Magnetic orientation in social insects

Toshio Ushiroguchi

Tuesday December 7th 2004

Table of contents

Abstract

Social insects rely on a variety of compasses to orient themselves in space. However, none of these compasses is as controversial as the magnetic compass, of which we have a relatively poor understanding. Studies have shown that social insects such as termites and honeybees rely on the magnetic fields of the Earth for orientation during nest building. This enables the insects to agree on an orientation of the inner cells of their nests. Termite and honeybee studies found shifting orientation of cells under deviated magnetic fields. When outside of their nests, termites, ants and honeybees also rely on magnetic cues. Termites use these when there is overlap or confusion in their pheromone trails since light cues are unavailable to the blind insects. Studies on ants were done in a darkened lab, in the field with blocked out sunlight, or in the field in overcast skies. In an anomalous field and in the absence of light, the insects shifted their orientation accordingly. Bees will use magnetic cues as a backup compass, or will use it in conjunction with other cues in order to gain maximum awareness of their surroundings. Magnetic field use is possible due to ferromagnetic magnetoreception, whereby the insect uses the magnetic particle alignment in its body to orient itself in a magnetic field. Earlier studies have shown that honeybees have higher magnetic resonance in their abdomen, and it was found that 10% of the granules in the fat body were magnetite, which is an ideal magnetoreceptor. However, more recent studies have shown that this may in fact be ferritin and its derivatives which would be unsuitable for magnetoreception. This led researchers to believe that magnetoreception was occurring in another region of the abdomen. Migratory ant (*Pachycondyla marginata*) magnetoreception is a little different in that studies have shown that most of the resonance was occurring in the head region. They were able to find that the antenna was the part of the head that had the highest magnetization, at 42% compared to the rest of the body. However, it is still unclear how this magnetoreception fits into the sensory system, and even the receptor which is believed to be magnetite, has not been confirmed. Future research should focus on physiological studies with electrodes in magnetic fields.

Introduction

Orientation is essential for proper navigation and homing, and enables an insect to control its behaviour in space. Insects use a variety of compasses to be able to achieve this aim. The honeybee relies heavily on the sun compass and learns the movement and direction of the sun with an internal clock. It then adjusts its path and angle of orientation while in flight, and can thereby figure out its direction based on where the sun is at a particular time of the day. When the sun is obscured by clouds but some blue sky is visible, insects that are aware of the sun’s polarization pattern will orient themselves once the polarized light hits the Dorsal Rim Area (DRA) of their eyes. Nocturnal insects such as moths will even track the movements of the moon and use it for orientation. However, this particular compass is rarely used since the moon is not always visible at all stages of its cycle. There is however a relatively poorly understood compass which exists, and it is the subject of much controversy. Despite its frequent use as a technical device by sailors and travelers, the magnetic compass is poorly accepted as an animal compass for several reasons. Firstly, humans are not consciously aware of magnetic fields. It is also hard to define and control magnetic conditions, and our poor understanding of this phenomenon has led us to poorly plan out experiments and results. Also, traditionally, the study of magnetic effects on organisms has been frowned upon by the scientific community and dismissed as a lesser science since the Mesmerists of the late 18th century (Kirschvink et al 2001). However, it is impossible to deny that magnetic fields are all around us and any organism that can potentially use these cues will be able to better cope with their environment, to forage and nest more easily, to save time and increase fitness. Though somewhat uncertain, it is believed that magnetic fields originated due to the Earth's fluid outer iron core (Wiltschko and Wiltschko 1995). This made the Earth a dipole with magnetic field lines radiating between the North and South magnetic poles. However, these field lines are not symmetrical like those of a simple bar magnet, since the magnetic content is not evenly distributed. Magnetic field lines at the poles either go straight up or straight down. They then curve around the Earth and go parallel to the Earth's surface at the magnetic Equator (Wiltschko and Wiltschko 1995; Fig. 1). Many organisms have been found to use magnetic fields for their orientation from magnetotactic bacteria to complex vertebrates like birds, which are by far the best studied group. Some animals show collective alignment in magnetic fields, which aids them in coordinating and organizing their group tasks. Social insects such as ants, termites and honeybees use magnetic fields for nest building and navigation outside of the nest thanks to the magnetic particles in their bodies.

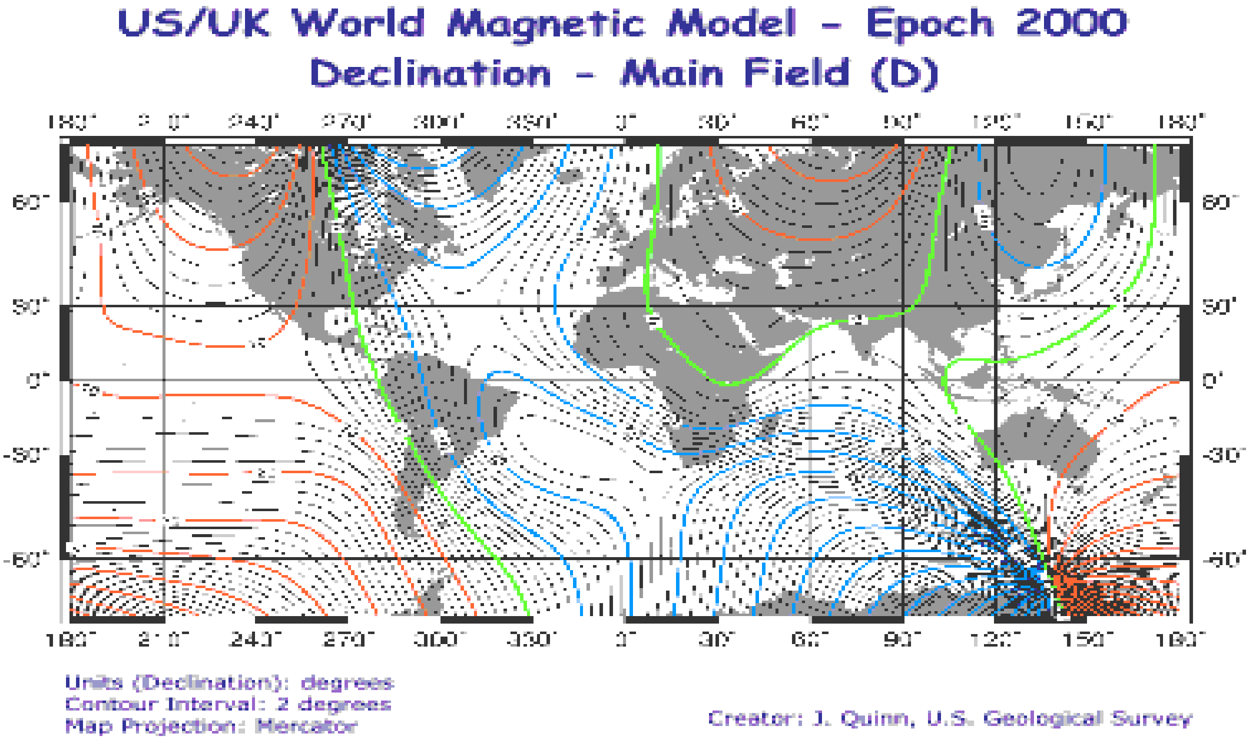

Fig 1: Magnetic fields of the Earth (Epoch 2000) (web source)

Use of magnetism for orientation in nest building

The nests of social insects such as termites and honeybees are very complex structures. The cells or combs are laid down by workers in a coordinated organized manner to make a functional, carefully crafted structure that is capable of housing several thousand inhabitants while standing the test of time.

The Australian compass termite (*Amitermes meridionalis*) which feeds on grass and which is native to Northern Australia, builds uniform, tombstone-shaped mounds that are 1.5-2.0m in height and with a long axis oriented in a North-South direction (Jacklyn and Munro 2002). One isolated sandy plain can have up to 100 such mounds more or less equidistant to each other, resembling a vast cemetery (Jacklyn and Munro 2002). The mounds are found only over a small range of Northern Australia, in plains that receive ample rain and even periodic flooding (Wiltschko and Wiltschko 1995). These “magnetic anthills” as the local populations call them, have complex internal structures composed of several cells which are laid down in parallel arrays (Wiltschko and Wiltschko 1995). Building the mounds is slow. *A. meridionalis* mounds take about 10 years to reach an elongated shape from an initial spike (Fig. 2; Jacklyn and Munro 2002).

Fig. 2: Growth of *A. meridionalis* mounds (Dark areas show new growth).(Jacklyn and Munro 2002)

The regularly structured internal architecture of these mounds, which is often oriented along the cardinal axis of the Earth, suggests that blind termite workers might be using geomagnetic cues for their construction (Jacklyn and Munro 2002).

To test whether Earth’s geomagnetic cues are important to the proper building of such mounds, a study compared the development of the mounds over a 7 year period by choosing 8 “initial spike” nests at random (Grigg et al 1988). Pairs of bar magnets were buried equidistant at 20cm from half of the early nests, while the other half had non-magnetic bars buried next to them in the same fashion. The treatment nests had an anomalous field 40-90º away from the Earth’s field (Grigg et al 1988). After a 7 year period, the researchers came back to the site and found that all control mounds had undergone regular development and had reached the characteristic elongated shape, while treatment mounds had eroded and were devoid of life (Grigg et al 1988). It was suggested by the authors of this paper that the treatment nest termites aligned according to a field with a different direction and strength, and this proved lethal to the colony's success. However, the study should have checked the progress of the mound construction more frequently to be able to assess what went wrong, and to be able to gauge how long it took for the building effort to cease or fall through. This study also doesn't explain how they used this magnetic information to position and direct their coordinated construction. In the interest of not destroying or harming these complex nests, the study elected to only use 8 nests for this experiment, which is too small a number to reach a definite conclusion, although the results were striking and the study was one of the first to employ an anomalous magnetic field on a natural termite plain.

Studies since this one have looked at the external orientation and found it to be not simply North-South directed as was previously thought. One study found that the mounds were not always oriented North-South but rather between 10ºgE and 349ºgW, depending on environmental conditions such as wind and shade, such that the Eastern face of the mounds were placed in a more stable, warmer location (Jacklyn 1992). However, this orientation gives a broad range and makes it difficult to draw conclusions on a species-specific axis used.

More recent work has been done on the internal structure of the mounds; focusing on mound construction and repair (Jacklyn and Munro 2002). Tops of mounds were cut off during the wet season, and mound repair was observed under artificial and natural magnetic fields (Jacklyn and Munro 2002). Measuring the orientation axis of caps, which takes a few months to repair (Fig.3), is different from measuring the whole mound's orientation because it is much easier for termites to use cues from the existing mound during repair (Jacklyn and Munro 2002).

Fig. 3: Repair of A. meridionalis mounds (Dark areas show new growth). (Jacklyn and Munro 2002)

Another more interesting aspect to measure is the orientation axis of the cells contained in the cap, since it has been suggested that orientation of the individual cells in the entire mound, much like the cells of our body, combine and function together to create a whole, integrated, cohesive entity. Thirty-two mounds were used and each was randomly assigned to 4 magnetic treatments (8 mounds per treatment): T1 had a 4ºgNNE magnetic field (natural magnetic North), T2 had the same orientation but was an artificial field, T3 was an artificial field oriented 45ºgNE (diagonal NE-SW) and T4 was an artificial field oriented 315ºgNW (diagonal NW-SE) (Fig. 4). The artificial fields T2-T4 were created by placing a ferric bar magnet on the center of the magnet, 50cm below the cut surface, producing a field 1.5 times stronger than the natural field (Jacklyn and Munro 2002). Orientation of cells were determined by examining enlarged photographs of cross-sections of the mounds. It was found that T1 and T2 cell orientations were clustered around the geographic North-South and East-West axes, with T2 having less pronounced clustering (Fig. 5). Treatments T3 and T4 had no clustering around the East-West axis, very indistinct clustering around the North-South axis, but significant clustering around

Fig. 4: Magnetic treatments of the mounds (gray ovals). Arrows represent the direction of magnetic field lines (declination). Treatment 1: natural geomagnetic field; treatments 2-4: artificial magnetic fields. (Jacklyn and Munro 2002)

Fig. 5: Distributions of cell orientations under natural (Treatment 1 and artificial (treatments 2-4) magnetic fields. The vectors inside the circles represent with their direction, the orientation of the mound cells, and with their lengths, the number of cells oriented into a specific direction. (Jacklyn and Munro 2002)

the NE/SW and NW/SE axes (Jacklyn and Munro 2002). Although the cap orientation was not affected by the magnetic anomaly, internal cells were heavily influenced by the magnetic conditions. The orientation trends were significant when comparing the T3 and T4 treatments to the natural geomagnetic treatment T1. However, the relationship was less evident when comparing the artificial magnetic treatment to the other artificial treatments T3 and T4, possibly because the bar magnet was less uniform than the natural field (Jacklyn and Munro 2002). This study appears to indicate that magnetism is central to mound construction. Termites appear to use the magnetic cues to orient cells and whole mounds along cardinal axes creating their symmetrical and resistant shape, which functions both in protecting the colony from the elements and housing the numerous colony members in an economical, organized fashion. However, it is possible that other thermal cues are jointly used by the blind workers. The authors of the study suggest that the magnetic orientation of nest building be done in the areas further away from the magnetic North or South, to see if orientation changes accordingly and proportionately to polarity (Jacklyn and Munro 2002).

The honeybee is also faced with organizing the construction of straight and parallel, vertically oriented combs by thousands of worker bees. This must be done efficiently, to rapidly house the colony. The bees must choose and agree on a planar orientation for the new combs, to be able to collectively construct a functional hive. Man has been fascinated by the complexity of the wax combs of honeybees from the ancient Egyptians to Darwin (1859). Nests of the honeybee (*Apis mellifera*) can be found in natural cavities like a hollow tree, a cave, and even a termite mound (De Jong 1982). Nowadays, beekeepers usually provide swarming bees with an artificial hive with frames built in wax sheets, which determine the direction of the future combs. If this isn't provided, the workers must build the new combs without light cues and must collectively agree on its orientation.

To understand what mechanism was behind this coordinated effort, several studies were undertaken but none until Dejong (1982) were successful at showing a magnetic influence. In this study, 25 swarms of feral honeybees were caught in bait-hives and transferred to separate artificial comb building hives. The hives were light-proof and did not have frames for orientation. Swarms were encouraged to build several times in succession since the comb building box was frequently replaced during the experimental period. A coil was placed around the comb building hives which, when turned on, caused a 90° deviation to the East of the natural magnetic field. Comb angles were measured by breaking off the combs within 1 cm of the hive surface and marking the orientation on a Plexiglas sheet placed overtop of the comb. The angle of the comb was then measured relative to the hive top. Since it was possible to age the swarms collected in the bait-hives, "young" bait-hive swarms, which were found to maintain comb direction unlike the "old" bait-hive swarms, were placed in the comb-building hives with the anomalous magnetic field. It was found that the comb direction was maintained to a significant degree relative to the anomalous field (De Jong 1982). It is also thought that the crucial part is the laying down of the first layer of combs with magnetic help, which then serves as a reference for future comb elaboration, which doesn't need to rely on magnetic cues. Another interesting finding in this study, was the pooled orientation data, which showed that the bees had a preferred axis running 76º-256º. Despite other studies conflicting with this axis, it could be that the wild-living bees chosen had an innate preference for the East-West axis and descended from a colony that used this orientation as a reference.

Use of magnetism for navigation

Social insects like termites, ants and honeybees need to make frequent trips from the nest to forage in order to keep themselves and the colony alive. They must often take long trips away from the nest, in indirect routes, and somehow find their way back as quickly and as directly as possible, to save energy and to be at minimal risk of attack from predators.

Magnetic orientation in foraging termites was found by Rickli and Leuthold (1988). The harvester termite (*Trinervitermes geminatus*) uses pheromone trails to guide it in trips around the nest. When these termites move in the open and encounter a fork of two different pheromone trails, they frequently choose the one that leads most directly back to the nest. To test whether magnetic cues were involved in this, Rickli and Leuthold (1988), directed returning foragers through a tube to an arena where 8 radially arranged pheromone trails were presented to them. The termites all chose the one which led closest to their nest. When the magnetic field was shifted in the arena using coils, their preferences were shifted according to the new field (Fig. 6).

Fig. 6: Orientation of homing foragers of the harvester termite (*Trinervitermes geminatus*) in the local magnetic fields, and when magnetic North was altered by 33º with the help of magnets. The bars indicate the distribution of direction of the termites along 8 radially arranged pheromone trails. Arrows mark ambient magnetic North. (Rickli and Leuthold 1988)

In this case, magnetic cues are used in conjunction with chemical cues, but pheromones take priority. For instance, when a forager loses a pheromone trail, he does not continue using magnetic cues, but instead searches for a new pheromone trail. It is possible that the pheromones contain some source information in their scent and chemistry, which guides the foragers to the nest so they need not rely as much on the magnetic cues.

Many studies have been done on different species of foraging ants which are found more commonly in open areas outside of the nest than their termite cousins. The fire ant (*Solenopsis invicta*) has a simple foraging process which is used in many other species of ants as well. First the scout workers leave the nest and explore the area; then after finding resources, orient and home in on the nest after recruiting other workers with pheromones, to help them carry an oversized load (Anderson and Vander Meer 1993). Mature fire ant colonies have as many as 200,000 workers living in a mound with radiating foraging tunnels with exit holes, allowing workers to reach the surface (Anderson and Vander Meer 1993). The ants forage at all times of the day, indicating they don’t always rely on light cues. Possible magnetic field orientation for foraging navigation was tested in the laboratory under total darkness. A test colony was placed in a tray within a helmholz coil, which when turned on, created a 180° reversal in the magnetic field (Anderson and Vander Meer 1993). A dead cockroach was placed a distance from the tray, and the time for the ants to form a trail from nest to bait was recorded. Four different conditions were tested depending on whether the coil was on or off (reverse or normal) in the acclimation period, and whether the coil was on or off (reverse or normal) after cockroach introduction (reverse/normal, normal/reverse, normal/normal and reverse/reverse) (Anderson and Vander Meer 1993). The results of the experiment showed that there was no difference in the time of trail formation when the magnetic field was constant (normal/normal or reverse/reverse). However the ants took significantly longer to form a trail when the magnetic field was changed during the experimental period. However there was no significant difference between the mixed field treatments (normal/reversed, reversed/normal) (Fig. 7).

Fig. 7: Comparison of time to trail formation under 4 different magnetic-field conditions (mean and standard error shown). Times when the magnetic field was held constant were not significantly different from each other. Times to trail formation where the magnetic field was changed were significantly different from times where the field was not changed. However the 2 reversed-magnetic-field situations were not different from each other. (Anderson and Vander Meer 1993)

This study shows that fire ants have a magnetic sense and that a change in magnetic fields will disrupt their homing ability. Moreover, in laboratory conditions, the ants are able to home in on a target regardless of the direction of the field, provided the field is held constant. However, it is debatable whether this result would be found if the field were shifted less than 180º, so that it was not on the same axis. Also, under natural conditions, it is questionable whether these results would stand since the laboratory environment is no comparable to what is seen in the wild. The laboratory setting is devoid of any natural obstacles; moreover, in more complex natural conditions, the distances traveled by ants to forage are much greater.

Similar studies were done on different species of ants, in their natural habitat. Camliepe and Stradling (1995) tested wood ant (*Formica rufa*) magnetic orientation under screened daylight and natural or artificially-induced magnetic fields. The artificial field was generated by a solenoid causing a 90º deviation from the natural fields. The ants were trained to visit a chamber with 4 collecting vessels, each pointing in a different cardinal direction, and prior to the experimental field, the chamber and vessels were washed periodically with ethanol to get rid of scent cues. The solenoid was either turned on or off depending on the treatment, and the ants that accumulated in each vessel were counted. The results of the study were promising since a significant number of foragers (64%) oriented towards the North arm when the long axis of the unenergized solenoid was oriented East-West. When the solenoid was energized, once again a significant number of foragers (45%) sought out the artificial North. To eliminate the possibility that the ants were responding to a property of the solenoid, the solenoid was shifted with its long axis in a North-South direction, and 80% oriented towards the geomagnetic North. This enhanced result was probably due to learning during the early trial period. However, the use of magnetic cues in this species seems evident, and it can be assumed that without the horizontal component of the magnetic field, the ants would disperse randomly in the vessels.

A similar study done on Weaver ants (*Oecophylla smaragdina*) yielded similar results; it also revealed that this particular species used magnetic cues as default cues when sunlight cues were absent, since the study tested orientation under shielded light and natural light conditions (Jander and Jander 1998).

It wasn’t until Banks and Srygley’s report (2003) that magnetic field orientation in ants was tested in fully natural light and sunless conditions (no opaque sun-shield). They used electromagnets to reverse polarity 180º in the field, and noted the orientation of leaf-cutter ants (*Atta colombica*) under sunny and overcast skies (Fig. 8).

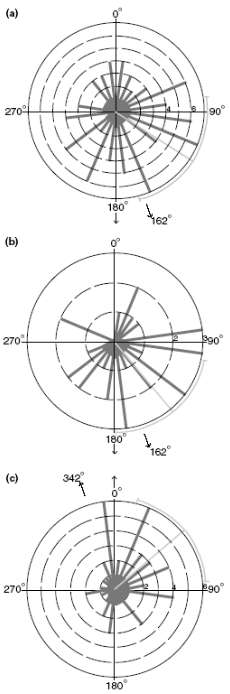

Fig 8: a) Controls (sunny, natural field) b) Reversed magnetic polarity (RMP) + sunny c) RMP and overcast. Each unit length along a radius represents one individual's mean orientation. (Banks and Srygley 2003).

It was found that under sunny conditions and reversed polarity, the orientation was not significantly different from controls (without the artificial field). However, under cloudy conditions, there was a shift in orientation, which while not in total reversal, was significant compared to controls and the first treatment under sunny skies (Banks and Srygley 2003). Although this study suggests that species like the leaf-cutter ant employ magnetic compass as a backup under low light, this interpretation becomes problematic when trying to quantify cloud cover as a sunless stage, since in some trials, sun or polarized light may have been a factor.

Some species of ant will use magnetic cues seasonally. The migratory ant (*Pachycondyla marginata*), which leaves its nest to raid termite mounds and predate on their inhabitants, has been found to have a preferred axis around 13º from the magnetic North-South axis during the dry/cold season (Acosta-Avalos et al 2001). However during the rainy/hot season they were markedly scattered in their orientation, and migrations did not show a preferred direction (Acosta-Avalos et al 2001). Although it is known that migration distances traveled in the dry/cold season are greater (Acosta-Avalos et al 2001), it is it is not known why they shift to the magnetic compass under these conditions.

Honeybees, also use magnetic cues when foraging. Schmitt and Esch (1993) caught bees as they exited their hive and tested their orientation in darkened laboratory conditions. In the natural magnetic field, the bees oriented in an Easterly direction with a mean direction of 71º, which was roughly the direction that the opening of their hive was facing. Under an artificial magnetic field deflected 90º, the bees also oriented towards the artificial magnetic East, with a mean direction of 60º. This shows that the bees use cues at the beginning of their foraging trips.

Collett and Baron (1994) also showed that magnetic cues are also used in the final approach phase to a familiar goal. In this study, bees were shown to face landmarks from a particular direction, which makes it easier for them to potentially remember their foraging and nest sites. First they were trained to face landmarks from a Southerly direction; then, when they were put under strong experimental fields, they were found to face the artificially induced magnetic South instead of the actual geographic South. The magnetic cues provide a directional reference allowing them to use visual landmarks from their memory in navigation.

However, no studies were found to show that bees use magnetic cues when they start their return trip. Kirschvink and Kirschvink (1991) tried to teach bees to leave the feeder and return towards the nest in a constant direction, under constant magnetic conditions, but the results were inconclusive.

Magnetoreception

In order to orient themselves during nest building and navigation outside of the nest, social insects rely on a form of magnetoreception. The first hypothesis, which was proposed by Leask in 1977, states that magnetoreception is light dependant and is associated with the visual system. Magnetoreception becomes possible when light raises macromolecules in the orienting organism to an excited state, which has a magnetic moment, and can interact with the magnetic field in several ways (Leask 1977). Leask assumed that the ordered array of molecules necessary for this interaction were the pigments of the retina. He suggested that magnetoreception is a by-product of the normal visual process (Leask 1977). He then encouraged researchers to test his hypothesis, by looking at the effects of varying light intensities on magnetic orientation. However, although studies on birds and insects such as drosophila support this hypothesis, no social insects have been shown to exhibit light dependant magnetoreception.

The most popular hypothesis in more recent times seems to be magnetoreception based on ferromagnetic particles. Magnetic properties of ferromagnetic materials come from the spin angular momentum of each atom (Wiltschko and Wiltschko 1995). Magnetoreception also depends on their size and shape (Wiltschko and Wiltschko 1995). If the particles are small enough, then they will have only one magnetic domain and will have a stable magnetic moment that is constant in time (Wiltschko and Wiltschko 1995). The best candidates for magnetoreception are particles with a single domain, and with stable magnetization. These can easily align themselves in a magnetic field (Wilschko and Wilschko 1995).

Magnetic iron oxide magnetite Fe_3O_4 has been found in various parts of the bodies of social insects. Honeybees (*Apis mellifera*) were found to have magnetic resonance in the front part of their abdomen (Gould et al 1978). Larvae and eggs were found to contain far less material compared to the adults (Gould et al 1978). A study by El-Jaick et al (2001) went one step further with new available technology, by submitting the particles in the abdomen to electron paramagnetic resonance, which has proved to be useful in identifying different structures in biomineralized magnetic systems. At least 4 different structures were identified: FeOOH, Fe^{3+}, isolated magnetite nanoparticles of 2 different sizes (single and multi-domain), and aggregates of these particles (El-Jaick et al 2001).

An early histological study by Kuterbach et al (1982), found iron-rich granules in the trophocyte of the fat body in the abdomens of post-eclosion adults. The size of the granules increased with age and was proportional to iron levels in the diet (Kuterbach 1982). Levels of iron reached a saturation point when bees were old enough to forage and use magnetic orientation (Kuterbach and Walcott 1986). Despite the fact that the form of iron found may not be suitable for magnetoreception, Hsu and Li (1994) found that 10% of the granules contained small particles of magnetite, a suitable magnetoreceptor. Some authors however disagreed with this hypothesis claiming that the "dense masses in the iron granules look[ed] like haemosiderin degradation products of holoferritin described in other insects" (Nichol and Locke 1995). Keim et al (2002), showed that the granules of *A. mellifera* were composed of apoferritin-like particles in the periphery, and clustered particles resembling holoferritin in the core. Electron spectroscopic images of the granules showed that iron, oxygen and phosphorus were also in the ferritin-like deposits (Keim et al 2002). This indicates that the iron granules of honeybees were composed of accumulated ferritin and its degraded forms (Fig. 9), and its degraded forms along with elements from the RER such as magnesium, calcium, and phosphorus (Keim et al 2002). The authors of this paper thought that the high levels of phosphate would prevent the crystallization of iron oxides into magnetite, making it impossible for this kind of magnetoreception to occur.

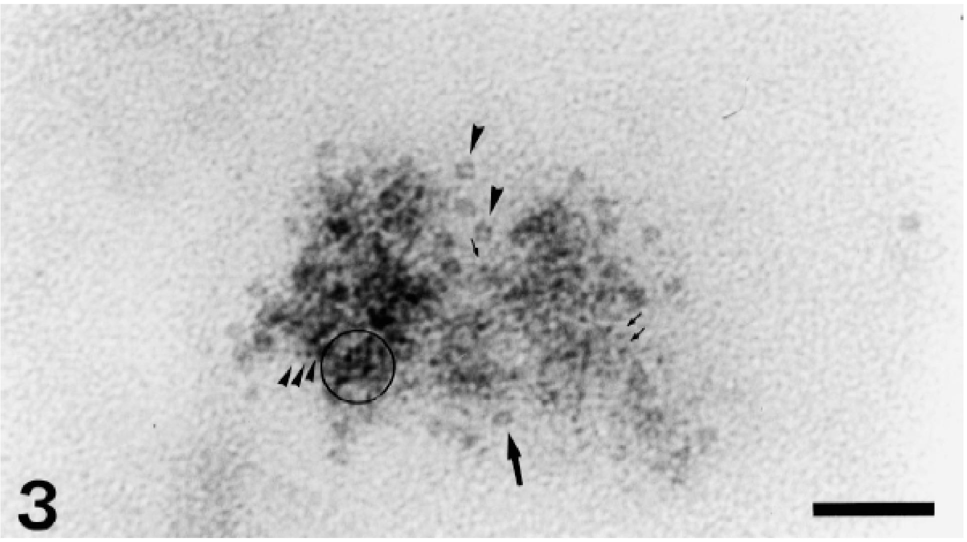

Fig 9: High magnification of a small granule from *A mellifera*. The large arrow indicates an apoferritin-like particle. Small arrows show individual electron dense deposits originating from the core of ferritin molecules. Small arrowheads represent ferritin molecules or ferritin cores. (Keim et al 2002)

Although magnetoreception in social insects has traditionally been biased towards honeybees, recent work has been done on ants and termites as well, to investigate the ferromagnetic hypothesis of magnetoreception.

Acosta-Avalos et al (1999) found magnetic iron oxides in the migratory ant (*Pachycondyla marginata*). Ants were separated in head, thorax and abdomen segments, and electron spectroscopic images for iron and oxygen were obtained for the extracted particles. Also, electron micrographs enabled accurate size distribution of particle estimates to be made. This revealed that the size distribution of the particles in the abdomen was different from that in the thorax and the head (fig 10).

However, the mean values for length and width were virtually the same in the 3 body segments (Acosta-Avalos et al 1999). It was also found that the ratio of iron/oxygen containing particles in each body segment (abdomen:thorax:head) was 3:1:2. Since the relative amount of particles in the thorax was low, there is a possibility that these could have resulted from contamination from the head/abdomen resulting from inexact cuts in the experimental phase (Acosta-Avalos et al 1999). Selected area diffracted analysis in the same study revealed the presence of the magnetic oxides magnetite and maghemite.

Alves et al (2004) did magnetic resonance studies on the same species of ant and its only termite prey (*Neocapritermes opacus*). This technique has enough sensitivity to record information on inorganic precursors and magnetic materials (Alves et al 2004). The study found that 99% of the magnetic material in the termite was in the body (abdomen and thorax). The ant on the other hand had only 34% of the magnetization coming from its body (Alves et al 2004). The authors proposed that the nanoparticles in the head of the ant were derived from "biomineralization or cuticular contamination processes", while the ones in the body could have resulted from the accumulation of ingested materials in the digestive apparatus. It was also found in the same study that a

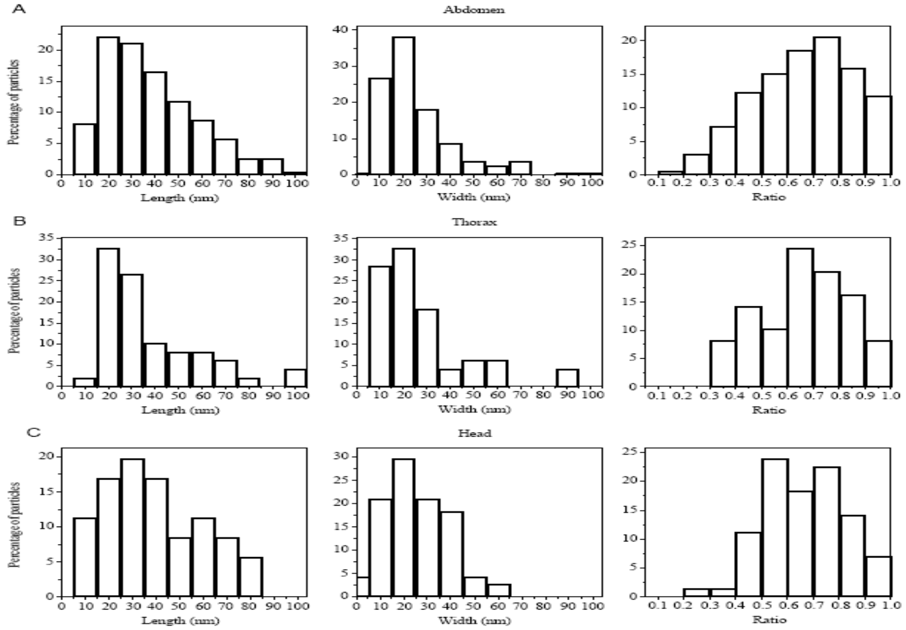

Fig. 10: Size distribution histograms from the particles extracted from the abdomen, thorax and head of *Pachycondyla marginata*. Size distribution in the abdomen is a single distribution, while there is bimodal splitting in the thorax and head. Mean values for length and width are approx. the same in the 3 segments. (Acosta-Avalos et al 1999)

much larger amount of nanoparticles within the magnetite single and multidomain region was found in the termite compared to the ant. Different magnetic diameters of isolated particles was also found between the 2 species, indicating that the predator does not directly use termite magnetic material that is ingested for its own magnetoreception (Alves et al 2004).

In a more recent study by Wajnberg et al (2004), it was found that the antennae on the head of the migratory ant accounts for most of the body's magnetism (Fig. 11).

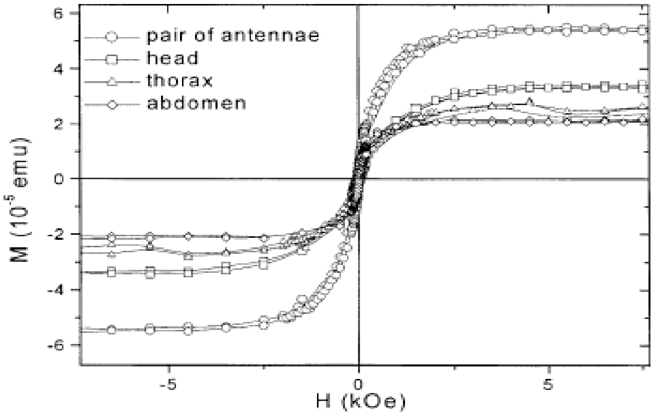

Fig 11: Hysteresis curves of four *Pachycondyla marginata* heads, abdomen, thorax and pairs of antennae, in a parallel magnetic field, showing how antennae have the highest saturation magnetization.(Wajnberg et al. 2004).

This observation is highly functional since the antennae of the ant are the insect's most anterior body part. It was found that the total saturation magnetization, based on hysteresis curve data was 42±3%, 24±3%, 19±3% and 15±3% for antennae, head, thorax and abdomen respectively.

Although there is good evidence for ferromagnetic magnetoreception in ants, termites, and the honeybee, findings are limited to resonance and histological studies which reveal magnetic components but do not show how they fit into the sensory system.

Conclusion

At the behavioural level, many studies have shown that social insects use magnetic cues for orientation. Termites like *Amitermes meridionalis* and the honeybee (*Apis mellifera*), use magnetic fields to align the cells or combs of their nests, although this is probably not the only cue they are using, since thermal cues are also present. Outside their nests, when the insects are foraging, they also rely on magnetic cues, but this time as a backup compass. Termites like *Trivitermes geminatus*l use them when pheromone trails intersect and diverge, creating confusion. Several species of antsl use them when light cues are unavailable. Finally, honeybees use magnetic cues when leaving the nest during foraging, but have not been shown to do so on their trips back to the nest. Honeybees usually rely heavily on the sun compass but are known to use many different compasses in combination, to gain the maximum awareness of their surroundings.

On a physiological level, however, studies are lacking. It seems highly likely, based on histological and resonance studies, that magnetoreception occurs due to single domain magnetite receptor in the abdomen of honeybees and in the antennae of ants such as the migratory ant. However, the extraction of magnetite from these areas has proved difficult, and recent reports in the honeybee have found mainly ferritin derivatives, which is not an adequate magnetoreceptor.

Another major problem remains. Even if the magnetite receptor is found to be responsible for magnetoreception, how it interacts with the sensory system is the next question that needs to be answered. The light-dependant magnetoreception hypothesis is convenient because we know it is associated with the retina and the visual system. However the ferromagnetic hypothesis, which is the favored hypothesis, is vague and doesn't propose an explanation for the physiology of the process. It is unclear how an organism whose iron oxides are lined up in a magnetic field can sense this alignment with its nerves and be able to use this to orient itself in space. This will in all likelihood be an area of future research, which is already underway in other organisms, but which is still in its early stages in social insects; in fact researchers are still searching for receptors. Studies should probably be done in the area of iron oxide alignments *in vivo* resulting from intense magnetization. Also, once the receptor and the region of magnetoreption in the body of the insect is discovered, electrode studies can be done on the organism, measuring resulting nerve impulses to artificial magnetic fields, in order to determine how the nervous system responds to magnetism.

Magnetoreception is thought to have been one of the first sensory systems to evolve due to the presence of magnetosomes and magnetosome chain in 4 billion year old carbonate blebs of a Martian meteorite, which is thought to have brought it to Earth (Kirschvink et al 2001). Also the resemblance of magnetosome structure in the different kingdoms supports the hypothesis that magnetite biomineralization arose in magnetotactic bacteria and was incorporated into eukaryotic cells by endosymbiosis (Kirschvink et al 2001). However we are just beginning to understand the complex physiology which is far from primitive.

References

Acosta-Avalos et al. 1999. Isolation of magnetic nanoparticles from *Pachycondyla marginata* ants. J. Exp. Biol. **202**: 2687-2692.

Acosta-Avalos, D. et al. 2001. Seasonal patterns in the orientation system of the migratory ant *Pachycondyla marginata.* Naturwissenschaften. **88**: 343-346.

Alves, O. C. et al. 2004. Magnetic material arrangement in oriented termites: a magnetic resonance study. J. Magn. Reson. **168**: 246-251.

Anderson J. D., Vander Meer, R. K. 1993. Magnetic orientation in the fire ant, Soleopsis invicta. Naturwissenschaften. **80**: 568-570.

Banks, A. N., Srygley, R. B. 2003. Orientation by magnetic field in leaf-cutter ants, *Atta columbica*. Ethology. **109**: 835-846.

Camliepe, Y., Stradling, D. J. 1995. Wood ants orient to magnetic fields. Proc. R. Soc. Lond. B. **261**:37-41

Collett, T. S., Baron, J. 1994. Biological compasses and the coordinate frame of landmark memories in honeybees. Nature. **368**: 137-140.

DeJong, D. 1982. Orientation of comb building by honeybees. J. Comp. Physiol. **147**: 495-501.

El-Jaick, L. J. et al. 2001. Electron paramagnetic resonance study of honeybee *Apis mellifera* abdomens. Eur. Biophys. J. **29**: 579-586.

Gould, J. L., Kirschvink, J. L. Deffeyes, K. S. 1978. Bees have magnetic remanence. Science. **201**: 1026-1028.

Grigg, G. C., Jacklyn, P. M., and Taplin, L. 1988. The effects of buried magnets on colonies of Amitermes spp. building magnetic mounds in northern Australian. Physiol. Ent. **13**: 285-289.

Hsu, C. Y., Li, C. W. 1994. Magnetoreception in honeybees (*Apis mellifera*). Science. **265**:95-97.

Jacklyn, P. M., Munro, U. 2002. Evidence for the use of magnetic cues in mound construction by the termite *Amitermes meridionalis* (Isoptera:Termitinae). Austr. J. Zool. **50**: 357-368.

Jander, R., and Jander, U. 1998. The light and magnetic compass of the weaver ant *Oecophylla smasmaragdina* (Hymenoptera; Formicidae). Ethology. **104**: 743-758.

Keim, C. N. et al. 2002. Ferritin in iron containing granules from the fat body of the honeybees *Apis mellifera* and *Scaptotrina postica*. Micron. **33**: 53-59.

Kirschvink, J. L., Kirschvink, K. A. 1991. Is geomagnetic sensitivity real? Replication of the Walker-Bitterman magnetic conditioning experiment in honeybees. Am. Zool. **31**: 169-185.

Kirschvink, J. L., Walker, M. M., and Diebel, C. E. 2001. Magnetite-based magnetoreception. Curr. Opin. Neurobiol. **11**: 462-467.

Kuterbach, D. A. et al. 1982. Iron-containing cells in the honeybee (*Apis mellifera*). Science. **218**:695-697.

Kuterbach, D. A., Walcott, B. 1986. Iron-containing cells in the honeybee (*Apis mellifera*). J. Exp. Biol. **126**: 389-401.

Leask, M. J. M.1977. A physico-chemical mechanism for magnetic field detection by migratory birds and homing pigeons. Nature. **267**: 144-145.

Nichol, H., Locke, M. 1995. Technical comments-honeybees and magnetoreception. Science. **269**: 1888-1889.

Rickli, M., Leuthold, R. H. 1988. Homing in harvester termites: evidence of magnetic orientation. Ethology. **77**:209-216.

Schmitt, D. E. and Esch, H. E. 1993. Magnetic orientation of honeybees in the laboratory. Naturwissenschaften. **80**: 41-43.

Wajnberg, E. et al. 2004. Antennae: the strongest magnetic part of the migratory ant. Biometals. **17**: 467-470.

Wiltschko, R., and Wiltschko, W. 1995. Magnetic orientation in animals. Springer Verlag. Berlin. P.1-3, 255-260.

Web sources:

Images from the world magnetic model: http://www.ngdc.noaa.gov/seg/WMM/image.shtml