrating under ice, the geomagnetic declination varies greatly with longitude, particularly at high latitudes, and thus it might serve as an occasional aid to the "map" when available.

Another third-level possibility would be to resolve the intensity and inclination into their horizontal and vertical components, respectively, as suggested by Yeagley (1947) and shown in Fig. 2D. However, it is not clear what additional information an organism would gain from this extra processing, as the Cartesian components of the field (horizontal and vertical) contain exactly the same information as the polar coordinates (intensity and inclination). It is difficult to conceive of "primary" organelles of any sort which would directly yield horizontal and vertical field estimates—this would require an organelle equally sensitive to both gravity and magnetism. For example, the large magnetite crystals which would be of use for gravity reception would of necessity be multidomain in size, making their net magnetic moments low and unsuitable for use as a ferromagnetic compass. For single-domain magnetite crystals, the magnetic energy of orientation typically exceeds that of gravity by factors of 10^2 to 10^4 , suggesting that the two senses are probably separate at the receptor level.

A final third-level possibility of this sort would be for the organisms to keep track of their positions in the vicinity of the release site while monitoring small shifts in the total intensity. In this fashion a local "map" of the intensity gradient field could be constructed and used as another component of a navigational grid. Some migratory and homing organisms like pigeons, turtles, and pelagic fish have been found to move in 100- to 200-m-diameter circular paths immediately after release in an unfamiliar area (Walcott, 1978; Rudloe, 1979); this behavior might be involved in the construction of such a gradient map.

For oceanic animals there is perhaps an even simpler arrangement for magnetic navigation which would involve using the marine magnetic lineations. Unlike the continents, *the geomagnetic field over the ocean basins has a regular and simple pattern composed of north-south-trending "ridges and valleys" produced by geomagnetic reversals recorded in the basaltic seafloor* (Vine, 1966). These could be used to keep track of relative changes in east-west position by counting local minima or maxima, while an inclination compass could keep track of north-south position. An even simpler strategy for animals with primarily north-south migratory routes (e.g., fin whales in the Atlantic) would be to stay on the magnetic lows. Kirschvink *et al.* (in press) have recently found that cetacean strandings along the eastern U.S. continental margin tend to happen where such minima intersect the coastline, suggesting that such navigational cues may actually be used (Fig. 2F).

In view of this discussion, it therefore seems most likely that any magnetic components to the "map" would involve functions of the total intensity, inclination, or declination from true north in this respective order of decreasing probability. This is consistent with the observation of Walcott *et al.* (1979) that between 10^7 and 10^8 single-domain magnetite crystals are present in homing pigeons, whereas only a few hundred to a thousand would be needed for the compass responses. Magnetite-based receptors involved in the measurement of either inclination or declination would be subject to the same Langevin-type constraints as discussed above for compass organelles. A similar theoretical approach for organelles involved in an intensity array is developed next, extending the thermally driven variance model proposed by Kirschvink and Gould (1981) and Kirschvink (1982).

2. The Thermally Driven Variance Model of Magnetic Intensity Reception

A geomagnetic intensity sense of the type outlined in Fig. 2 must somehow minimize the directional aspect of the earth's field and extract only its scalar magnitude as would, for example, a proton-precession magnetometer. Two approaches seem possible for this. The simplest would be to use organelles which are only sensitive to some function of the intensity. An integrated signal from a large number of such receptors would similarly be free of directional dependence. A second approach would be to start with a less-than-perfect organelle, one that responds to components of both intensity and direction. By using a large number of such structures with random (e.g., uniformly distributed) spatial orientations, the directional effects should average out and leave only an intensity-dependent response for the overall system.

The total intensity of the field is probably not responsible for most of the map and time responses, however. The K-index correlations of Keeton *et al.* (1974) and Southern (1978) are best interpreted in terms of a sensitivity to small fluctuations in the background field, and this interpretation looks plausible for the honeybee circadian rhythm data of Lindauer (1977) as well as the pigeon magnetic anomaly effects (Walcott, 1978; Papi *et al.*, 1978). The ability to monitor small shifts in the background field would be of equal use to a migrating animal as would monitoring total intensity.

Magnetite-based sensory organelles are in principle capable of generating the intensity-dependent signal required for this type of system. A small particle in a fluid medium will move randomly in response to thermal bombardment from molecules in the surrounding fluid. This "Brownian" motion causes the moment of the particle (μ) to deviate from the direction of the external magnetic field (B) with a directional probability density given by the Boltzmann distribution, $\exp(\gamma \cos \theta)$. If this field is strong, the parameter $\gamma (= \mu B/kT)$ will be large and μ will closely align along the direction of B . An organelle which fires as some repetitive function of grain orientation would produce a uniform frequency of action potentials. In weaker fields, γ will be small and the position of the grain will wander greatly; signals resulting from the organelle would occur with irregular frequency. Although the mean firing frequency of an organelle would yield information about direction, the variance around the mean frequency from such a receptor would be a function of intensity. Several explicit organelle configurations which could produce this type of response have been discussed elsewhere (Kirschvink and Gould, 1981).

The sensitivity of a variance-based intensity system which responds to background fluctuations may vary strongly with the magnetic moment of each organelle. The best moment is clearly that at which the variance of the Boltzmann distribution changes the most with small fluctuations in γ . Components of the variance parallel and perpendicular to the external field are

$$\sigma_{\perp}^2 = (2/\gamma) L(\gamma)$$

$$\sigma_{\parallel}^2 = 1 - (2/\gamma) L(\gamma) - L^2(\gamma)$$

where $L(\gamma)$ is the Langevin function as before. Similarly, it is straightforward to differentiate σ_{\perp} and σ_{\parallel} with respect to γ , yielding

$$\frac{\partial \sigma_{\perp}}{\partial \gamma} = \frac{1}{\gamma \sigma_{\perp}} \left[L'(\gamma) - \frac{L(\gamma)}{\gamma} \right]$$

$$\frac{\partial \sigma_{\parallel}}{\partial \gamma} = \frac{-1}{\sigma_{\parallel}} \left[L(\gamma) L'(\gamma) + \sigma_{\perp} \frac{\partial \sigma_{\perp}}{\partial \gamma} \right]$$

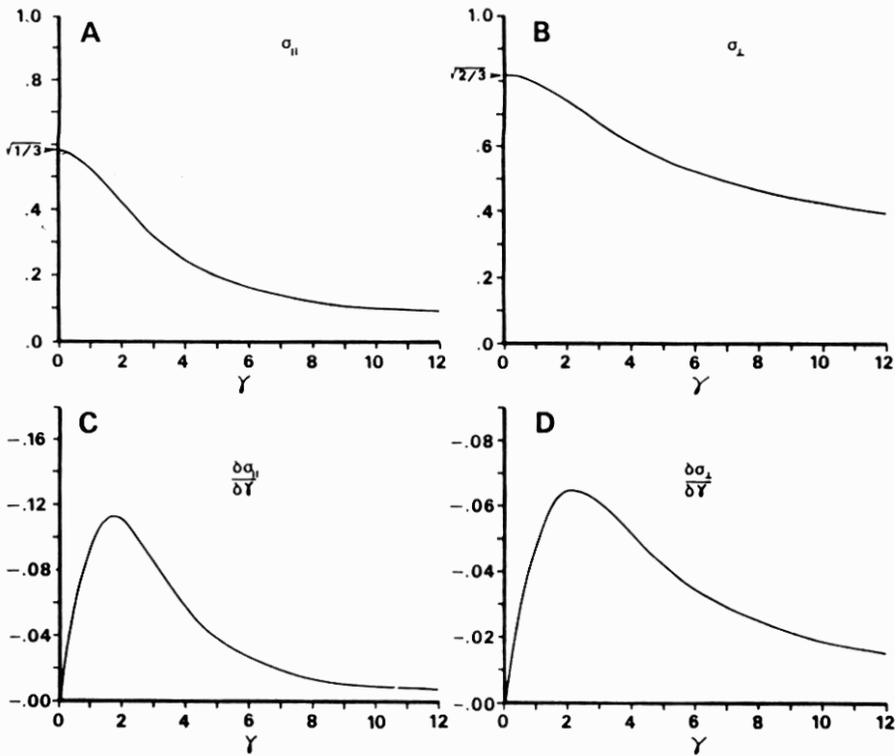


Figure 3. Variance of motion components of the Langevin function, and the optimum moment for an intensity receptor. A and B show the parallel and perpendicular components from equilibrium calculated from Eqs. (1) and (2). The optimum moment for these receptors will be where these functions change the most with small fluctuations in γ . These derivatives, calculated from Eqs. (3) and (4), are shown in C and D and both clearly peak around $\gamma = 2$. Because Eq. (6) depends on σ/σ' , the optimum may be broadened somewhat and shifted to slightly larger γ .

These quantities are shown as a function of γ in Fig. 3. For very small organelle moments where γ is near zero, both perpendicular and parallel components of the thermally driven deviation (Fig. 3A,B) approach constant values of $(2/3)^{1/2}$ and $(1/3)^{1/2}$, respectively. Small fluctuations in γ therefore will not yield an appreciable change in the variance, and an array under this condition will not be very sensitive. A similar situation holds for big magnetite crystals where γ is large and the thermal deviations asymptotically approach zero. As can be seen in Fig. 3C and D, the best organelle moment for both cases is near $\gamma = 2$, which is several times smaller than that predicted above for a compass organelle. Note that this analysis does not depend on how the transduction between the magnetite and the nervous system is achieved; any system which is subject to thermally driven variance should be similarly constrained.

The sensitivity of such an array can be estimated in a straightforward fashion. Let $f(\gamma)$ be a typical signal received from one of these organelles, and $\sigma(\gamma)$ be the associated standard deviation around it (σ^2 is the variance, and γ is as before). By integrating over N of these identical organelles, the detectable standard deviation $\sigma(\gamma)$ can be reduced by a factor of $N^{1/2}$. Each grain will also have a characteristic rotational time constant, τ , and by integrating over a time length I the resolution of an array similarly improves by a factor of $(I/\tau)^{1/2}$. The sensitivity for the entire array to small fluctuations in γ , given by $\Delta\gamma$, can now

be found by assuming, for example, that the organism will be able to detect 1 S.D. shift in the mean response, or:

$$\frac{\sigma(\gamma)}{[N(I/\tau)]^{1/2}} = f(\gamma + \Delta\gamma) - f(\gamma)$$

Dividing both sides by $\Delta\gamma$ and assuming it is small relative to γ leads to

$$\frac{\sigma(\gamma)}{\Delta\gamma[N(I/\tau)]^{1/2}} = \frac{f(\gamma + \Delta\gamma) - f(\gamma)}{\Delta\gamma} = f'(\gamma)$$

implying that

$$\Delta\gamma = \frac{\sigma(\gamma)}{f'(\gamma)[N(I/\tau)]^{1/2}}$$

As expected, Eq. (6) shows that the resolution of a magnetosensory system can be improved by increasing the number of organelles (N), the integration time (I/τ), or by maximizing the magnitude of $f'(\gamma)$ by selecting a suitable value for γ . Of course, the functions $f(\gamma)$ and $\sigma(\gamma)$ will be determined by the particular model under consideration. According to the intensity model outlined here, the function $f(\gamma)$ would reflect some component of thermally produced variance generated by motion of the magnetite grain such as those shown in Fig. 3A and B. The function of $f'(\gamma)$ would then correspond to either Fig. 3C or D. With a constant temperature, the sensitivity to the magnetic field, ΔB , would be given by $\Delta\gamma kT/\mu$ or $B\Delta\gamma/\gamma$. For example, an array sensitive to the perpendicular variance component averaging for about 3.5 sec ($\sim 100\tau$) over the 10^8 particles found in pigeons (Walcott et al., 1979) should be able to detect an intensity fluctuation of less than 1 nT, in good agreement with Yorke (1981) and Kirschvink and Gould (1981).

Finally, it should be noted that an intensity array of this sort would also be sensitive to small fluctuations in temperature. If the magnetic field strength is held constant, the resolvable temperature change ΔT would be $-T\Delta\gamma/\gamma$, where $\Delta\gamma$ is given by Eq. (6). For the pigeon system, this translates into a 0.006°C change across about 3.5 sec ($\sim 100\tau$). Small temperature fluctuations might therefore be confused with magnetic field changes, unless an independent correction system with separate thermoreceptors is used. It seems, however, that the thermal inertia in birds is adequate to substantially dampen external temperature shocks. For example, Torre-Bueno (1976) monitored by radio telemetry the core temperature of starlings flying in a wind tunnel. By abruptly changing the air temperature from an abnormally high 35°C to a more normal 16°C , he was able to produce a rate of core temperature change of about $1^\circ\text{C}/\text{min}$ ($0.05^\circ\text{C}/100\tau$). This change is slightly more than 8 times the theoretical sensitivity that the variance-based system would have in pigeons, but is comparable to the 10-nT level implied by their behavioral experiments. Birds rarely encounter such extreme conditions in the wild, however, and the typical steady-state shifts reported were much lower than this. Thermal correction of this sort is therefore not likely to pose much of a problem for larger vertebrates, particularly if the receptors are in thermal equilibrium with large volumes of internal fluid (blood, cerebrospinal fluid, etc.).

On the other hand, Martin and Lindauer (1977) observed temperature effects in the magnetic behavior of honeybees, although at the time they interpreted their results as supporting an unspecified paramagnetic transduction mechanism. The smaller volume of

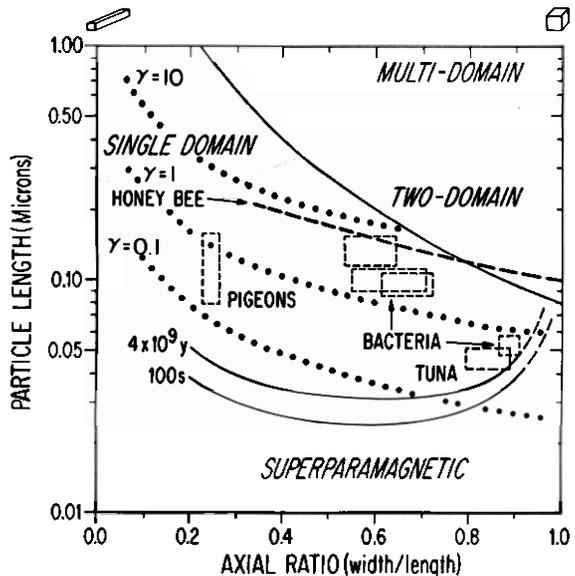
the bee implies that it would have less thermal inertia to ambient temperature fluctuations, and thermal effects might therefore be expected for them.

3. Discussion

The above analysis suggests that the total magnetic moment of an organelle could be an important factor in discriminating between the compass and intensity sensory functions of a magnetoreceptor. We can test this prediction by comparing the ratio $\mu B/kT$ with the size ranges of magnetic crystals detected in the pigeons, honeybees, fish, etc. on the Butler-Banerjee diagram (Fig. 4). Each point in Fig. 4 specifies the size and shape of a magnetite parallelepiped, and therefore its magnetic moment is fixed as well. Superimposed are three dotted curves which represent constant grain moments corresponding respectively to $\gamma = 0.1$, 1, and 10, assuming the grain is in the earth's magnetic field ($50 \mu\text{T}$ or 0.5 gauss) at body temperature (310°K). As shown in Fig. 4, the bulk of these crystals fall slightly below the $\gamma = 1$ curve in the pigeons and fish, indicating that they are in the main individually too small for compass organelles, and may be too small for the intensity organelles in the pigeons.

There are at least two ways by which particles of sufficient moment for compass receptors could occur. The crystals could be individually large enough to possess moments sufficient to act as compass receptors. Unless they are relatively few in number, below 10,000 or so, these crystals should be detected in the coercivity spectra. It is interesting to note, however, that Yorke (1979) and Kirschvink and Gould (1981) predict that up to 1000 single-domain magnetite crystals are sufficient to provide organisms with a very sensitive compass receptor, and that such a small number of crystals could not be detected by currently available magnetometers. Extraction of the crystals and analysis of their particle-size distribution are needed to test this point. On the other hand, if systems B, C, and D of Fig. 2 are used in conjunction with A or as part of the map, more of these compass forms might be present, although still not necessarily in sufficient numbers to be detectable.

Figure 4. Magnetic stability diagram for rectangular parallelepipeds of magnetite (after Butler and Banerjee, 1975, and Kirschvink and Gould, 1981). Solid lines represent the theoretically and experimentally determined boundaries between multidomain, single-domain, and superparamagnetic crystal sizes, with the approximate size and shape ranges for observed biogenic magnetites superimposed. The three dotted lines crossing the single-domain and superparamagnetic areas represent contours of equal grain volume and hence constant magnetic moment μ . Each curve is scaled such that the ratio $\mu B/kT$ ($= \gamma$) is respectively 0.1, 1, and 10 at body temperature in the geomagnetic field.



The second means by which the moment of receptor organelles can be increased is by linking the crystals into chains to sum their moments. Examination of the electron micrographs referred to by Walcott *et al.* (1979) suggests that the crystals are grouped in chains several particles in length, making their total magnetic moment compatible with that required for an intensity receptor. As yet there is no suggestion of longer chains such as those which have been reported from magnetotactic bacteria (Balkwill *et al.*, 1980), although the possibility that they may have been sheared to a smaller size during the extraction process cannot be ruled out. Like the larger crystals, chains should be detectable through measurements of intergrain interactions. Walker *et al.* (1984, and Chapter 20, this volume) demonstrate the presence of such effects in fish. Whether the chains are of sufficient moment to serve as compass receptors is unknown, but if they are, it would suggest that the compass sense might have higher resolution than behavioral experiments have demonstrated so far.

Some behavioral tests of the hypotheses are also possible. Kirschvink (1981) shows that the horizontal honeybee dance data of Martin and Lindauer (1977) and Gould *et al.* (1980) are compatible with a single-domain ferromagnetic organelle with γ near 6. With this receptor moment the accuracy of the bees' dance plotted against external field strength quantitatively resembles the Langevin function, being poor in weak fields and asymptotically improving in higher fields. The shape of the curve indicates the size of the moment involved; for the bee compass receptor this moment is about 9×10^{-16} A m².

A similar test should be possible for the intensity sense if and when a behavioral assay for measuring sensitivity to small-intensity fluctuations is developed [the circadian rhythm experiment of bees (Lindauer, 1977) is a possibility]. As discussed above, the best grain size for use in an intensity receptor is that at which the variance of the Boltzmann distribution changes the most with small variations in γ (see Fig. 3). With fields in the normal geomagnetic range, the moment of the receptor is optimal when $\gamma = 2$. Outside this range, this does not hold and sensitivity should decline. Tests for threshold sensitivity to small-intensity changes over a range of external field values should therefore resemble the optimized moment plot ($\partial\theta/\partial\gamma$ vs. γ) and so enable γ to be estimated.

As noted by Nesson and Lowenstam (this volume), biomineralization of magnetite occurs within the confines of an organic matrix which appears to control the size and shape of the crystals. Within a given organism like bacteria, chitons, or tuna, the magnetite crystals are all very similar in size and shape. Individually, the crystals do not have sufficient moment to orient the bacterial cells, but their alignment in chains gives them sufficient net moment to enable them to cause the bacteria to take up appropriate orientation (Frankel and Blakemore, 1980). On the basis of this observation, we could predict that the moment required, and hence the length of the magnetite crystal chain, is dependent on cell size. Larger cells should therefore have longer chains of magnetite crystals. In the case of the unicellular magnetotactic organisms, the length of the chain of magnetite crystals has been determined by natural selection for sufficient net magnetic moment to bring about the orientation of the cells.

Like the bacteria, the crystals of magnetite in metazoans have been found or inferred to be similar in size and shape within species. The responses to magnetic fields by animals fall into compass and map categories that can be easily explained by the magnetite-based magnetoreception hypothesis. A corollary of this hypothesis is that there are separate, optimum receptor moments for the two receptor types predicted here. These moments can be produced by different sized crystals or the arrangement of similar sized crystals into chains of different lengths. By arguments similar to those for the bacteria and algae, we predict that the magnetoreceptors of metazoans will have been subject to selection for optimum receptor moments for compass and map receptors and that size and shape of the crystals will be under close genetic control. We would therefore expect to see convergence on receptors of similar magnetic moments even though the magnetite crystals within the

receptors will be of different sizes and chain lengths in different species. We anticipate that this will be a productive area for future research.

4. Summary

A variety of behavioral experiments suggest that many organisms are able to sense the geomagnetic field. Many of these same organisms are also known to precipitate biochemically the mineral magnetite, which is a suitable material for transducing the geomagnetic field to the nervous system. These behavioral experiments suggest that there are at least two separate forms of magnetoreception, one which resolves the axial field direction or maximum dip angle and one which monitors extremely small fluctuations in geomagnetic intensity. An extension of the thermally driven variance hypothesis of magnetic intensity reception suggests that the permanent magnetic moments for organelles of each type may differ in size by factors of 3 or more, and leads to a variety of testable predictions for magnetite-based magnetoreceptors.

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