

Chapter 2

BEOS: A tool for experimental design

2.1 Introduction

When designing visual experiments, one important aspect to be considered is the visibility of the stimuli to the experimental animal. In our case we have to be sure that the bees in our trainings and tests perceive the patterns we are offering them the way we think they do. As I will demonstrate below, the bee's eye is by no means a simple and uniform structure. This means that, if we want to get a reasonably accurate idea of how an image in front of the bee appears on the bee's retina, we cannot simply filter the input image with an uniform filter. This is where BEOS comes into play.

BEOS (Bee Eye Optics Simulation) is a program I developed as a tool for designing experiments in bee vision. It allows us to view a flat pattern in front of the bee through an approximation of the optics of the bee's eye. By using the simulation, we can check whether a pattern that is planned to be used in an experiment is adequate and appropriate for the question that is being posed.

In his chapter I will first give a brief survey of the theoretical basis of the optics of compound eyes and review the relevant literature, reaching back in time by more than one and a half centuries. I will then describe BEOS in detail and, finally, discuss its application in the last section of this chapter.

2.1.1 The theory of vision in compound eyes

The bee has two different types of eyes. One type, the ocellus, is a small, single lens eye of which the bee has three. The other type, the compound eye, is the one we will be concerned with here, since the ocelli are not involved in the visual tasks we are interested in (Wilson 1978, Stange 1981). A compound eye consists of a number of single units, or ommatidia. Each ommatidium has its own dioptric apparatus and a set of light receptors which receive light from a limited portion of the outside world.

The spatial resolving power of any eye is potentially limited by three factors: (i) the quantity of light available to the eye, (ii) the quality of the eye's optics and (iii) the spatial sampling frequency of the receptor mosaic. Since most of the behavioural experiments reported in this thesis were conducted in broad daylight, the first factor has little relevance here and is therefore not dealt with in detail. Instead – as have most of the authors in this field – I will concentrate on the optical and anatomical limitations.

Optics. A lens can never form a perfect image exactly reproducing the original object. The reasons for this inherent imperfection are spherical aberration, chromatic aberration and diffraction. The effects of the first two factors are relatively small in lenses with

small apertures such as the bee's facets, but with diffraction the opposite is true. Parallel light passing through a lens with small aperture is not focused onto a single point, but is dispersed into the so called Airy diffraction pattern, in which the intensity distribution shows a central peak (called the Airy disc) surrounded by concentric rings of much smaller amplitude. The halfwidth (width at half height) of the Airy disc is

$$\Delta\rho_1 = \lambda / D, \quad (2.1)$$

where λ is the wavelength of light and D is the diameter of the aperture (Hecht 1987, Warrant and McIntyre 1993). This dispersion of light has the effect, that the distal end of the rhabdom (positioned on the optical axis) receives some light even if incident rays enter the ommatidium at an angle to the optical axis. If we convolve the Airy disc with the acceptance function of the rhabdom, we get the theoretical angular sensitivity function of the ommatidium (Snyder 1979). The actual sensitivity function, however, does not only depend on the Airy disc and the rhabdoms acceptance function, but also on waveguide effects (if the rhabdom is narrow enough to act as a waveguide, which is the case in the bee) and possible light spread in the retina (Warrant and McIntyre 1993). The angular sensitivity function can usually be approximated by a two-dimensional, circularly symmetric Gaussian function of halfwidth $\Delta\rho$, the acceptance angle of the ommatidium.

The Fourier transform of the angular sensitivity function, the modulation transfer function (MTF), tells us what range of spatial frequencies the dioptric apparatus of the ommatidium can transmit. The frequency at which this function reaches zero is called the cut-off frequency (ν_{co}). This frequency is (Land 1989)

$$\nu_{co} = \frac{D}{\lambda}. \quad (2.2)$$

Any intensity modulations at spatial frequencies above ν_{co} are not perceived by the retina. This is the optical limitation to the spatial resolving power of the compound eye.

Anatomy. The spatial sampling frequency (ν_s) of a compound eye is a function of the interommatidial angle $\Delta\phi$ (ie. the angle between the optical axes of neighbouring ommatidia). According to the Whittaker-Shannon sampling theorem, the highest spatial frequency an array can resolve is

$$\nu_s = \frac{1}{2\Delta\phi} \quad (2.3)$$

for a square array (Snyder 1977) or a hexagonal array along one of its axes (ie. parallel to one of the diagonals of an individual hexagon). If the grating is oriented perpendicularly to an axis of a hexagonal array, then (Snyder 1977)

$$\nu_s = \frac{1}{\sqrt{3}\Delta\phi}. \quad (2.4)$$

In these situations each period of the grating would be sampled by two receptors. In other words, the receptors could be aligned with the extrema of the grating, such that a sequence of neighbouring receptors would view alternately dark and light areas.¹

¹ On the other hand, if the receptors are aligned to view the edges of the gratings, the whole array of receptors would perceive a uniform grey.

Eye parameter. In an ideal eye, the sampling frequency of the receptor mosaic should be lower than or equal to the cut-off frequency of the optics. A higher sampling frequency would be useless, since higher frequencies never reach the retina. If we combine equations (2.2) and (2.3) we get (Land 1989)

$$v_{co} \geq v_s, \text{ or } \frac{D}{\lambda} \geq \frac{1}{2\Delta\phi}, \text{ or } D\Delta\phi \geq \frac{\lambda}{2}. \quad (2.5, 2.6, 2.7)$$

The eye parameter $p = D\Delta\phi$ (Snyder *et al.* 1977) is a measure of how close the eye comes to the diffraction limit. With 500 nm light its minimal value (when $v_{co} = v_s$) is 0.25 μm , but real p values range from about 0.3 μm in the fovea of some insects (eg. the sand wasp *Bembix*; Horridge 1977) to 31 μm in the king crab *Limulus* (Land 1989). In other words, most compound eyes undersample their environment. One reason for this is that, if the amount of information in the image is to be maximised, the eye parameter is a function of the light level at which the eye operates (Snyder *et al.* 1977). Accordingly, animals active in bright daylight often feature low values of p , while the highest p values are found in nocturnal and marine animals (Horridge 1977).

In this section we have only covered the resolving power of the lenses and the spatial resolution of the retina. The visual acuity, ie. what the animal perceives and acts upon in a behavioural experiment, depends on many more factors such as the angular velocity of the pattern, its contrast and colour, as well as on the mechanisms underlying subsequent processing. Neural and behavioural mechanisms that might improve or impair visual acuity include lateral inhibition, neural pooling and temporal scanning. These aspects will not be covered here, since BEOS is a simulation of the bee's optics only.

2.1.2 Bee vision

The interommatidial angle $\Delta\phi$. Götze (1927) and Baumgärtner (1928) were the first to make quantitative measurements on the compound eyes of the bee. Götze determined the extent of the bee's visual field by assuming that the hairs on the cornea of the compound eye are parallel to the adjacent ommatidial axes (which led to an underestimate of the visual field and binocular field). He also made some fairly crude measurements of the interommatidial angles, using histological sections in various planes. Baumgärtner's measurements of $\Delta\phi$, although based on the same technique, are much finer. Figure 2.1 (broken lines) shows Baumgärtner's mean $\Delta\phi$ as a function of the ommatidium number.

It is obvious that the interommatidial angles are not uniform. The angles vary between 1.7–7.5° in the vertical section² and between 2.7–4.0° in the horizontal section. The minima correspond to ca. 8° down from the horizontal and 60° to the side from the frontal direction, respectively (Baumgärtner 1928; not directly inferable from Figure 2.1.). However, since the sections were made relative to the eye's shape, and not relative to its natural position in space, we cannot directly apply these resolution optima to the bee's behaviour. Baumgärtner had some indications from behavioural experiments (see

² Baumgärtner's definition of the vertical interommatidial angle – as well as del Portillo's later on – corresponds to half of $\Delta\phi_v$ as it is used here. Their data have been converted to match the definition of $\Delta\phi_v$ given in Figure 2.3b.

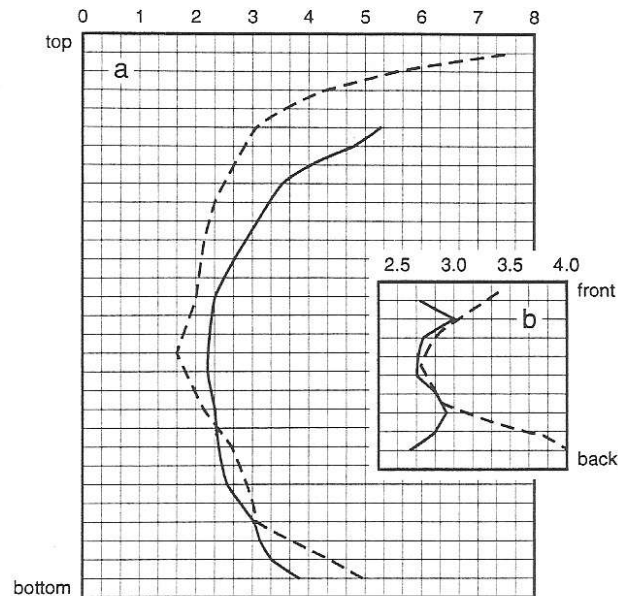


Figure 2.1: Baumgärtner's and del Portillo's measurements of $\Delta\phi$ in the bee's eye. Abscissa: interommatidial angle $\Delta\phi$ in degrees. Broken lines: Baumgärtner's data. Solid lines: del Portillo's data. **a:** Vertical $\Delta\phi$. Vertical section containing ca. 144 ommatidia. (1 unit = 5 ommatidia) The lower end of the scale corresponds to the ventral rim of the eye. **b:** Horizontal $\Delta\phi$. Horizontal section containing ca. 48 ommatidia. The lower end of the ordinate corresponds to the posterior rim of the eye. (Redrawn from del Portillo 1935).

Chapter 1) of where in the bee's visual field these optima should lie and suggested that the bee might align them by tilting its body.³

The main difficulty in applying Baumgärtner's measurements to the bee's visual acuity is that the ommatidium's anatomical axis does not necessarily correspond to its optical axis, i.e. the ommatidium is often looking in a different direction from the one to which it is geometrically aligned. Baumgärtner (1928) measured differences of up to 40° (at the ventral rim of the eye).

Del Portillo (1935) repeated Baumgärtner's measurements of $\Delta\phi$ (Figure 2.1, solid lines). In the vertical sections his results are slightly different, as he was cutting in a different plane (through the middle of the eye rather than along a plane through both eyes as Baumgärtner did). He reports the vertical $\Delta\phi$ to range between 2.2° and 5.2° . In the horizontal plane his measurements basically match Baumgärtner's, except for the border regions, where he found smaller values. He attributes this phenomenon to "developmental deficiencies".

It was not until almost fifty years later that more accurate (i.e. non-histological) measurements of the bee's interommatidial angles were performed. Seidl (1982; Seidl and Kaiser 1981) mapped out the bee's visual field by studying the pseudopupil under

³ He filmed bees approaching a vertical pattern and found that the angle between the longitudinal axis of the bees and the horizontal varies between $15\text{--}30^\circ$.

antidromic illumination.⁴ This optical technique permitted the determination of the optical axis of each ommatidium in a coordinate system centred on the bee's head which can be related to the external world. Since the measurements were done on whole heads, they can be expected to be much more accurate (less artefact prone) than measurements on histological preparations. Seidl's results are depicted in Figure 2.2.

Seidl's $\Delta\phi_h$, ie. the interommatidial angle in the horizontal plane, shows little variation along the vertical. It ranges from 2.1° to 4.6° (Seidl 1982) and its minimum along a given latitude is mostly located between ca. 30° and 45° to the vertical midline. $\Delta\phi_v$ ranges from 1.2° to 4.9° . It shows a minimum at the equator, increasing towards both the dorsal and the ventral rim of the eye. It is quite uniform along a given latitude, except at the equator, where it decreases towards the anterior and the posterior rim of the eye, and the dorsal rim, where the opposite is the case.

These optical measurements (Figure 2.2) compare quite well with the older histological data (Figure 2.1). The overall pattern in all of them is the same: both horizontal and vertical interommatidial angles are minimal somewhere in the centre of the eye and increase towards the borders.

The acceptance angle $\Delta\rho$. The visual field of individual *Apis mellifera* ommatidia have been measured optically and electrophysiologically and calculated using ray-tracing techniques. The results of these studies can be grouped into two distinct classes with $\Delta\rho$ values differing by a factor of two. The first class includes Kuiper's (1962) and Varela and Wiitanen's (1970) studies. Kuiper measured the acceptance angle optically on "scalps" cut from the eye while frozen in liquid air. He found a bell shaped acceptance function with a halfwidth (width at half height) of about 6.5° and a total width of about 20° . Varela and Wiitanen measured the refractive indices of the different parts in the ommatidium, as well as their dimensions and relative position, and used this data to calculate an admittance function⁵ using both ray-tracing techniques and the Gaussian thick lens formula. The resulting function had the shape of a Gaussian with halfwidth $\Delta\rho = 5.55^\circ$.

The second class of studies found acceptance angles of only half this width. The acceptance functions measured using optical techniques by Wiedemann (1965, see also Autrum and Wiedemann 1962) and Eheim (1972, see also Eheim and Wehner 1972) had a halfwidth of 2.60° (Eheim 1972) and a total width of ca. 7° (Wiedemann 1965, Eheim 1972). Laughlin and Horridge (1971) measured $\Delta\rho$ electrophysiologically and found it to be 2.6° as well. Ohly (1968, cited in Eheim and Wehner 1972) used the pseudopupil under antidromic illumination to determine the total width of the acceptance function to be about 8° . The exact results of all these studies are summarised in Table 2.1.

It is not clear what caused the difference between the first two studies listed in Table 2.1 and the remaining studies in the list. Kuiper's results might contain an artefact caused by the freezing of the preparation. It has been pointed out (Laughlin and Horridge 1971) that Varela and Wiitanen failed to take diffraction effects within the

⁴ Antidromic illumination reverses the path of the light through the eye's optics. The insect's head is illuminated from inside, so that the light follows the rhabdom to its distal tip and leaves the ommatidium through the dioptric apparatus.

⁵ Varela and Wiitanen's (1970) "admittance function" is defined as the percentage of rays reaching the rhabdom of those falling onto the ommatidium as a function of angle of incident.

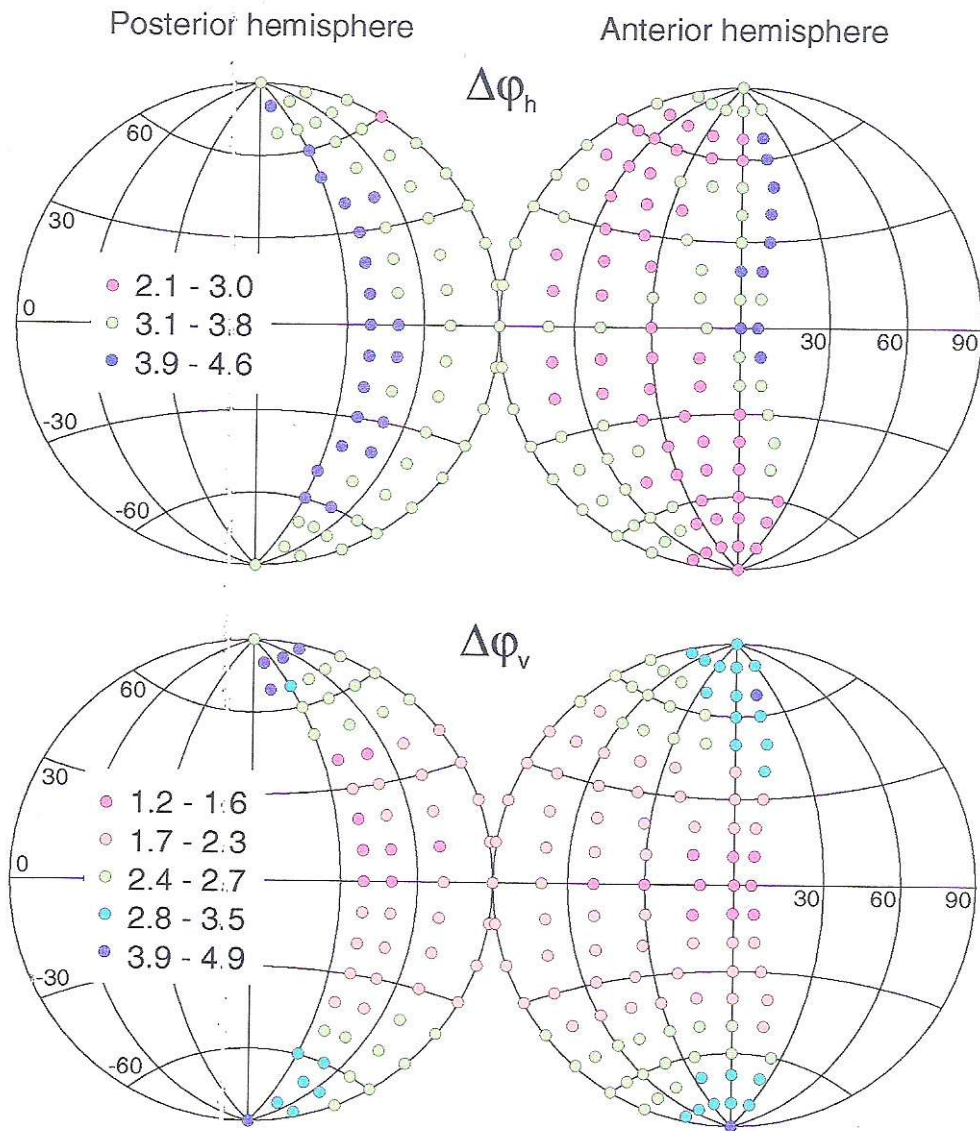


Figure 2.2: Seidl's measurements of $\Delta\phi$ in a bee's right eye. The angular space around the bee is represented by the posterior (left) and anterior (right) hemisphere. Each dot represents a measurement. Upper half: horizontal interommatidial angle ($\Delta\phi_h$). Lower half: vertical interommatidial angle ($\Delta\phi_v$). (After Seidl 1982).

cone tip into consideration, which might account for the difference between their admittance function and the intensity distributions measured in the last four studies listed in Table 2.1. All in all I prefer to rely on the second class of results with a $\Delta\rho$ of 2.6° .

Some of the studies summarised in Table 2.1 differentiated between acceptance angles in the horizontal and vertical direction, respectively. None of them found a significant difference between the two directions. Furthermore, Wiedemann (1965) and Eheim (1972) report slightly larger angles in the horizontal, while in Laughlin and

Horridge's (1971) results the opposite is true. It can therefore be assumed that the acceptance function of the bee's eye is radially symmetric.

Finally, one of the studies (Eheim 1972) took the adaptation state of the eye into account as well. The results show that $\Delta\rho$ in the dark adapted state (marked as (d) in Table 2.1) is slightly larger than in the light adapted state (l). However, this difference was not statistically significant.

All the measurements listed above were done on ommatidia in the central eye region, ie. the region looking sideways. We do not know how $\Delta\rho$ varies across the eye. From the theoretical point of view of an ideal match between interommatidial angle and ommatidial acceptance angle one might expect $\Delta\rho$ to vary with $\Delta\phi$, but so far there is no experimental evidence for that.

Table 2.1: Summary of measurements of the acceptance function of honeybee ommatidia. h: horizontal halfwidth. v: vertical halfwidth. l: light adapted. d: dark adapted.

Study	Technique	Halfwidth ($\Delta\rho$)	Total width
Kuiper (1965)	optical on frozen prep.	ca. 6.5°	ca. 20°
Varela and Wiitanen (1970)	ray-tracing	5.55°	ca. 15°
Wiedemann (1965)	optical on frozen prep.	—	h: 7.2° ± 1.4° v: 6.7° ± 1.1°
Eheim (1972)	optical on fresh prep.	h: 2.56° (l); 2.78° (d) v: 2.53° (l); 2.75° (d)	h: 7.42° ± 0.24° v: 6.68° ± 0.14°
Ohly (1968)	pseudopupil	—	ca. 8°
Laughlin and Horridge (1971)	electrophysiology	h: 2.5° ± 0.4° v: 2.7° ± 0.8°	ca. 7°

Acuity measured in behavioural experiments. The first behavioural measurements of visual acuity in honeybees were performed by Baumgärtner (1928). He trained bees to distinguish between squares of different colours in the vertical plane and then moved the colour patches further into tunnels, away from the bees. He then recorded at what distance the bees were not able to discriminate the colours from outside the tunnels any more, ie. when the bees entered the wrong tunnel equally often as the right one.

This approach is likely not to measure the bees' acuity, but rather their intensity discrimination ability, since an object could give rise to a mean intensity difference in a single ommatidium even if it is much smaller than $\Delta\phi$. It is well known (Hertz 1934, Palka and Pinter 1975) that the ability to resolve a periodic grating (which is the usually accepted measure of visual acuity) is not directly related to the ability to detect a single spot. Baumgärtner's experiments will be considered further in Section 2.3.2.

The same shortcoming applies to the experiments of Wolf (1931). He changed the interval length of a sequence of rectangular landmarks along the flight path of the bees, thus varying the angular size of each landmark seen from the previous one in the

sequence. The time it took the bees to find their way along this succession of landmarks was then interpreted as an indication of whether the bees could see a landmark when they passed the previous one.

A better approach to behavioural acuity measurements is to use extended sources such as gratings. A point source (such as a single rectangle) has a broad spatial frequency spectrum with no lower limit. Therefore it is impossible to determine the cut-off frequency of an optical system with a single spot. A perfect grating, on the other hand, does not contain any frequencies lower than its fundamental frequency, or only the fundamental frequency in the case of a sinusoidal grating.

Most studies of visual acuity in insects and crustaceans using gratings rely on the optomotor reflex. This reflex causes the animal to follow any wide field movement the eyes perceive, ie. to stabilise the image of its surroundings on the retina. In the natural situation this helps a moving animal to stabilise its path in a stationary environment. Under experimental conditions the optomotor response can be utilised to determine whether a pattern (usually a grating) on the inside of a rotating cylinder can be resolved by the animal located at the centre. If the animal attempts to follow the movement of the cylinder, it perceives the pattern; if it does not move or moves in the wrong direction, it is not able to resolve the pattern and sees either a uniform mean luminance or some geometric interference pattern.

The first researcher (and to my knowledge the only one) to use optomotor experiments to measure visual acuity of honeybees was Hertz (1934).⁶ She placed her bees in the centre of a rotating, striped cylinder under a glass dome just big enough for the bee to turn in place. Using rather subjective criteria to interpret the ambiguous response of the bees she determined the minimum resolvable angular wavelength of the grating to be 4–5°. Kunze (1961) performed an extensive study of the optomotor response in bees. However, when testing gratings of different wavelengths he limited the bees' sampling interval artificially to 5°. His results are therefore not useful in determining the anatomical sampling frequency of the bee's eye.

It can be argued that measuring the limits of the optomotor response only reveals the acuity of this visual subsystem and not necessarily the optical acuity of the bee's eye. To overcome this problem Srinivasan and Lehrer (1988) trained bees to discriminate between two patterns in a Y-shaped testing apparatus similar to the one shown in Figure 3.1. Entering the Y at the "trunk", the bees had to decide between a black and white grating at the end of one of the branches of the Y and a uniformly grey area at the end of the other branch.⁷ By making the branches progressively longer and thereby moving the two patterns farther and farther away from the bees, the angular wavelength of the gratings as seen from the "decision chamber" (the branching point of the Y) could be reduced. The minimum spatial frequency at which the bees could just perceive the modulation of the grating was determined to be 0.27 c/deg (which corresponds to a

⁶ Hecht and Wolf (1929) performed similar experiments, but these seem to have measured a different behaviour. Their bees crawled on an "inclined transparent surface" below which a luminous grating was moved. The response of the bees was "a sudden change in the direction of [their] progression, which [was] opposite in sign to the movement of the pattern." The minimal spatial wavelength of the grating to elicit this behavioural response at the maximal level of illumination was about 2°.

⁷ They also trained bees to discriminate between horizontal and vertical gratings, but the acuity measured that way, of course, potentially only reflects that of a subsystem as well, namely orientation discrimination.

grating wavelength of 3.7°). A detailed account of this study will be given in the discussion of this chapter.

The Wiitanen-Varela model. Computer simulation of the optics of the bee eye has been attempted previously by Wiitanen and Varela (1971). However, their matrix based simulation has two major shortcomings. Firstly, it assumes the ommatidia to be arranged in a regular hexagonal array with a constant interommatidial angle of $\Delta\phi = 1.5^\circ$ (which we now know to be the absolute minimum $\Delta\phi$ in the bee's eye, applying only to $\Delta\phi_v$ along the equator).⁸ And secondly, the acceptance function it uses has a halfwidth of $\Delta\rho = 5.55^\circ$ (based on the results of Varela and Wiitanen (1970) obtained by ray tracing analysis).

Apart from these weaknesses the program might have been suitable for the tasks to which it was applied (but see Discussion). However, it is not appropriate for more general use, that is to simulate the bee's view of any arbitrary pattern. For example, the projection of the pattern to be viewed onto the surface of the model eye has to be done manually. It is apparent from the results presented in Wiitanen and Varela (1971) that this is a considerable source of error.

2.2 Description of BEOS program

BEOS (Bee Eye Optics Simulation) is a computer program that simulates the view through the optics of a honeybee's eyes. It was developed as a tool to aid the design of experiments on bee vision.

2.2.1 The model eye

BEOS is based on a single model eye with an array of sampling stations (the model ommatidia) approximating the bee's array of ommatidia as described by Seidl (1982). The visual field of the single eye covers the frontal hemisphere of the model bee. The left half of this visual field corresponds to the portion of the visual field between the frontal and the lateral median of the left eye, while the right half corresponds to the equivalent portion of the visual field of the right eye. The array of sampling stations is created by the following procedure. Starting with a frontal ommatidium, ommatidia are progressively added to the left and to the right, spaced by the interommatidial angle $\Delta\phi_h$ which is a function of the azimuth (α , see Figure 2.3a). At $\alpha = 0$ (frontal) $\Delta\phi_h$ is 3.7° . With increasing α , $\Delta\phi_h$ decreases linearly down to 2.8° at $\alpha = 45^\circ$, after which it increases, again linearly, back to $\Delta\phi_h = 3.7^\circ$ at $\alpha = 90^\circ$. When α reaches 90° (the limit of the frontal hemisphere) it is set back to 0 and ε , the elevation (Figure 2.3a), is set to $\varepsilon = \Delta\phi_v / 2$ to commence the creation of the next row (see Figure 2.3b for explanation). To create a hexagonal array α is now set to $\Delta\phi_h / 2$ before the first two (almost frontal) ommatidia of this row are added. The row can then be completed in the same way as the first one. The rows at $+\varepsilon$ and at $-\varepsilon$ are created simultaneously. After completion of the second row α is set back to 0 again, ε is set to $\Delta\phi_v$ and the process starts over. In this

⁸ The definition of this $\Delta\phi$ corresponds to $\Delta\phi_h$ in BEOS (see Figure 2.3). Due to the regularity of their hexagonal array Wiitanen and Varela's $\Delta\phi_v$ can be calculated to be $\Delta\phi_v = \sqrt{3} \cdot \Delta\phi_h = 2.6^\circ$.

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