INSECT NAVIGATION BY POLARIZED LIGHT

F. J. Smith
School of Electronics, Electrical Engineering and Computer Science, Queens University, Belfast, N. Ireland

Keywords: Polarization, Skylight, Navigation, Clouds, POL, Insect celestial map, Robot navigation.

Abstract: Many insects can navigate accurately using the polarized light from the sky. A study of a large number of experiments on the behaviour and anatomy of insects has led to a simple algorithm for navigation by skylight, suitable for a robot or drone in lightly clouded skies. The algorithm is based on the special ability of insect eyes to measure the position of the 4 points in the sky at which the polarization angle, i.e. the angle χ between the polarized E-vector and the meridian, equals $\pm\pi/4$. The azimuths of these 4 points are possibly the only measurable quantities that are invariant to variable cloud cover, provided that polarized light is still detectable below the clouds. It is shown that the sum of these 4 azimuths can be turned into a celestial compass in a few short steps. A simulation shows that the compass is accurate as well as simple and well suited for a robot or drone. It can also explain many of the experimental results published on insect navigation.

1 INTRODUCTION

Due to the scattering of light within the earth's atmosphere, skylight is partially linearly polarized, discovered by the Irish Scientist Tyndall (1869). Two years later a mathematical description of the phenomenon was given by Lord Rayleigh (1871) for the scattering by small particles (air molecules) in the atmosphere. That an insect can use this polarization to navigate was first discovered in experiments with bees by Karl von Frisch (1949).

It took another 25 years before the nature of the insect's celestial compass began to be clarified (Kirshfeld et al., 1975; Bernard and Wehner, 1977). It depends primarily on a specialized part of the insect compound eye, a comparatively small group of photoreceptors, typically 100 in number, situated in the dorsal rim area. Further insight on these photoreceptors came from Wehner and co-workers working with desert ants and bees (Labhart, 1980; Rossel and Wehner, 1982; Fent and Wehner, 1985; Wehner, 1997). It was found that each ommatidium in the dorsal rim of the compound eye has two photoreceptors with axes of polarization at right angles to one another and each strongly sensitive to the E-vector orientation of plane polarized light. The axes of polarization of these ommatidia have a fan shaped orientation that has been claimed from experiments to provide an approximate map for the polarized sky, a map which the insect can use as a compass (Rossel, 1993). The variation in E-vector orientation has also been traced within the central complex of the brain of an insect (Heinz and Homberg, 2007).

Although much is known about this insect compass little is known about the underlying physical processes that require these 100 photoreceptors, the subject of this research. One attempt has been made to design a navigational aid for a robot based on the compass; this uses 3 pairs of photoreceptors (Wehner, 1997; Lambrinos et al, 1998), simulating the accumulation of results from many photoreceptors in three different parts of the fan of receptors used by an insect. This system is reported to work well in the desert but it is not clear that it would be accurate under a variable cloudy sky. NASA has also built robots navigating by skylight, but these apparently use a different process based on 3 photoreceptors with 3 different axes of polarization on a horizontal plane (NASA, 2005). Few details have been released publicly on this system or its performance.

This paper proposes that the fan of photoreceptors is scanning the sky to find the four points in the sky where the polarization angle, χ, the angle between the meridian and the polarized E-vector in the sky, equals $\pm\pi/4$. We propose that the anatomy of the eyes of bees, ants, and many other

Smith F. (2009).
INSECT NAVIGATION BY POLARIZED LIGHT.
In *Proceedings of the International Conference on Bio-inspired Systems and Signal Processing*, pages 363-368
DOI: 10.5220/0001553503630368

insects are designed precisely to detect these four points, probably the only measurable quantities invariant to variable light cloud cover. We also show that the direction of the sun can be found quickly by a simple algorithm well within the capacity of the insect brain for all orientations of the head.

In a previous work-in-progress paper (Smith, 2008) a simulation of this insect compass was attempted using an algorithm involving 16 elements in a 4X4 array in which all possible solar elevations were examined one after the other until the correct elevation was found. Probably this was too difficult for the brain of an insect and in further studies of previous experiments on insects it was found that when insects view the sky through two different windows they obtain solar azimuths equal to the average of the two azimuths obtained from each window (Wehner, 1997). This could not be explained as part of the above algorithm. In addition a mapping of the celestial compass in the insect brain by Heinz and Homberg (2007), although it too involved sets of arrays of 16 elements, indicated that the processing of polarized light in the brain involved simple pairing of contributions from different sources. These facts led to the discovery of a new much simpler algorithm in this paper and to a better understanding of the invariance of the algorithm to cloud conditions.

In the following we first summarise the derivation of mathematical expressions for the light intensities measured by the insect photoreceptors. This is brief as more details are given in the previous paper (Smith, 2008). We then show how these intensities can give the direction of the sun in the new algorithm

2 THEORY

2.1 Measured Intensities

In an ideal sky with no cloud, as shown by Rayleigh (1871), the light observed from any patch of sky is partially polarized, with an elliptical profile for the electric vector, **E**, in which the major axis of the ellipse is at right angles to both the direction of the sun, represented by the unit vector, **S,** and to the direction of the observed patch of sky, **k'. T**he electric vector in the direction of the major axis is the E-vector. In the ideal situation where all of the light observed is scattered once only, the ratio of **E** in the directions of the minor axis to the major axis is cos *(θ)* where *θ* is the scattering angle between **S** and **k'**.

When this partially polarized light enters an ommatidium in the dorsal rim its intensity is measured by two photoreceptors, each of which can measure polarized light with parallel structures called microvilli. The two directions of the microvilli are at right angles to one another, and define two orthogonal axes of polarization for these X and Y photoreceptors. In Figure 1 we illustrate the orientations of the microvilli in the dorsal rim of the honey bee by Sommer (1979), as redrawn by Rossel (1993). The fan shape of the microvilli is apparent.

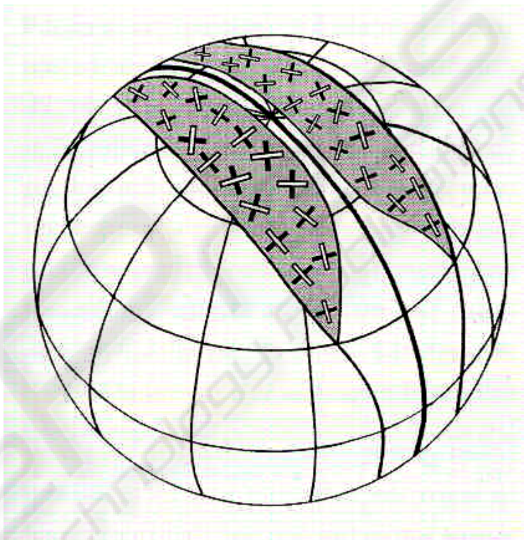

Figure 1: The paired orthogonal photoreceptors in the dorsal rims of a bee. The axes of polarization of the Y photoreceptors are dark, the X photoreceptors light.

The centres of the patches of sky being observed by the photoreceptors are on the opposite side of the head, i.e. contralateral (Sommer, 1979). An examination of Figure (1) shows the axes of the X photoreceptors are approximately parallel to the meridians passing through these patches of sky contralaterally. The same approximate parallel pattern was found in desert ants by Wehner and Raber (1979). It follows that the angle that the X polarization axis makes with this meridian always equals zero. The discovery that this angle is zero, learned from the anatomy of bees and ants, turns out to be critical, and it greatly simplifies the expressions for the light intensities, S_X and S_Y, measured by the two receptors, X and Y. But before writing down these expressions we note that in the real world the sky is not blue, but has a degree of haze or cloud differing with direction. The light then entering the ommatidia can be viewed as made up of two components, one partly polarized as in Rayleigh's equations, and the second totally unpolarized due to multiple scattering. We let U be the intensity of unpolarized light measured by both photoreceptors. Then the 2 light intensities are:

$$S_X = P\left[1 - \sin^2(\theta)\sin^2(\chi)\right] + U \quad (1)$$

$$S_Y = P\left[1 - \sin^2(\theta)\cos^2(\chi)\right] + U \quad (2)$$

where the factor P depends on terms derived by Rayleigh (1871) and on the measuring capability of the photoreceptors.

It has been shown by Labhart (1988) that the brain of a cricket records the difference between the two signals, S_Y and S_X or rather the difference between the log of the two signals; so the recorded signal is

$$S_{YX} = Log(S_Y) - Log(S_X) = Log(S_Y / S_X) \quad (3)$$

To illustrate the variation in these signals as the azimuth angles of the ommatidia vary we set $P = 1$ and $U=0$ in the top of Figure (2). In the bottom we include simulated clouds by putting $U=0.5\ sin^2(a_o)$ with $P=1-U$. The curves change with cloud cover but uniquely the zeros in S_{YX} are always the same, as evident mathematically by equating Equations (1) and (2).

2.2 Solar Azimuth and Elevation

To proceed further we need the polarization angle, χ, in terms of the solar azimuth, a_s, and solar elevation, h_s. We need also the known azimuth, a_o, and elevation, h_o, of the centre of the patch of sky being observed by the photoreceptors.

We also know that the E-vector, in the direction **i'**, is at right angles to the plane containing the solar unit vector, **S**. So **i'.S** = 0. In our previous paper (Smith, 2008) it is shown by substituting for **S** and **i'** that this becomes:

$$\cos(\chi)\cos(h_O)\sin(h_S) - \cos(\chi)\sin(h_O)\cos(a)\cos(h_S) - \sin(\chi)\sin(a)\cos(h_S) = 0 \quad (4)$$

where $a = a_s - a_o$ is the azimuth of the sun relative to the azimuth of the observed sky. We use this equation later.

2.3 A Compass for a Cloudy Sky

We need to know why insects are measuring the difference S_{YX} between the signals from the two orthogonally polarized photoreceptors in each ommatidium. First, the absolute value of the difference S_{YX} is between logs of intensities as in Equation (3) and since this equals the log of the ratio

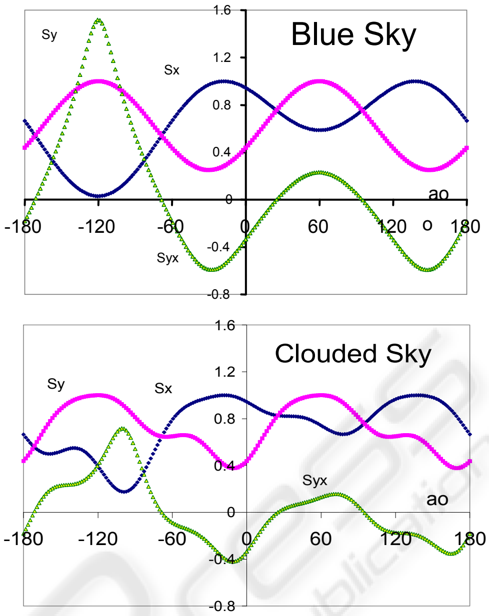

Figure 2: Illustration of the signals S_X S_Y and S_{YX} in a perfect blue sky [U=0] and a sky with simulated clouds [$U=0.5\ sin^2(ao)$], as they vary with the azimuth, a_o, of the fan of observations measured from the central axis of the insect with solar elevation h_s=30°, and azimuth a_s=60°. Note that there are 4 azimuths a_o where S_{YX}=0 or $Sx=Sy$, called zeros, and that these are unchanged by the cloud.

of S_T to S_X an examination of Equations (1) and (2) shows that it reduces the effect of the unknown unpolarized light intensity U caused by clouds, but it does not remove it. So little reliable information can be obtained from the absolute values of S_{YX}. Instead, the ommatidia are probably measuring the positions of features in the measured intensities rather than the values of the intensities. As these ommatidia scan the sky through 360° S_{YX} goes through a maximum towards the solar meridian, then a minimum, then a maximum towards the antisolar meridian and finally a second minimum. Between these four extrema are four directions in which S_{YX} equals zero. So there are two possibilities: that the ommatidia are looking for the positions of the 4 extrema or for the positions of the 4 zeros.

(a) 4 Extrema

As explained above the difference S_{YX} in Equation (3) goes through maxima in the directions of the solar meridian, a_s, and of the antisolar meridian, a_s+π. This is because the signal S_Y goes through a maximum in these directions while S_X goes through a minimum. So the difference between them enhances the maximum in S_Y Labhart (1988). If at least one of these 2 maxima is found then it immediately gives the direction of the sun or the opposite direction. Other clues can then tell the insect which of the two directions is correct.

The positions of the other 2 extrema, the 2 minima cannot be used so easily. Although the minima of S_Y occur at $a_s \pm \pi/2$ the maxima in S_X do not, and may be as much as 20^o different. This is partly because in these directions the factor $sin^2(\theta)$ in Equations (1) and (2) is not stationary as it is in the directions a_s and $a_s+\pi$. So the 2 minima in S_{YX} cannot be used in the celestial compass

Although a maximum in S_{YX} gives the positions of the sun, the finding of the exact position of a maximum, even enhanced, is not easy; so small errors are likely. But a bigger problem comes from cloud. As evident from Figure (2) variable cloud can shift the position of a maximum or produce false maxima, causing further errors. The wide window of observation used by insects minimises this effect but does not remove it. Simulations with a wide window and real cloudy skies by Labhart (1999) have shown that the errors caused by cloud in the positions of the maxima were small, mostly 3^o or less, but a few larger errors occur. Nevertheless this approximate position of the sun is a valuable check or an alternative to what we now describe.

(b) 4 Zeros

The second possibility is that S_{YX} is measuring the 4 zeros. Firstly zeros can be measured more accurately than the positions of maxima, and secondly the positions of zeros are almost completely unaltered by variable cloud, provided only that there is some polarized light detectable below the cloud. So the two sources of errors in the positions of the maxima are removed. We now show how we can use these 4 accurate measurements of zeros to calculate the sun's position.

Putting S_{YX} = 0 or S_X=S_Y in Equations (1 to 3) brings about a large simplification eliminating the unknowns U, P and θ in one step and reduces the equations to simply: $\sin^2(\chi) = \cos^2(\chi)$. This makes $\chi = \pm\pi/4$. So finding the zeros where S_{YX} =0 tells us the precise azimuths $a_o = Z$ where $\chi = \pm\pi/4$. Examples of zeros for different solar elevations for a constant window of observation between elevations 45^o and 89^o are shown in Figure (3). There are almost always 4 zeros if the window of observation is at a constant elevation. However, when the solar elevation is high there may be no zeros. In this case a robot or insect might increase the elevation of observation (although this reduces the accuracy).

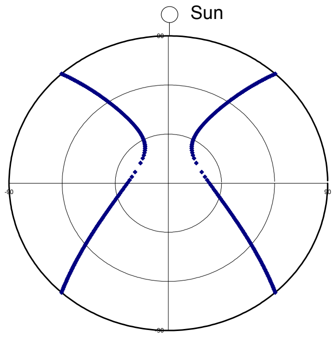

Figure 3: Projection of the sky showing for each solar elevation the 4 azimuths relative to the sun, of zeros where S_{YX}= 0 and χ=$\pm\pi/4$. These zeros are invariant to cloud cover. The circles represent elevations of 0^o, 30^o and 60^o.

Therefore, noting that cos(χ) = 1 and sin(χ) = ±1 at the zeros, Equation (4) simplifies to:

$$\begin{aligned} &\cos(a_s - a_o)\sin(h_o) \\ &\pm \sin(a_s - a_o) = \cos(h_o)\tan(h_s) \end{aligned} \qquad (5)$$

Solving this for a_s, the azimuth of the sun, gives expressions for a_s, for the 4 zeros where a_o=Z:

$$a_s = Z \pm \gamma \pm \delta \qquad (6)$$

in which $\delta = arccos(tan(h_s)cos(h_o)/K)$ and $\gamma = arcsin(1/K)$ where $K^2 = 1 + sin^2(h_o)$. If the robot scans the sky at a constant elevation h_o then the angles γ and δ are also constant, simplifying the algorithm (Smith, 2008). The angle γ depends only on the elevation of the observation, it is large, >π/4, and known to the insect or robot. The angle δ depends on the solar elevation and when the sun is on the horizon it equals $\pi/2$. It can be calculated by a robot from the above equation for δ, which needs the solar elevation, known from the latitude and time; fortunately we now show that this difficult calculation is not needed by an insect.

The 4 alternatives in Equation (6) correspond to the four zeros as illustrated in Figure (4), which we write as

$$a_s = Z_1 + \gamma - \delta,\ a_s = Z_2 - \gamma - \delta \qquad (7)$$

$$a_s = Z_3 - \gamma + \delta,\ a_s = Z_4 + \gamma + \delta \qquad (8)$$

where the signs are chosen by symmetry in the geometry in Figure (4). Note that all of these quantities are angles in [0,2π]; so the sums are all modulus 2π.

If we sum these 4 expressions the γ and δ terms cancel and we get $4a_s$= Z_1+Z_2+Z_3+Z_4, mod 2π. Dividing by 4 gives a_s, but because of the cyclic nature of the summation (350^o + 20^o = 10^o) an uncertainty of mπ/2 occurs where m=0, 1, 2 or 3.

This uncertainty can be resolved by noting in Figure 4 that (1) $Z_2 - Z_1 = Z_4 - Z_3$ and (2) the two zeros Z_1 and Z_4 nearest to the sun are closer together than the other two. These two conditions are used in the following algorithm to calculate a_s from 4 measured zeros, Y_1, Y_2, Y_3, and Y_4, where at first the order is not known, i.e. which one of them is Z_1 in Figure 4.

So the algorithm is simple:

1. find the 4 zeros in $[0, 2\pi]$ where $S_X = S_Y$;
2. put in order Y_1, Y_2, Y_3, and Y_4;
3. find the sum: $S = Y_1 + Y_2 + Y_3 + Y_4$;
4. *put* i=1; m=0;
5. *if* $y_2 - y_1 <> y_4 - y_3$ then $i=2$ and $m=1$;
6. *if* $y_i - y_{i+3} < y_{i+2} - y_{i+1}$ then $m=m+2$;
7. $a_s = (S/4 + m*\pi/2) \bmod 2\pi$.

(Note that differences are cyclical and clockwise.)

For example, for a solar elevation $h_s = 60^o$ and observation elevation $h_o = 70^o$ we find 4 zeros at 84^o, 120^o, 213^o, and 351^o. Following the algorithm we find that $m=3$ and the 4th one is Z_1, S=768°, S/4=192° and a_s=192°+270°=462°=102°, the correct solar azimuth. Simulations with about 5000 examples have shown that this algorithm succeeds in almost every case with no ambiguity within a tolerance of 1 degree. Errors occur only at low or high solar elevations ($\leq 2^o$ or $> h_o$), as long as four zeros are found.

2.4 Less than 4 Zeros

If 4 zeros cannot be found because part of the observed sky is obscured a robot can use the average of the detectable zeros, along with the known values of γ and δ, to calculate the solar azimuth. Other clues, such as light intensity, are needed for the signs of the corrections, remembering that the corrections are large. An insect, not being able to calculate δ, puts $\delta=\pi/2$, assuming that the sun is on the horizon (Rossel & Wehner, 1982), and uses the average of the available values: $z \pm \gamma \pm \pi/2$. Since γ is known this leaves an error of $\pm(\delta-\pi/2)$ if one zero only is observed. If 2 zeros are observed then the average of the two zeros gives an error of $\pm(\delta-\pi/2)$ or, if they are symmetric about the solar meridian, an error of zero. Calculated values of these errors are in general agreement with experiments with insects (Wehner, 1989). This supports our proposal that the insect compass is based primarily on the 4 zeros.

An insect may use only two zeros based on the equations: $2a_s = Z_1+Z_4$ and $2a_s = Z_2+Z_3$ deduced from Equations (7) and (8). We were lead to this pairing of zeros and to our algorithm by structures

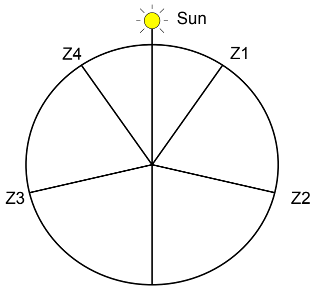

Figure 4: Example of the approximate azimuths (directions) of the 4 zeros where $S_{YX} = 0$ relative to the direction of the sun for a solar elevation $h_s = 60^o$.

found within the brain of an insect observing polarized light by Heinz & Homberg (2007).

2.5 Robot Design

For a robot the greatest difficulty in building our skylight compass is finding the direction of the four zeros. One design (mimicking an insect) uses about 100 pairs of photoreceptors in a circle round the robot. A problem is that each pair has to observe a patch of sky with an accurate azimuth and elevation. In another design the robot has one pair of photoreceptors which is rotated through 360° (like radar) measuring the azimuth as it moves at a constant high elevation (e.g. 70°). This single pair of photoreceptors can be made highly sensitive to small differences in polarization. This would be made easier by the use of ultraviolet light which can penetrate cloud more easily than visible light; it is the light used by most insects (Pomozi et al., 2001).

Although an insect views the polarized sky contralaterally (for reasons that are unclear) it is more straight forward for the robot to scan the sky ipsilaterally, but with the orientations of the polarization axes in the same directions as an insect.

3 CONCLUSIONS

We have shown that an accurate celestial compass for a robot can be built round the principle of finding in skylight the 4 zeros at a constant elevation. The algorithm was discovered after studying published experiments on insect navigation and anatomy. The algorithm is simple and accurate and well within the capacity of the insect brain. It also allows an insect to navigate continuously without turning its head. It explains many experiments on insect behaviour.

Besides the simplicity and accuracy of the method its greatest advantage is that it is accurate in hazy and partially clouded skies, because the position of the zeros is unchanged by cloud. No other method shows this invariance.

However, much remains uncertain about insect navigation. For the algorithm to be accurate the top of the robot or drone must be pointing towards the zenith. Insects may do this using the 3 ocelli on the top of their heads (Goodman, 1970). But how they would do this is not clear. Many insects also have ommatidia in sets of three with the polarization axes of the 3 sets differing by about $\pi/3$ (Labhart, 1988; Wehner, 2001). There are several possibilities. If 3 ommatidia from different sets point at the same patch of sky they could be used to calculate the polarization angles χ, even in a cloudy sky. Alternatively they might help identify in one of them the signs of the corrections $\pm\gamma$ and $\pm\delta$ if less than 4 zeros are visible. Yet another possibility is that they are looking also for the 4 zeros where $\chi = \pm\pi/4 + \pi/3$ and the 4 zeros where $\chi = \pm\pi/4 - \pi/3$. The algorithm above might then be repeated for each of the 3 sets of zeros, giving 3 different approximations for the solar azimuth. All these possibilities are being investigated.

REFERENCES

Bernard, G D, Wehner, R, 1977. Functional similarities between polarization vision and color vision, Vision Res., 17, 1019-28.

Fent, K, Wehner, R, 1985. Ocelli: A celestial compass in the desert ant Cataglyphis, Science, 228, 192-4.

Goodman, L. J., 1970. The structure and function of the insect dorsal ocellus. Adv. Insect Phys., 7, 97-195.

Heinze, S, Homberg, U, 2007. Maplike Representation of Celestial E-Vector Orientations in the Brain of an Insect, Science, 315, 995-7.

Kirschfeld, K, Lindauer, M, Martin,H, 1975. Problems in menotactic orientation according to the polarized light of the sky, Z. Naturforsch, 30C, 88-90.

Labhart, T, 1980. Specialized Photoreceptors at the dorsal rim of the honeybee's compound eye: Polarizational and Angular Sensitivity, J Comp. Phys., 141, 19-30.

Labhart, T, 1988. Polarized-opponent interneurons in the insect visual system, Nature, 331, 435-7.

Labhart, T, 1999. How polarization-sensitive interneurones of crickets see the polarization pattern of the sky: a field study with an optoelectronic model neurone, J. Exp. Biol., 202, 757-70.

Lambrinos, D, Maris, M, Kobayashi, H, Labhart, T, Pfeifer, P, Wehner, R, 1998. Navigation with a polarized light compass, Self-Learning Robots II: Bio-Robotics (Digest 1998/248) IEE, London, 7/1-4.

NASA, 2005. www.nasatech.com/Briefs/Oct05/ NPO_41 269.html

Pomozi, I, Horvath, G, Wehner, R., 2001. How the clear-sky angle of polarization pattern continues underneath clouds, J. Expt. Biol, 204, 2933-42.

Rayleigh, Lord, 1871. On the light from the sky, its polarisation and colour, Phil Mag,, 41, 107-20, 274-9.

Rossel, S, 1993. Mini Review: Navigation by bees using polarized skylight, Comp. Biochem. Physiol, 104A, 695-705.

Rossel, S, and Wehner, R, 1982. The bee's map of the e-vector pattern in the sky, Proc. Natl. Acad. Sci. USA, 79, 4451-5.

Sommer, E W, 1979. Untersuchungen zur topo-graphischen Anatomie der Retina und zur Sehfeldoptologie im Auge der Honigbiene, Apis mellifera (Hymenoptera). PhD Thesis, Un. Zurich.

Smith, F J, 2008. A new algorithm for navigation by skylight based on insect vision, in Biosignals 2008, 2, Eds. P Encarnacao & A Veloso, Madeira, 185-90.

Tyndall, J, 1869. On the blue colour of the sky, the polarisation of skylight, and on the polarisation of cloudy matter, Proc. Roy. Soc., 17, 223.

Von Frisch, K, 1949. Die Polarization des Himmelslichts als Orientierender Faktor bei den Tanzen der Bienen, Experientia, 5, 142-8.

Wehner, R, 1989. The hymenopteran skylight compass: matched filtering and parallel coding, J Exp. Biol., 146, 63-85.

Wehner, R, 1997. The Ant's celestial compass system: spectral and polarization channels, In Orientation and Communication in Arthropods, Ed. M. Lehler, Birkhauser, Berlag, Basel, Switzerland, 145-85.

Wehner, R, and Raber, F, 1979. Visual spatial memory in desert ants, Cataglyphis bicolor (Hymenoptera: Formicidae), Experientia, 35, 1569-71.

Wehner, R, 2001. Polarization vision – a uniform sesory capacity, J. Exp. Biol., 204, 2589-96.