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The magnetic and electric fields induced by superparamagnetic magnetite in honeybees

Magnetoperception: an associative learning?

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Abstract. Hairs on the abdomen of honeybees contain dendrites and a rod and ring structure composed of black particles, presumed to be superparamagnetic (SPM) magnetite. The rod and ring were divided into compartments and each compartment approximated by a dipole. The magnetic fields were calculated at a point *P* at various locations for a change of the external geomagnetic field from zero to 0.5 G in 0.1 s. The magnetite amplifies the external field at the rod/ring–dendrite interface. The induced electric field and potential difference for a small circular area are in the order of 10^{-7} V/m and 10^{-13} V respectively. Mechanisms are proposed for amplifying the electric fields in the dendrite and in an integrating nerve fibre. A hypothesis is developed for associative learning of visual and magnetic stimuli. If magnetic and visual inputs are associated in the ganglion and in the brain, very small changes of either magnetic or visual inputs could be perceived. A bee could sequentially follow the images associated with magnetic gradients on a cloudy day and find the food source.

1 Introduction

It has been known for several years that many animals, perhaps including humans, can perceive intensity gradients in the geomagnetic field (for reviews see Kirschvink 1989; Kirschvink et al. 1992). The animals most studied with respect to magnetic sensitivity are bees. The sensitivity seems to be linked to magnetite crystals present in two dimensions: single domain (SD, permanent magnets) and superparamagnetic (SPM). Without an external magnetic field the magnetization of SPM magnetite is zero, in an external field it is larger than that of paramagnetic material. SD crystals are believed to determine a compass sense, SPM crystals a *learned* navigational map sense of magnetic intensity gradients (Gould 1985) (i.e. learning the recognition of magnetic gradients in their environment). Nothing is known about the transduction process for either of the magnetite structures. We suggest that SPM magnetite is involved in gradient detection by amplifying *locally* changes of the external magnetic field.

Responses of neurons in the second abdominal ganglion of bees have been described (Schiff 1991). This ganglion underlies a line of short, black hairs on the dorsal abdomen (Fig. 1a). In that part of the dorsal

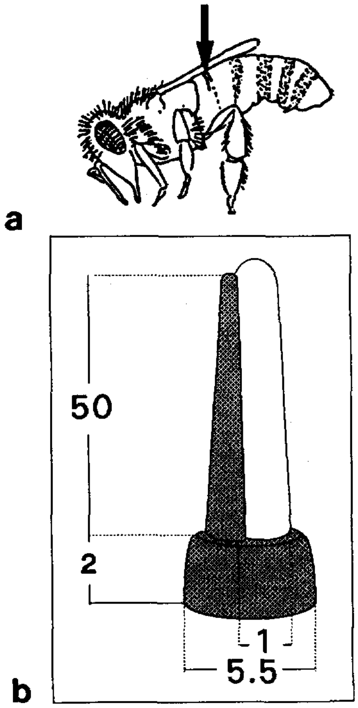

Fig. 1a,b. The *arrow* indicates the position of the black hairs containing electron-dense material. This is also the region where magnetic material had been localized and where little wires glued to the bee destroy magnetic field perception. Neuron responses were recorded in the ganglion of this segment. **b** Diagram of one hair and its dimensions in μm. The shaded areas are the two structures presumably composed of SPM magnetite

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This paper is dedicated to the memory of the late Prof. Dr. W. Reichardt, an outstanding scientist and personality, who will be greatly missed by all who knew him and his work abdomen magnetite has been localized by SQUID (super quantum interference device) measurements of remanence and identified on the basis of its Curie temperature (Gould et al. 1978; Walcott et al. 1979) as well as by behavioural experiments (Walker and Bitterman 1989a). In the hairs black particles which had about the dimensions of SPM particles were observed in transmission electron microscopy (TEM) (Schiff 1991)[1]. Assuming the particles to be SPM magnetite a hypothesis was proposed for inductive processing in the transduction of geomagnetic information.

In this paper we calculate the increase of the magnetic field provoked by the SPM magnetite as a function of particle sizes, distance from the magnetite structures and the directions of the external magnetic field. We then calculate the induced electric fields and potential differences. The resulting numerical values are indicative of the order of magnitude of the magnetic induction and of the electric fields and potentials induced by the magnetite. Further, we wanted to study how far from the magnetite magnetic and electric fields would extend and in which way they would decay. While the magnetic field at a point P near the magnetite is greatly increased, the resulting electric fields are very small due to the small area we considered for the magnetic flux. Therefore, we proceed to indicate the processes amplifying the electric fields by integrative nervous processing. We propose a model for associative learning and the development of specific activation patterns in a neuron population. This model is similar to a combination of the model for learning correlations between simultaneous inputs in adjacent synaptic patches (Alkon et al. 1990) and the EEG recordings showing the activity of neuron ensembles in the vertebrate olfactory system (Freeman 1991). The model thus derived would explain some of the mysteries in the electrophysiological recordings from single neurons as well as in experiments involving training of bees (Kirschvink et al. 1992). We consider only SPM magnetite, which is assumed to be responsible for the map sense of bees, disregarding SD magnetite, which is presumably linked to the compass sense.

2 Materials and methods

2.1 The structures

A line of black hairs on the anterodorsal abdomen of bees contains two agglomerates of black particles which we assume to be SPM crystals (Schiff 1991). Each hair contains a dendrite and a rod of particles resting on the dendritic membrane at the posterior side of the hair. At the base of the hair the dendrite is tightly surrounded by a ring of the same particles. Figure 1b shows the arrangement and dimensions of these structures.

2.2 Neuronal responses

Single neurons in the abdominal ganglion underlying the hairs respond to about 30% changes in the intensity of the magnetic induction by increase and/or decrease of the spontaneous firing frequency. Such intensity modulation simulates the motion of a freely flying bee passing through field gradients of magnetic anomalies. The best responses were observed for sinusoidal variations of intensity at frequencies between 0.01 and 1 Hz. Firing frequency increased especially at the flex points, but increases were observed also for the maxima and minima of the sinusoidal modulation. Responses to step function changes of the magnetic induction were less clear. An initial decrease was usually followed by an increase in frequency and successive oscillations.

2.3 The calculations

SPM magnetite crystals are tiny dipoles with dimensions between 10 and 30 nm. In a magnetic field the magnetic moments of these crystals align along the field lines. If the magnetic field is strong all crystals are aligned. In a low-intensity field thermal motion will disalign a large proportion of the dipoles. We calculate the magnetic moment μ of the magnetite particles from $\mu = M_s \cdot \text{vol}$ where M_s is 480 electromagnetic units (emu)/cm^3, the saturation magnetization of the SPM magnetite, and vol the volume of the spherical particles with different diameters.

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[1] An anonymous reviewer has cited (apparently unpublished) TEM investigations which have failed to replicate the results on the magnetite content in the hairs of the bees and affirms that probably most of the iron is ferrihydrite, the iron core of the protein ferritin. Ferrihydrite is presumably the precursor of magnetite after a reduction process. Ferritin is well known as the molecule transporting iron in organisms. The presence of ferrihydrite, even in large amounts, would be expected in the vicinity of magnetite. Ferrihydrite is magnetizable and aligns in a magnetic field but has no remanence. Whether the iron material is all magnetite or a mixture of magnetite and ferrihydrite the effects might be rather similar. From the large quantities of hydrous iron oxide in the bee abdomen only 0.33% of the total iron in the form of magnetite would be enough to account for the magnetic moments in bees (Kuterbach et al. 1982). Nesson and Kirschvink (1992) found 10–20 ng of magnetite (SD and SPM together) per bee. If 10^8 SPM magnetite granules with diameters of 10 nm were present in the bee, and if all of these were located in 100 hairs, this would constitute 10–20% of the total magnetite content, of which 0.1–0.2% would be in each hair. It has even been suggested (Kirschvink and Gould 1981) that if magnetite connected to extracellular fluid were oxidized on one side (ferrihydrite) and reduced on the other (magnetite) this would imply electron flow and consequently electrical currents. The diffraction patterns of ferrihydrite and magnetite would be superimposed (Nesson and Loewenstam 1985) and the large amount of ferrihydrite might overshadow the magnetite pattern. Two other considerations can be made in favour of the presence of magnetite in the hairs: Firstly, during preparation for TEM the small crystals may have been washed out, and secondly the iron structures may be present only at certain ages of the bees. When the bees undergo metamorphosis, iron would have to be transported by ferritin and deposited in the hairs. After that it would still have to be reduced to magnetite. Bees sectioned in May and August may have quite different proportions of magnetite and ferrihydrite in that region of the abdomen. Nesson and Kirschvink (1992) have extracted SPM magnetite from the whole homogenized bee abdomen. Homogenization and magnetic concentration of magnetite (both SD and SPM together) would destroy any existing structures of magnetite and could possibly result in conglomerates of magnetite in differently shaped structures. As described by Schiff (1991) there are many different types of crystals and agglomerates of crystals below the hairs in the bee abdomen.

The mean alignment or the fraction of the total magnetization that will be aligned by an external magnetic field of strength H at a given temperature T (in degrees Kelvin) is given by the Langevin equation:

$$M/M_0 = \coth(\mu/kT) - kT/\mu = L(\mu H/kT)\,,$$

where M is the total magnetic moment per unit volume, M_0 is the maximal possible magnetic moment for the sample, **H** the external magnetic field aligning the particles, kT the kinetic energy disaligning the particle moments (with k the Boltzman constant) and μ the magnetic moment of the single particles each contributing $(\mu \cdot \cos\theta)$ to the magnetization. The ratio M/M_0 indicates the degree of alignment in the sample, i.e. the number of magnetic moments aligned within an angle between θ and $\theta + d\theta$. θ is the angle between the external field and the dipole moments.

The total magnetic moment **U** for each hair is a function of the number of particles n and their magnetic moments μ and, in an external magnetic field, is given by:

$$U = n \cdot \mu \cdot L(\mu H/kT)\,.$$

The magnetic field in gauss at a point P at distance d from a dipole with magnetic moment μ was calculated from:

$$H_r = (2 \cdot \mu \cdot d \cdot \cos\theta/d^2 - r^2)^2 \qquad \text{(radial component)}$$

$$H\theta = (\mu \cdot \sin\theta/d^2 + r^2)^{3/2} \qquad \text{(angular component)}$$

where θ is the angle between the dipole axis and a line of length d connecting the dipole centre to the point P and r is half the length of the dipole. The total magnetic field strength resulting in P is given by the sum of the two components:

$$H = (H_\mathrm{r}^2 + H_\theta^2)^{1/2}$$

plus the external magnetic field which induced the dipole fields. **H** has a direction angle α relative to the line between the dipole and the point: $\alpha = \arctan H_\theta/H_\mathrm{r}$. Each dipole contributes $(\mu \cdot \cos\alpha)$ to the magnetic field in P.

The induced field E was derived from the electromotive force (emf) V which is (in **MKS**):

$$V = -\mathrm{d}\Phi/\mathrm{d}t = \int_\mathrm{L} \mathbf{E} \cdot \mathbf{dl} = \int_\mathrm{L} E \cdot \cos\theta\,\mathrm{d}l \cong -\Delta\Phi/\Delta t\,,$$

where Φ is the magnetic flux through a surface S delimited by the closed integration path L:

$$\Phi = \int \mathbf{B}\,\mathbf{ds} = \int_\mathrm{S} B \cdot \cos\theta\,\mathrm{d}s = B \cdot S$$

($\mathbf{B} = \mu_0 \cdot \mu_\mathrm{r} \cdot \mathbf{H}$ is the magnetic induction. μ_r, the magnetic permeability for magnetite is about one, thus: $\mathbf{B} = \mu_0 \cdot \mathbf{H}$, μ_0 = magnetic permeability in vacuum.)

$$V = -\mathrm{d}\Phi/\mathrm{d}t = \int_\mathrm{L} E \cdot \cos\theta\,\mathrm{d}l = -d\Big(\int_\mathrm{S} B \cdot \cos\theta\,\mathrm{d}s\Big)/\mathrm{d}t\,,$$

where θ is the angle between **E** and **dl** and α between **B** and the normal to **ds**. For a closed circular path of radius r:

$$V = -\mathrm{d}\Phi/\mathrm{d}t = 2 \cdot \pi \cdot rE = -\pi \cdot r^2 \cdot \mathrm{d}B/\mathrm{d}t \qquad \text{and}$$

$$E = -(1/2) \cdot r \cdot (\mathrm{d}B/\mathrm{d}t) \cong -r \cdot \Delta B/\Delta t \qquad \text{(in V/m)}\,.$$

The electric potential difference was calculated in approximation from $(\Delta B/\Delta t) \cdot r^2$ in volts.

3 Results

The total number of SPM particles has been estimated to be between 10^6 and 10^8 (Gould et al. 1978; Kirschvink and Gould 1981). Taking the larger value and about 100 hairs, i.e. receptor organs, each hair would contain 10^6 particles, of which about 60% would belong to the ring and 40% to the rod. The distances between the centres of the spherical SPM particles would be 28 nm. A 10 nm particle has a volume of $4.2 \cdot 10^{-18}$ cm^3. We assume a constant temperature of 20°C and the magnetic field of the earth to be 0.5 G. The values for $\mu H/kT$ and $\mathrm{L}(\mu H/kT)$ are 0.0243 and 0.0081 respectively. Table 1 and Fig. 2a show the values for the magnetic moments for magnetite particles with different dimensions and Fig. 2b shows the total magnetic moment as a function of the external field and the number of particles. The total magnetic moment of each hair is about 10^{-11} emu. According to the data retrieved from the waggle dances of the bees, the magnetic to thermal ratio for the whole bee (not specifying SD or SPM magnetite) is estimated to be about 6, which yields values of $5 \cdot 10^{-13}$ emu for the average magnetic receptor (Kirschvink et al. 1992). From the total magnetic moment we assign $0.98 \cdot 10^{-11}$ emu to the ring and $0.65 \cdot 10^{-11}$ emu to the rod. We then divide the rod in $n = 30$ compartments, divide the total magnetic moment for the rod by n and approximate the particles contained in each compartment to a dipole with magnetic moment μ/n (Fig. 3a). The ring was subdivided first into four equal quarters. Each quarter was further divided into $n = 10$ compartments, each represented by a dipole (Fig. 5a). For the ring, the moments assigned to the 10 compartments in a quarter correspond to the volume of each compartment. The external field was changed from zero to 0.5 G in 0.1 s.

3.1 The magnetic field of the rod

This magnetic field was calculated at a point P for three cases: (1) The external magnetic field is horizontal with

Table 1. SPM magnetite particles of different sizes: values for the magnetic moment μ in an external magnetic field of 0.5 G, the ratio of magnetic to thermal energy, the numerical values for the Langevin function and the total magnetic moment of 10^6 granules

	Radius (nm)		
	7.5	10.0	12.5
μ granule	$8.48 \cdot 10^{-16}$	$2.01 \cdot 10^{-15}$	$3.93 \cdot 10^{-15}$
$\mu \cdot H/k \cdot T$	0.0102	0.0243	0.0474
$L(\mu \cdot H/k \cdot T)$	0.0034	0.0081	0.0158
μ total	$2.9 \cdot 10^{-12}$	$1.63 \cdot 10^{-11}$	$6.21 \cdot 10^{-11}$

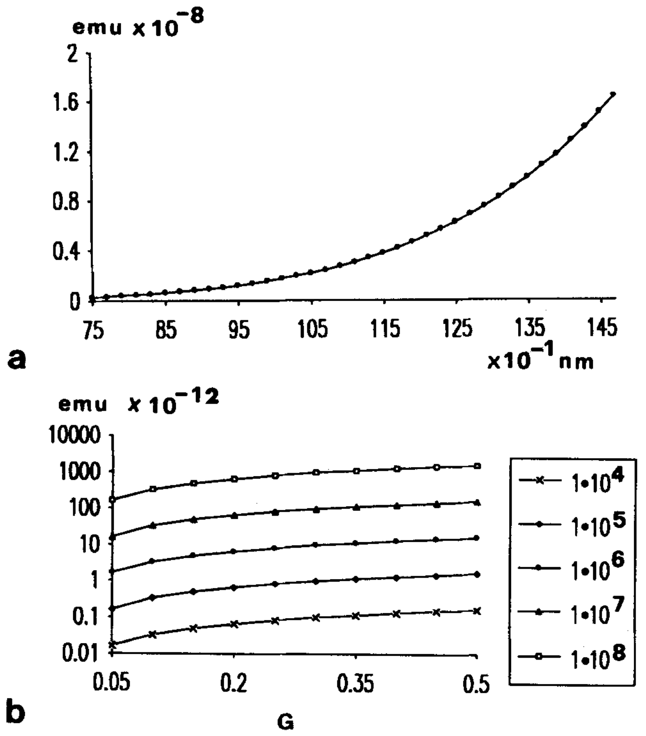

Fig. 2a,b. The total magnetic moment increases with the diameter of the particles in the range between 10 and 20 nm. **b** Maximal magnetic moment as a function of the magnetic induction of the external field given in gauss and of the number of particles immersed in a non-magnetic material. The scale is logarithmic

the dipoles directed from the magnetite towards the dendrite (along the y-axis in Fig. 3a). P is also along the y-axis. (2) The external field and dipoles are horizontal but parallel to the x-axis and P is on the y-axis. (3) The external field is vertical and the rod is magnetized vertically (along the z-axis in Fig. 3a). For these cases we calculate the magnetic field at a point P at various distances from the dipoles using the equations given above. The length of the rod is about 50 µm and its diameter 1.8 µm. The hemidistance of each dipole r was thus taken to be 0.9 µm and the point P was located at 25 µm, i.e. half the length of the rod. Each compartment or dipole contributes a component to the magnetic field in P but, obviously, the dipole aligned with P contributes most (Fig. 4a). Figure 3a, b shows for three particle sizes the magnetic fields in gauss as a function of the distance of the point P from the dipoles. Near to the rod at distances of 10–20 nm, the thickness of the nervous membrane, the field can be very intense: for 10 nm particles it is $1.7 \cdot 10^3$ G and $1.10 \cdot 10^3$ G for the two cases of an horizontal external field, but only 6.5 G for a vertical field. The magnetic field decays rapidly with the distance from the rod and at 0.1 µm distance the field intensity is almost zero. The magnetic field across the nervous membrane, i.e. near to the rod, increases considerably with particle size. For 12.5 nm particles the near magnetic field reaches values in the order of 10^4 and 10^5 G. Thus, if a horizontal external field is applied, the magnetite amplifies it and

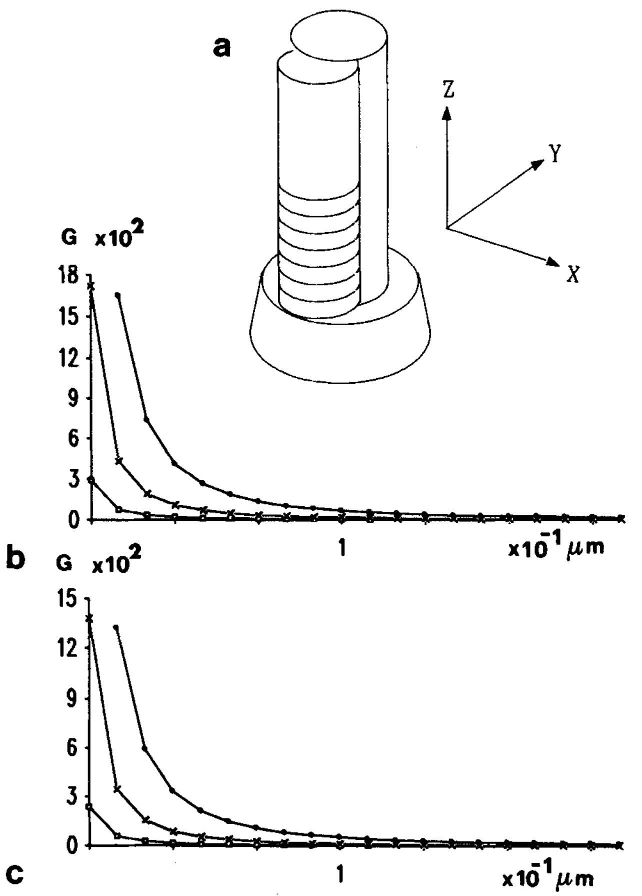

Fig. 3a–c. The magnetic fields in gauss at a point P at the distances from the centre of the magnetite rod given on the abscissae. The external field **H** is assumed to change from zero to 0.5 G in 0.1 s. **a** Diagram of the dendrite and the magnetite rod with their long axis parallel to the z-axis. **b** The external field is horizontal and parallel to the y-axis. The magnetic induction was calculated at a point P located on the same axis. For particles $\geqslant$ 10 nm the magnetite provokes a strong magnetic field decaying rapidly with distance. **c** The external magnetic field and the directions of the dipoles are parallel to the x-axis. The magnetic field has been calculated at a point P on an axis parallel to the y-axis. The magnetic fields provoked by the compartmental dipoles are similar to those shown in **b**. If the external magnetic field **H** is vertical, parallel to the z-axis, the magnetic field produced by the rod at a point P at the centre of the dendrite is only 6.5 G (assuming $\mu = 0.65 \cdot 10^{-11}$ emu, $r = 1$ µm and $d = 0.2$ µm), —□— 12.5 nm; —×— 10.0 nm; —○— 7.5 nm

generates a strong gradient between the rod and the dendrite, whereas vertical fields have negligible effects.

3.2 The magnetic field of the ring

The external magnetic field is vertical, parallel to the length of the dendrite. Figure 5 shows the magnetic fields resulting from particle alignment, evaluating it parallel to the dendrite length (Fig. 5b, P on the z-axis in Fig. 5a) and perpendicular (Fig. 5c, P on the y-axis). In a horizontal magnetic field (x–y plane) the vectors **B** on opposite sides of the ring would have equal but opposite effects on the dendrite and would cancel each other (Fig. 5d). There would be a small enforcement of the rod magnetic field by the ring quarters aligned with the dipoles in the rod.

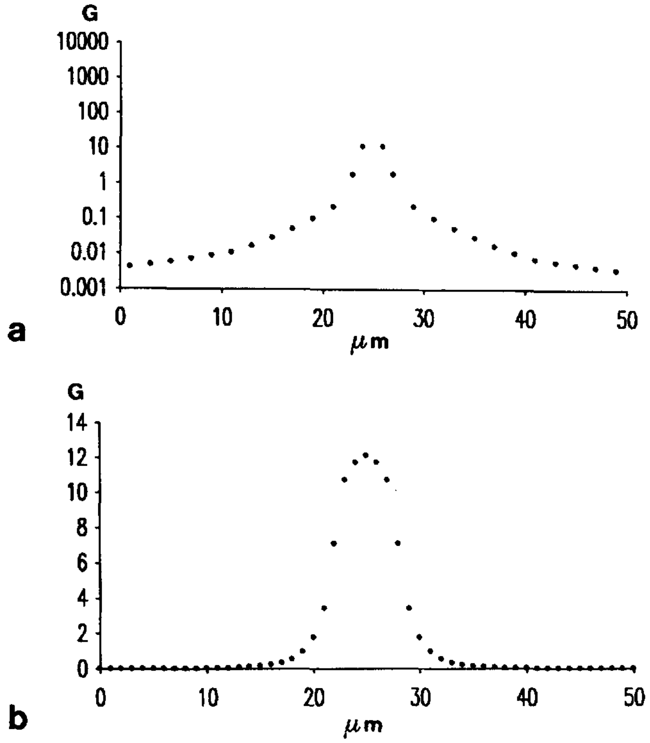

Fig. 4a,b. Contributions by the single compartments to the magnetic field at a point P on an axis parallel to the y-axis and at a position corresponding to the centre of the rod length: **a** for 30 compartmental dipoles; **b** for >1000 compartmental dipoles. Actually these magnetic fields are generated at each point along the rod-dendrite interface and the total magnetic field would be represented by a cumulative gaussian curve

3.3 The magnetic field considering more than 1000 compartments

The magnetic field at the point P calculated for $n = 1000$ to 3000 compartments (dividing the total magnetic moment by 1000 or more) is smaller by a factor of 10 with respect to that with $n = 30$. For the rod in a horizontal external field it is $1.5 \cdot 10^2$ G (instead of $1.7 \cdot 10^3$ G) and rapidly decays to $0.1 \cdot 10^2$ G (Fig. 4b). The central part of the contributions of the n dipoles at point P becomes smoother (Fig. 4b) than that for 30 dipoles. The maximum for one contribution is 12 G with a total maximum for all contributions of 151 G decaying to 0.03 G for the contributions 500 dipoles away from the centre. For the ring quarter with 1000 compartments (dipoles) in a vertical field, evaluated perpendicular to the external field (along the y-axis in Fig. 5a), the result is $1.8 \cdot 10^2$ instead of $1.4 \cdot 10^3$ G as for the 10-dipole approach.

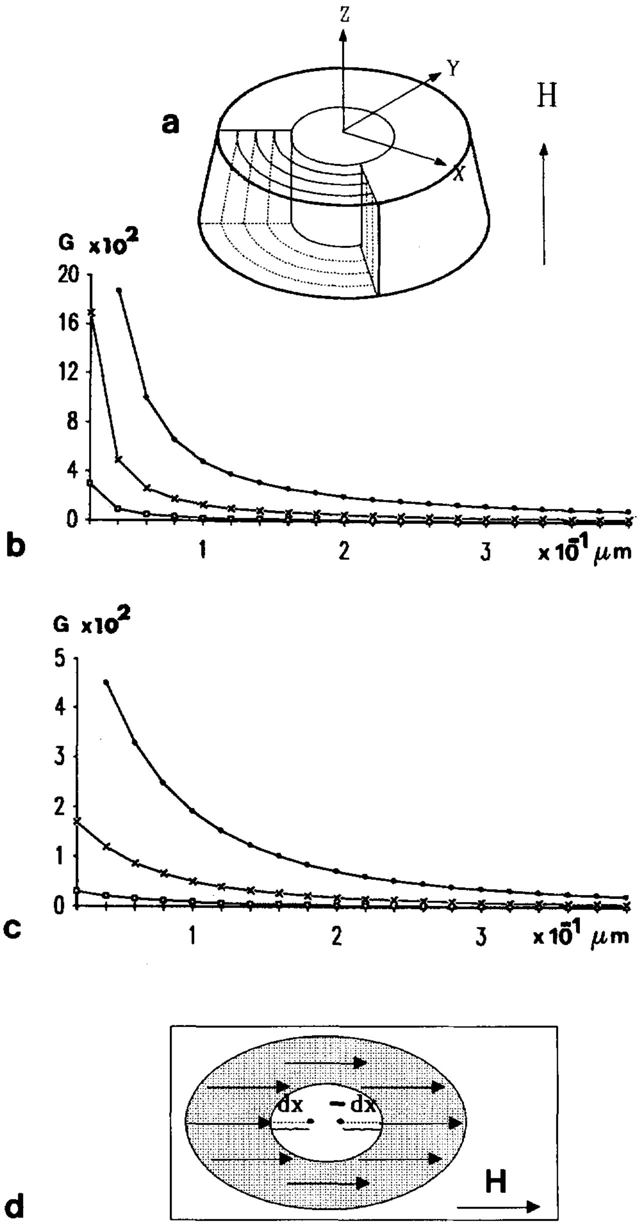

Fig. 5a–d. The magnetic field provoked by the ring. **a** The magnetic induction was calculated for a quarter of the ring with n compartments (dipoles). **b** The external field and the dipoles are vertical, parallel to the z-axis. Large values of the magnetic field decay rapidly with distance of the point P from the ring. P is located on the z-axis. **c** Considering the magnetic field at a point P on the y-axis and the dipoles aligned with the z-axis: the magnetic field starts with smaller values than in the other cases but decays less steeply. **d** A horizontal, external magnetic field would align the particles as shown by the *arrows*. The gradients dx through the dendritic membrane at the two opposite sides of the ring would be of equal size but opposite sign, and the effects on the dendrite would cancel each other

3.4 Transduction and dendrite depolarization

Since **B** decays quickly with distance from the magnetite rod we had to choose which value of **B** to use. Two cases were considered: using $\mathbf{B}(r)$, the value of **B** at distance r (radius of the integration path in the x–y plane) or using the mean, $\mathbf{B}_{\mathrm{med}}$, between the maximal value $\mathbf{B}_{\mathrm{lim}}$ and that of $\mathbf{B}(r)$ (Fig. 6a). The external field and the dipoles are aligned with the z-axis. In the first case (Fig. 6b) the electric field decreases from a maximum of $1.7 \cdot 10^{-8}$ V/m. In the second case (Fig. 6c) the electric field increases with distance from $1.8 \cdot 10^{-9}$ V/m to 10^{-7} V/m. The potential difference calculated from $\mathbf{B}_{\mathrm{med}}$ starts at values of 10^{-16} V (Fig. 7a) near the dendritic membrane and increases to 10^{-13} V at a distance of 0.5 μm from the rod. Using the value $\mathbf{B}(r)$, the electric field remains almost constant at about 10^{-16} V (Fig. 7b).

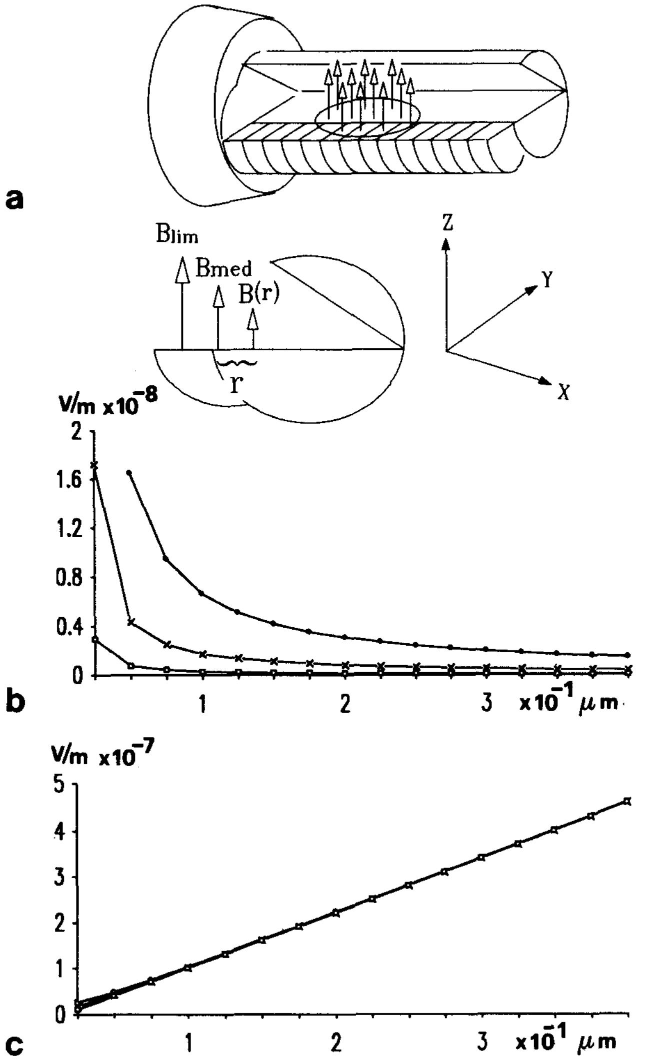

Fig. 6. **a** The electric fields and potentials are calculated for a small area with radius r in the x–y plane. The magnetic fields of the magnetite dipoles are parallel to the z-axis. $\mathbf{B}(r)$ is the value of $\mathbf{B}$ at distance r, $\mathbf{B}_{\mathrm{lim}}$ the maximal value and $\mathbf{B}_{\mathrm{med}}$ the mean value between $\mathbf{B}(r)$ and $\mathbf{B}_{\mathrm{lim}}$ used for calculating the electric fields and potentials. The external magnetic field is parallel to the z-axis. The electric field is calculated for a circular integration path of radius r in the x–y plane. In **b** the value $\mathbf{B}(r)$ is used to calculate the induced electric field. The induced electric field has maximal values of 10^{-8} V/m near the membrane and decays as quickly as the magnetic field due to the rapidly decreasing value of $\mathbf{B}(r)$. In **c** the mean, $\mathbf{B}_{\mathrm{med}}$, was calculated and used for determining the electric field which increases with the radius r, i.e. with the area considered. The curves for particles of different dimensions are almost identical

4 Discussion

4.1 The magnetite structures

When using classical physics it is assumed that the magnetic field decays with the cube of the distance d. Considering a rod and a ring of agglomerates of the small SPM magnetite spheres, the magnetite field may decay more slowly at distances smaller than the diameter of the structure, similar to the magnetic field generated by an action potential in a nerve fibre (Wikswo 1985). The curves of Figs. 3 and 5 would then have a somewhat less steep descent. It is important, though, that the magnetic field provoked by the magnetite should decay within short distances such that the effect, i.e. generation of electric fields, acts only on the dendrites and not on other nervous structures, for example the central nervous system. The rod would amplify horizontal gradients of magnetic induction, the ring vertical gradients. Horizontal gradients are associated with the forward flight of the bee, vertical gradients with the height above ground at which the bee is flying (assuming that the magnetic fields derive from the magnetic situation in or on the ground).

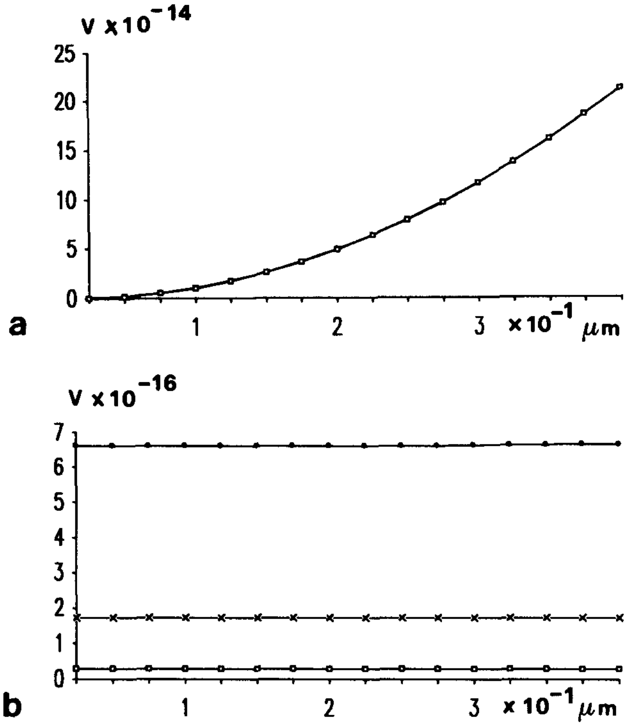

Fig. 7a,b. The same conditions as in Fig. 6. The potential difference between any two points on the integration path can be calculated. **a** With $\mathbf{B}_{\mathrm{med}}$ the potential difference increases with r identically for all particle sizes. **b** With $\mathbf{B}(r)$ there is almost no change with increasing r

4.2 The magnetite-dendrite interface

The values for the electric field and potential seem rather small. Several considerations may explain an action on the dendritic membrane even with such small potentials. We have calculated the fields for one point (magnetic) or a very small area (electric). It should be taken into account that a magnetic and consequently an electric field and potential are generated at each point along the magnetite-dendrite interface such that many curves such as those in Fig. 4 would be superimposed. The cumulative sum of all contributions along the dendrite would be a sort of flattened gaussian curve (Σ in Fig. 8a), larger than the simple sum of contributions. Thus, the potential should be integrated in space over that part of the dendritic membrane which is in close

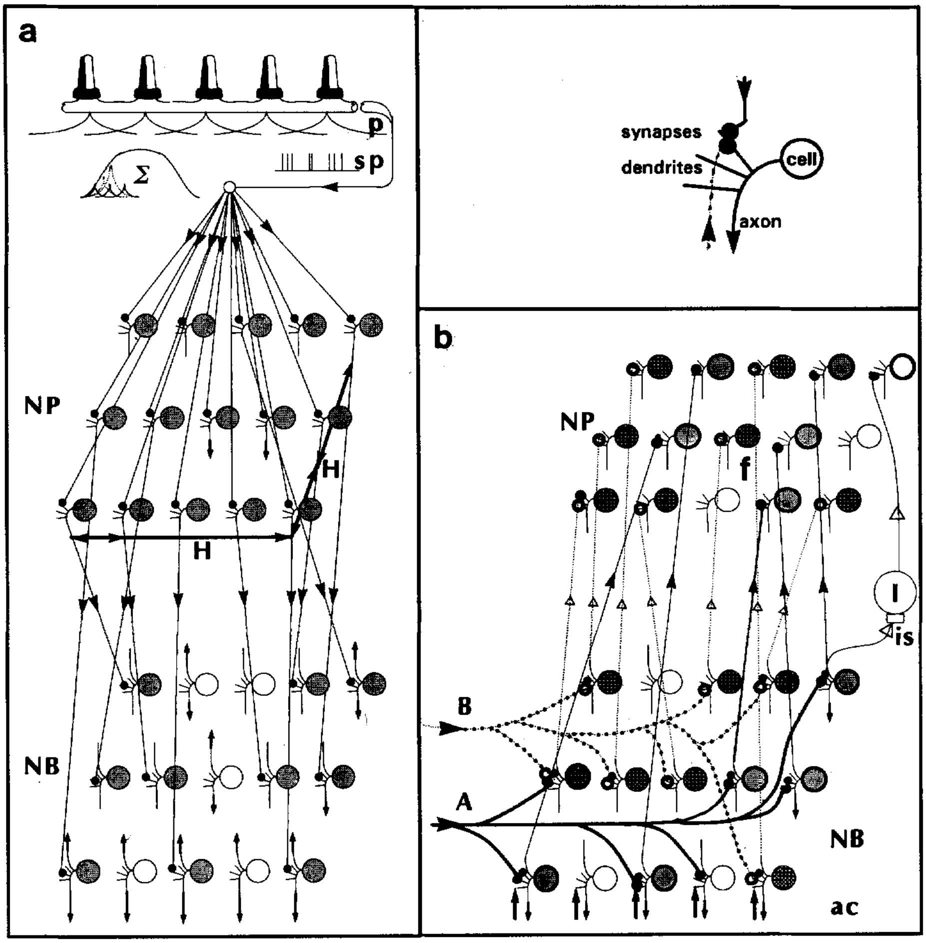

Fig. 8a, b. A hypothesis for associative learning in the bee. **a** A magnetic gradient is amplified by the magnetite. In the dendrites small electric potentials (*p*) are generated. Potentials are summed (Σ) in time and space in the integrating fibre and produce spike discharge patterns (*sp*). A neuron population (*NP*) in the abdominal ganglion receives simultaneous inputs from the fibre and sends signals to a neuron population (*NB*) in the brain. Shaded cells are those receiving magnetic inputs. Hebb synapses (*H*) between the neurons in the ganglion would further amplify and expand the activity of the neuron population in the ganglion. **b** The neurons in the brain which receive inputs from the magneto-sensory neurons in the ganglion also receive the visual inputs *A* or *B*. The visual inputs arrive at a particular configuration of neurons. This configuration of activated neurons might be determined by features in the visual environment. The synaptic patches (●) for the visual and the magnetic inputs are adjacent and would transmit signals simultaneously. The coincident inputs modify the synaptic membranes such that signal transmission is facilitated. Reafferences from the (more or less) activated neurons in the brain contact an ensemble of neurons (a subset of the population) in the ganglion. These neurons would then associate the visible image with the magnetic gradients. *Shaded cells with heavy circles* receive magnetic and visual inputs from *A* and constitute the associative neuron ensemble in the ganglion and in the brain. The neurons of the ensemble associating magnetic gradients with inputs from *B* are drawn with a different pattern. Note that some neurons may participate in associations with both *A* and *B*. Once the association was learned, a small magnetic *or* visual input alone could activate a certain configuration of neurons and provoke a specific spatio-temporal activity map. After learning, inputs might be retrieved also from the associative centres (*ac*) in the brain. Additional, spontaneously firing neurons (*I*), contacted by inhibitory synapses (*is*), would provide the possibility of anticorrelation

contact with the magnetite. The potential should be integrated also in time, as graded stimuli seem more effective for the neuron responses (and in behavioral tests, Leucht 1984) than a step function change of the magnetic intensity. Furthermore, prolonged electric stimulation needs less voltage (or current) than short stimuli.

4.3 Amplification in the dendrite

The voltage gradient through the magnetite and the high-resistance dendritic membrane will change due to the steep gradient of the magnetic field and the gradient of the electric field over the 10 nm membrane. This alone might be enough to provoke the opening of some ion channels which in turn provokes the opening of more channels. Once ionic channels open, a depolarization would be generated over large part of the dendritic membrane.

4.4 An integrating fibre

Let us assume that all dendrites in the hairs belong to the same fibre or have contacts to the same neuron. When the bee flies over a structure where the intensity of the magnetic induction varies (Fig. 9a), all dendrites will be exposed simultaneously to this magnetic, time varying intensity gradient. At the interface between the

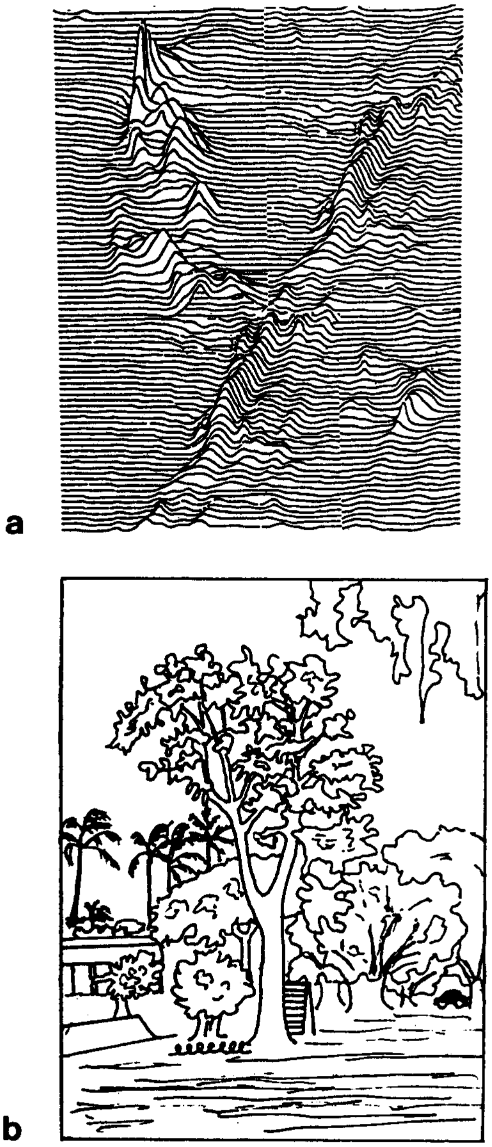

Fig. 9a,b. Magnetic and visible landscapes which might be associated in a neuron population

magnetite and part of the dendritic membrane the magnetite will almost instantly generate a gradient much higher than the external one. This generates small electric fields. Currents will flow through the magnetite and the extracellular fluid with low resistances as well as through the high-resistance dendritic membrane. A small graded depolarization of the dendrite decays with the time constant τ and the space constant λ. Space constants have a wide range, depending on the nerve tissue characteristics, but are usually in the range of millimetres. Thus, if all dendrites are connected to the same nerve fibre, small potentials will arrive simultaneously at many points along the fibre (p in Fig. 8a). These are graded potentials, but the decrement will be almost zero, because the length of the dendrite is about 100 times smaller than the space constant. If the external magnetic gradient is not a sharp edge or peak (i.e. step function gradient, an unnatural if not impossible situation for a flying bee) the dendrites will be exposed over some length of time to the magnetic gradient with continuously changing intensity (for example in a sinusoidal modulation). Time constants in crayfish visual neurons range from about 1–5 ms in nerve fibres to 500 ms for the synapses (Waldrop and Glantz 1985). The modulation $\Delta B/\Delta t$ will occur during several hundred milliseconds to seconds (for a speed of flight of the bee of about 6 m/s). Therefore, simultaneous adjacent inputs will sum spatially on the integrating fibre. Successive inputs will sum in the dendrites *and* in the integrating fibre. Contributions from all dendrites are summed in the integrating fibre. [Calculations for a similar integrating process have been described in Iacino et al. (1990); Di Stefano et al. (1990).] As long as the depolarization is above threshold, spikes (sp in **Fig. 8a)** will be generated.

In behavioural research it was observed that bees were unable to learn intensity modulations faster than 20 Hz (Walker and Bitterman 1989b). Kirschvink et al. (1992) succeeded in obtaining criterion performance (correct choices, i.e. 50% sugar solution paired with magnetic anomaly, in 6 choices in a row or 7 of 8 choices) in response to 60-Hz modulations of the magnetic field from seven of nine bees in a replication of the Walker and Bitterman two-choice experiments. In electrical recording from neurons in the abdominal ganglion underlying the line of hairs, the effects of sinusoidal variation of magnetic induction are already strongly reduced at one Hz (Schiff 1991). These data were obtained by calculating the *means* and the regression of all responses to 10–20 modulations of the magnetic field. In experiments on vertebrates and with different techniques, and stimulating with vertical instead of horizontal magnetic fields, magnetically influenced responses of neurons to 100-nT modulations have been recorded (Semm and Beason 1990) though means for longer time periods were not shown. In our experiments effects were observed mainly after some seconds or even minutes of exposure to a magnetic modulation. (Effects last for about 1–2 min then firing becomes erratic or oscillatory.) This seems to indicate an integration over time, which increases the firing rate at the maxima, minima and flex points of a sinusoidal stimulation as well as the delay of responses in a step-function stimulation. The superposition and cumulative effect of the magnetic and electric fields and of the graded potentials in the dendrite and in the fiber may be the amplification necessary for the neuronal responses to the 20–30% changes of the external magnetic induction.

4.5 Collateral effects

In a complex system such as the magnetite-dendrite system there are several interacting magnetic and electric fields generated by the magnetite and the dendritic potentials, these last influencing in turn the magnetic (and electric) fields in the magnetite. These will be in different directions enforcing or opposing the magnetic gradients due to the magnetite alone. When ionic channels open, current flows between the dendrite, the extra- and intracellular fluid and the magnetite. We would then have a Hall effect which would induce an electric field on its own and would change the magnetite-induced field, probably opposing it. Another phenomenon difficult to evaluate may be parasite currents (Foucault currents). These phenomena may explain the oscillations in spike frequencies and the only temporary response of the neurons.

4.6 Association and learning

Integrative effects can be observed in the ganglionic neurons for 20–30% intensity modulations of the magnetic field. But the whole animal can be taught to perceive modulations as small as 0.06% (Walker and Bitterman 1989c) of intensity changes. In bobolinks some neurons responded to 0.4% changes of the geomagnetic field (Semm and Beason 1990), and it was suggested that neural averaging could produce the high sensitivity. In that system the number of magnetically stimulated neurons as well as the amount of magnetic (SD and SPM not specified) is probably much larger than both of these in bees.

From research in the last few years it emerges that sensory systems act as cooperative ensembles (e.g. Burnod 1991; Gilbert and Wiesel 1991) or chaotic generators (Freeman 1990). Associative learning, shown in many instances, occurs in the synapses of the ensembles in a geometrical distribution which depends on the input pattern. If inputs from different origins arrive simultaneously in adjacent synapses the synaptic membranes are altered, incorporating short- and/or long-term memory. Each memorized input pattern provokes a specific activity pattern in a neuron population. We propose a process for acquisition of the extremely high sensitivity in bees and for learning a map sense which would also explain some of the still unresolved problems in bee behavior. The proposed model offers an easy way of checking whether the magnetic field perception in bees follows the above-mentioned neural processing. The processing would start in those neurons in the ganglion which receive inputs from the integrating fibre (**Fig. 8a**). The firing pattern in this fibre depends on the intensity, speed and direction of modulation of the magnetic field. We assume that the patterned output of spikes is distributed to a neuron population (NP) in the ganglion which receives simultaneous inputs. If there is a lateral interaction with Hebb-type synapses (H), the neural activation of the whole cell population will increase and expand and successive inputs would be facilitated.

The activity of the neuron population may be transmitted to the brain, where another neuron population (NB) would be activated. These neurons also receive inputs from other sensory modalities (A, B), e.g. from vision, which may be associated with the magnetic inputs. When the bee flies over a certain magnetic gradient or anomaly on a clear day it simultaneously receives information on the position of the sun and the visible environment (Fig. 9). The visual inputs are not the same for all neurons but will activate certain configurations of neurons (Fig. 8b), each of which may respond to certain features in the visual environment. The magnetic field sensors may be a subset of the visual feature detector population. Then for each image, a certain configuration of neurons will receive visual and magnetic inputs simultaneously. On repetition, synaptic patches on these neurons may memorize the coincidence of such inputs (Alkon et al. 1990) from vision and from the magnetic sensors. Correlation could be associatively learned, such that with an overcast sky the magnetic input alone may be enough for determining the position of the sun or, vice versa, the visual input alone may be enough for orientation. Pigeons with mounted magnets (which compensate the external magnetic field) orient normally on sunny days (Gould 1985).

From the EEG measurements from the vertebrate olfactory system (Freeman 1991) it seems that there is a reafference from the brain to the ganglionic neurons after learning and association of inputs. For the bee this means that the neurons which have already associated different inputs or receive inputs from associative centres would then contact those ganglionic neurons which receive the inputs from the integrating fibre connected to the dendrites. The inputs from the brain contact only a certain configuration of neurons and do not activate all neurons (Fig. 8b). Neither are the neurons activated in the same measure. A new input from the magnetosensors would then be correlated to an image (or the position of the sun) and would excite a certain predisposed configuration of neurons. Thus, a specific ensemble of activated neurons in the ganglion as well as in the brain would represent each learned association, the single neuron being only a small component of the ensemble activity. Extremely small changes of inputs could now alter such a simultaneous and cooperative ensemble activity. The configuration of the patches in a neuron population determines the configuration of activity in the neuron population. Associative learning by simultaneous inputs to two nearby synaptic patches has the advantage of not involving the whole neuron. Therefore, the same neuron can participate in many configurations of active neuron ensembles in different associations. Adding one more neuron (*I*) for each correlative path adds the possibility of anticorrelation, i.e. interpretation of a missing input (no magnetic anomaly) as correlated to an image.

4.7 Unsolved problems in behaviour and the possible use of magnetoperception

Some of the unresolved questions in ethological research might be explained by our model. Behavioural responses in most animals tested were observed only within a certain range of intensities and frequencies (bees: Martin and Lindauer 1977; Walker and Bitterman 1989b; birds: Keeton et al. 1974; tuna: Walker 1984; rays: Kalmijn 1974). Misdirection of dancing bees is observed for variations of 0.1–1 γ/min. This gives an indication of the sensitivity, the saturation values and the frequency ranges of the system. Thresholds are very low, but the bees seem to be sick or disturbed (Towne and Gould 1985) at values much larger than the earth's magnetic field (>5 G for bees). At high intensities the magnetite particles would be oriented and the system would be saturated. High-frequency changes (> 1 Hz for neuron responses, Schiff 1991; > 20 Hz for the whole animal, Walker and Bitterman 1989b) may be followed by the SPM magnetite but not by the nervous system and do not occur in the natural environment, where frequencies are below 10 Hz.

The misdirection in the waggle dance communication has been studied extensively (Martin and Lindauer 1977). Without a magnetic field in the hive there is no misdirection (Towne and Gould 1985). Thus, it is possible that magnetic gradients outside the hive could be communicated with respect to the magnetic situation inside the hive. Magnetic gradients or anomalies on the route to a food source would be associated with the position of the sun and/or the images encountered during flight. Therefore, inside the dark hive, both the visual and the magnetic environment might be communicated and might reinforce each other for flight correction. A bee might be able to find the food source on a cloudy day by sequentially following the magnetic gradients and their associated images. Misdirection then would be necessary for communicating the flight direction as well as the sequence of images associated with the corresponding magnetic gradients relative to the hive situation.

There is no misdirection if the waggle dance direction coincides with the inclination of the geomagnetic field at the hive, i.e. at "zero-points" of inclination (Martin and Lindauer 1977). Inclination is therefore taken to be the reference for the magneto-sensors. But if a light stimulus is given at the zero-points of geomagnetic inclination, misdirection reappears (Leucht 1984). When the geomagnetic field is compensated, not only the magnetically induced misdirection but also the light-induced misdirection disappears. These experiments show that there actually is a strong correlation between the magnetically and the visually induced misdirection, i.e. that magnetic and visual inputs are strongly linked. The light-induced misdirection is provoked only by green and blue photoreceptors, the colours predominating in images seen by the flying bee, which lacks red receptors.

Stationary bees could not be trained to perceive magnetic anomalies (Walker et al. 1989), and flying bees do not "learn properly" (Kirschvink et al. 1992), i.e. do not *associate* the magnetic anomaly with stronger or weaker sucrose concentrations. A stationary bee cannot fly through a magnetic gradient and cannot associate it with a visual cue. If the association is with vision, then the bees would first require training with a visual cue and should thereafter be able to distinguish the right sugar solution on the basis of magnetic anomalies alone. The configuration of the activated neuron ensemble would be specific for particular magnetic-visual situations. Recruitment of other bees may be possible with magnetic field cues alone provided the bees are well trained. We would expect that in appropriately trained bees a nerve cell would respond to very small changes of the magnetic field without other inputs inasmuch as each change would excite the whole neuron ensemble which has learned a correlation or anticorrelation.

Similar systems might be possible in other animals if SPM magnetite were present near (i.e. resting on) nerve membranes of selected localized neuron populations. If biogenic SPM magnetite amplifies gradients in the geomagnetic field, it may influence the activity of a small, localized neuron population onto which it has been deposited near to dendrites or nerve membranes. According to our model the development of magnetic sensitivity would require a learning process.

Hall sensors, used in technical applications for magnetic sensing in control systems, e.g. switches and vicinity detectors, could possibly be improved by applying neural networks similar to the one which we propose for bees.

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