

‘Matched filters’ – neural models of the external world

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A. Introduction

In her late days, Gertrude Stein is reputed to have inquired, “What is the answer?” Getting no reply, she said, “In that case, what is the question?”

In trying to understand the mechanisms of animal behaviour, e.g. the way of how animals get around in their visual, olfactory, or acoustic world, neurobiologists are often inclined to ask the sort of question that is quite different from the one which animals had to answer during their evolutionary history. Yet without knowing these evolutionary answers, and without appreciating them as specific adaptations tailored to the animal’s particular behavioural needs, one will hardly be able to ask the proper questions about the underlying neurobiological mechanisms.

What is the answer? The key point in referring to Gertrude Stein’s paradoxical inquiry in this context is that the genes do not supply an animal’s brain with the general ability to solve problems, but provide it, from the outset, with specific rules of sensorimotor coordination suitable for steering particular actions. The answer is the odd mechanism and the chance solution. As natural selection is inherently opportunistic, the neurobiologist must adopt the attitude of the engineer, who is concerned not so much with analyzing the world than with designing a system that fulfils a particular purpose. But to whom do I tell this in the presence of Hansjochem Autrum celebrating his jubilee?

Almost fifty years ago, Autrum (1940) realized that grasshoppers had to employ mechanisms of directional hearing that were quite different from the ones used by mammals: for the simple reason that grasshoppers, like all insects, were small animals – small with respect to the wavelength of the sound wave. If a pure pressure receiver is smaller

in diameter than about half of the wavelength of the sound wave, it is non-directional and, as a consequence, biologically almost useless. Insects have solved this problem in two ways. Their ears act either as pressure gradient transducers, at least at low frequencies, or as particle-velocity receivers (for recent reviews see Michelsen 1983; Lewis 1983; Bennet-Clark 1984). Still other problems of directional hearing arise in fish. A fish may reach the same size as a mammal, but as it is surrounded by a medium of about the same density as its own body, it is acoustically transparent. Furthermore, the fact that the sound-pressure receiver of a fish is an unpaired organ (the swimbladder) should render a fish completely insensitive to the direction of sound. Nevertheless, fishes can localize a sound source directionally quite well and, as we now know (Schuijff and Buwalda 1980), do so by exploiting the particle movement that is necessarily associated with a sound-pressure wave. As this movement is picked up directly by the otolithic apparatus of the fish’s inner ear, and as particle velocity is vectorial, directionality is an intrinsic property of such an ear.

How have sensory systems managed to solve the particular problems posed by the idiosyncrasies of the environment within which they operate? This is the basic question underlying Hansjochem Autrum’s multifaceted research through many years, and so it comes as no surprise that the organizers of the symposium held in honour of his 80th birthday have chosen just this topic as the unifying theme. By the same token, Autrum’s life-long occupation with this topic, and his fundamental contributions to what is now often referred to as ‘Sensory Ecology’ (Ali 1978), make me wonder whether he is really 80 years old: His wisdom and perception require at least twice that many years.

My contribution to Hansjochem Autrum’s aca-

demic birthday party may seem a bit unconventional, at least to those who like to think in terms of optimal design and general organizational principles. The view I shall champion is that animals solve their problems of spatial orientation not by resorting to abstract computations performed within three-dimensional Newtonian space, but by adopting approximations, shortcuts, and simple tricks. To us, such solutions might appear incomplete and vulnerable to certain kinds of navigational error; to us, they might cover only some partial aspects of the more comprehensive geometrical problems we would like to envisage; but to the animals they are always the full solutions to the very problems with which they must contend.

The topics discussed in this chapter are grouped into sections focusing on six different aspects of spatial orientation, but a number of common themes span these sections. Among them is the notion that a great deal of spatial information used by an animal to guide its activities within its world is handled and processed at rather peripheral levels within the nervous system. In particular, I shall argue that in many cases it is already the spatial design of the receptor layer at the outermost periphery of the nervous system, that 'solves' a particular problem. Arrays of receptors may form 'matched filters' – to borrow the engineer's term (e.g. Goodman 1968) – in which the spatial layout of a population of receptors is matched to a certain spatial aspect of the navigational problem to be solved. In that respect, let me take the poetic freedom to use the term 'matched filter' in a somewhat metaphorical sense. Of course, perceiving the world through such a 'matched filter' severely limits the amount of information the brain can pick up from the outside world, but it frees the brain from the need to perform more intricate computations to extract the information finally needed for fulfilling a particular task. *Algebra gives way to geometry.*

I hope that the approach I shall entertain in this chapter will be successful in analyzing and explaining certain rather complex phenomena in animal orientation. At least, I aim to take a stand on matters which, as I hope, will continue to spark professional debate.

B. Case studies

1. Measuring the volume of a sphere

Ichneumonid wasps of the genus *Trichogramma* lay their eggs into the eggs of other insect species, mainly lepidopterans, which they use as hosts for

their larval stages. The exact number of eggs a female wasp deposits into her spherical host depends on the size of the host. If too many eggs are injected into too small a host, the reproductive success of the wasp will be reduced due to larval competition for the limited nutrients available. On the other hand, the wasp's benefit/cost ratio deteriorates, if an inappropriately small number of eggs is deposited, because then the female wasp must spend more time in localizing and manipulating her hosts. For *Trichogramma* it is all the more important to keep the overall search time down, as the wasps are gregarious and thus are probably subject to strong competition among females.

But how do the wasps determine the sizes of their hosts? In principle, they could do so by examining the surfaces of their spherical hosts and measuring the curvatures of the spheres. For example, while manipulating a host with her legs, the female wasp could trace out a spherical triangle, measure some angles and distances within this triangle, and then use these data to compute the radius of the sphere. Of course, the wasp's brain does not perform such feats of computation, but relies on a simple trick. When two Canadian entomologists (Schmidt and Smith 1986) took photographic pictures of ovipositing female wasps they realized that each wasp assumed a stereotyped body posture when manipulating her host. Irrespective of the size of the host, the height of the wasp's pronotum above the surface of the host ($ME - r$ in Fig. 1) was constant, and so was the angle between the thorax and the head (angle DCE). Under these conditions, the position of the legs necessary for maintaining the preferred body height could provide the wasp with some measure of the host's curvature, but would do so, with fair precision, only for a limited range of host sizes – and unfortunately, not for the sizes accepted by the wasps. Furthermore, if the wasp – like most walking insects (Delcomyn 1981) – used the alternating tripod gait, adjusting the position of the legs could not provide her with any information about the curvature of a sphere. This is because then only two ipsilateral legs would be in contact with the substrate at any one time. But the wasp does use the alternating tripod gate (Schmidt and Smith 1986).

Instead of the legs, it is the antennae with which the ovipositing wasp measures the curvature of the host eggs. While manipulating the eggs with their legs the wasps investigate the surface by continuous drumming movements of their antennae. During these movements, the angle between head and scapus (angle BCD , η) is strongly correlated with

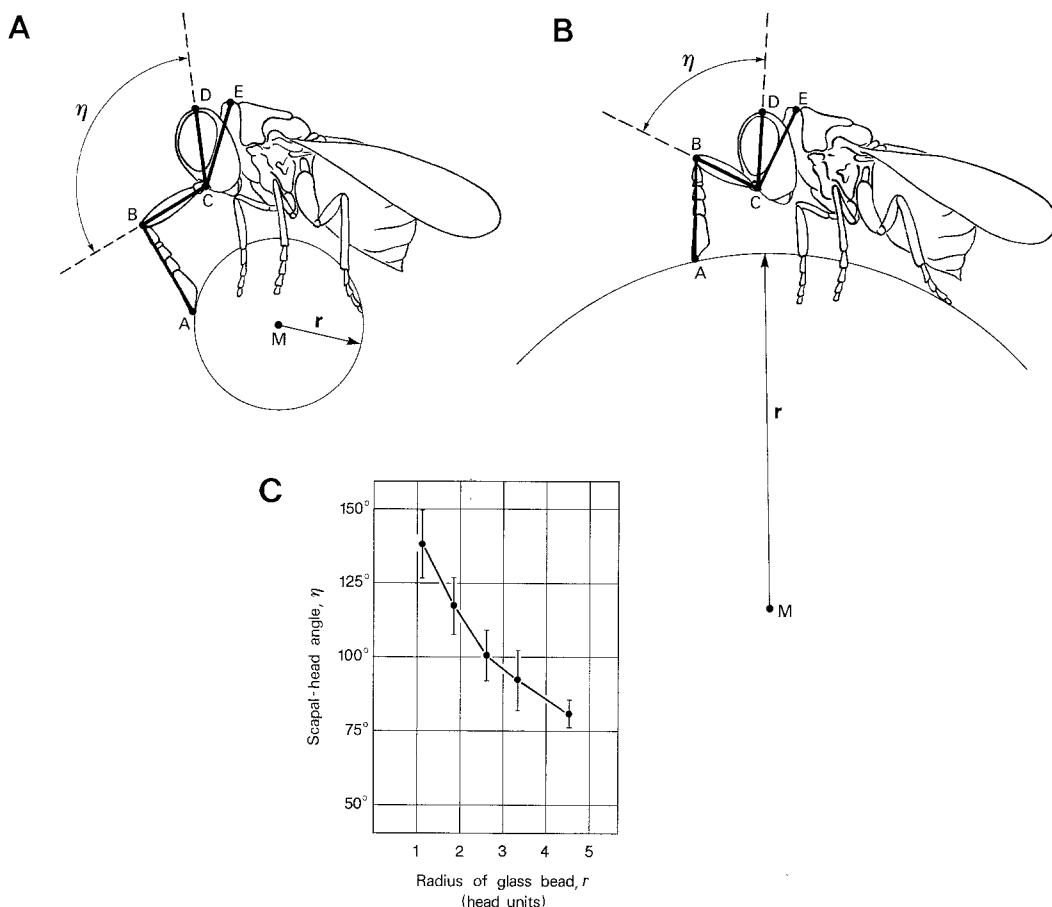


Fig. 1A–C. Parasitoid wasps of the genus *Trichogramma* (Ichneumonoidea) use the surface curvature of their hosts (insect eggs) to determine the number of progeny allocated to the host. **A** and **B** Profile views of female wasps examining glass bead models of different sizes. **C** Scapal-head angles observed for different sizes of glass bead models. The angles were determined by analyzing photographs taken through a dissecting microscope. η Scapal-head angle (angle BCD); M centre of spherical glass bead; r radius of glass bead. A redrawn and modified from Schmidt and Smith (1986), **B** and **C** designed and computed by using data of Schmidt and Smith (1986)

the radius r of the host: the larger r , the smaller η (Fig. 1A–C).

Now, an attractive hypothesis emerges: The wasp determines the radius, and thus the volume, of her host not by performing some kind of spherical trigonometry, but by taking a single measure: the head/scapus angle η monitored most probably by the mechanosensory bristles located at the joint between head and scapus. (Notice, however, that relying on the measurement of η alone is useful only when the wasp adjusts her body position so as to keep two other measures constant: the height of the thorax above the surface, and the angle between thorax and head.) In theory, the hypothesis could be tested by manipulating η experimentally and counting the number of eggs deposited by the wasp into a flat surface. I say 'in theory', because the wasp's minute size (less than a millimetre in length) renders the necessary manipulations a rather tricky exercise.

However elegant the wasp's way of determining the volume of a sphere might appear, there is little chance that it will make its way into the textbooks of geometry. The range of curvatures over which the wasp's mechanism works with fair precision is rather small (see Fig. 1C) – but it covers exactly the sizes of the hosts preferred by *Trichogramma*.

This introductory example, in which an important aspect of a parasitoid wasp's three-dimensional world is represented by a one-dimensional scale, the η -scale, might appear trivial. If this is so, it has fulfilled its purpose: to prepare the reader for the more complex studies to be described next. With one exception, and unlike the *Trichogramma* case, they are taken from the animals' visual world. There are obvious reasons for this choice: Vision is the spatial sense *par excellence*. It exceeds by far any other sensory system in its capacity to resolve fine spatial detail. The physical nature of light is the ultimate reason for this supremacy.

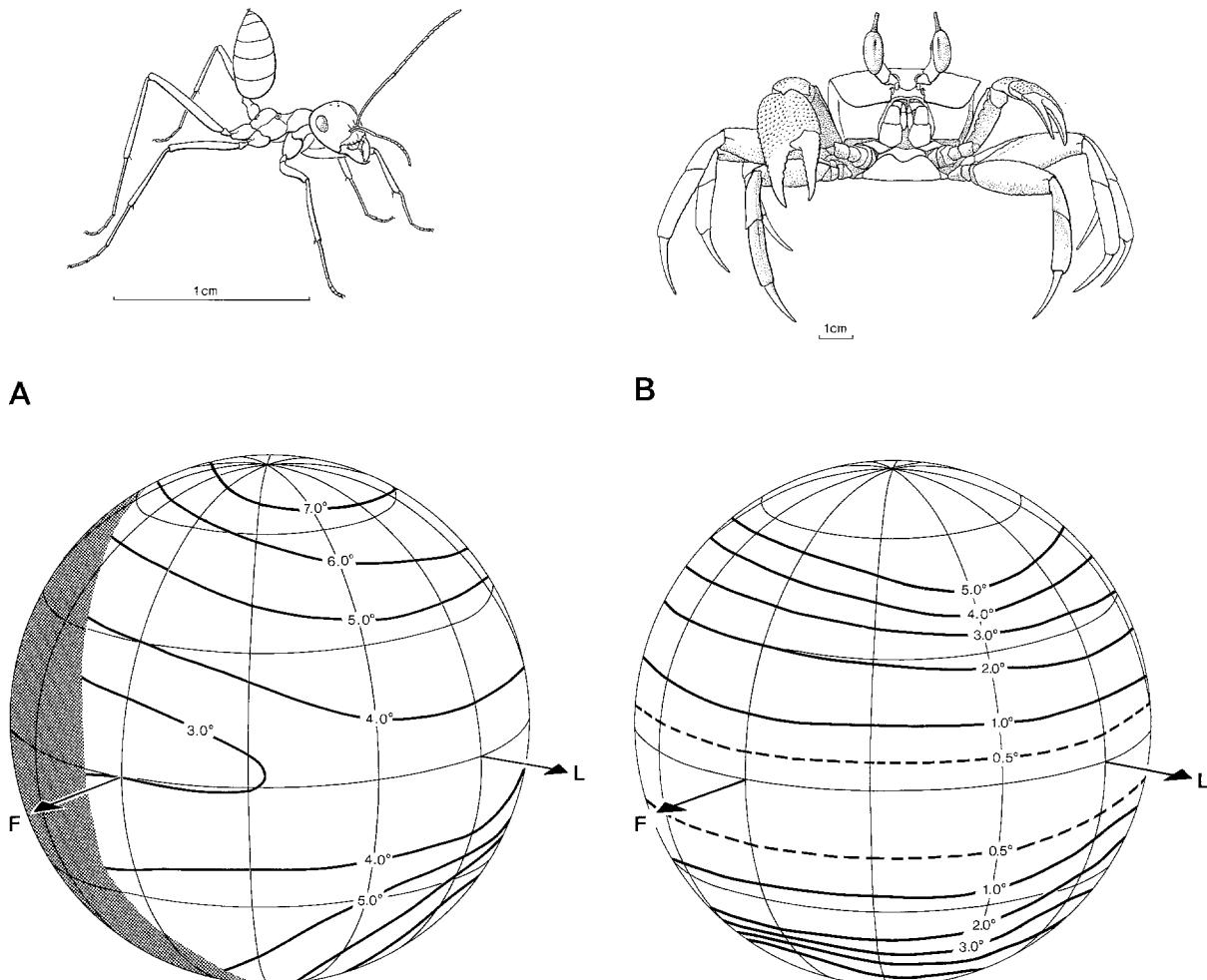


Fig. 2. Visual spheres and 'visual streaks' of desert ants (*Cataglyphis bicolor*, A) and shore-living crabs (*Ocypode ceratophthalmus*, B). In the lower graphs the visual fields of the left eyes are projected onto a sphere. Within these fields of view, the spatial distribution of the interommatidial distances (=receptor spacing) is depicted by the heavy isolines. The arrows F and L point in the forward and lateral direction, respectively. The interommatidial angles (numbers associated with isolines) were determined by ophthalmoscopic (pseudopupil) measurements in the live eyes of ants and crabs (A: Wehner and Srinivasan 1984; B: Zeil et al. 1986). The inclinations of head (*Cataglyphis*) and eyestalks (*Ocypode*) were taken from photographic pictures of walking ants and crabs

2. Looking at the horizon

Let us first consider the visual world of two groups of arthropods inhabiting the exceedingly flat terrains of the Saharan salt pans and the intertidal sand and mud flats of the seashore: the desert ants, *Cataglyphis*, and the semi-terrestrial crabs, *Ocypode*, respectively. The visual world of these arthropods is dominated by the horizon, and it is there – within a narrow strip just above and below the horizon – that amazingly accurate discriminations are made between differently sized skyline landmarks (*Cataglyphis* ants: Wehner and Räber 1979) and conspecifics (*ocypodid* crabs: Greenspan 1980; de Brooke 1981). This visual capacity is directly related to the optics and overall structure

of the eye, in which a disproportionately large number of photoreceptors is looking at the horizon.

To the uninitiated, this may seem surprising. The multiple-lens compound eyes of insects and crustaceans have so much come to epitomize bulky hemispheres covered by uniform arrays of functionally identical visual subunits (ommatidia) that the idea of optical inhomogeneities and receptor gradients in compound eyes is a strikingly counter-intuitive notion. In fact, however, such inhomogeneities occur in many compound eyes (Horridge 1978; Land 1981; Wehner 1981). Optical investigations of the eyes of *Cataglyphis* ants and *Ocypode* crabs have revealed pronounced band-like zones of especially high visual acuity indicated by mini-

mum values of interreceptor spacing (Fig. 2). In running ants and crabs, these 'visual streaks' are perfectly aligned with the horizon, irrespective of the load an ant may carry (Wehner 1982), or the gravitational input a crab may receive from its statocysts (Zeil et al. 1986).

On closer inspection of the maps of interommatidial angles in Fig. 2 one realizes that the maximum visual acuity within the visual streak is considerably larger, by almost one order of magnitude, in the crab than in the ant. Actually, interommatidial angles of 0.3° as found in *Ocypode ceratophthalmus* (Zeil et al. 1986) are the smallest recorded in any compound eye. In spite of this exceptionally high visual acuity implied by these small angles, there is nothing special about the eyes of crustaceans as compared to those of insects. *Ocypode* just happens to be much larger than *Cataglyphis* (see insets and scales in Fig. 2). Larger animals can afford to have larger eyes, and for simple optical reasons (e.g. Land 1981), larger eyes allow for higher visual acuities.

Visual streaks are by no means restricted to compound eyes. They occur in the single-lens eyes of vertebrates as well (Walls 1942; Hughes 1977). In fact, in some reptiles, birds and mammals – and even in fish (p. 518) – narrow horizontal bands of high visual acuity occur, in which the vertical receptor gradients are much more pronounced than in insects and crabs. All animals in which visual streaks occur live in open habitats. Visual streaks are therefore common adaptations to the geometrical potentialities and constraints that visual systems and their owners encounter in a world dominated by a horizontal skyline.

In some compound eyes, the adaptations to living in a flat world are much more intricate than the mere presence of a visual streak may indicate. For example, thanks to the work of Zeil and his collaborators (1986) we know a fair amount about how the receptor spacing varies at right angles to the visual streak of *Ocypode* crabs. According to these investigations the vertical distribution of interommatidial angles is such that objects that appear near to the horizon and are of constant absolute size are seen by a constant number of ommatidia, irrespective of the distance between the object and the eye (Fig. 3A, B). Hence, by avoiding the need of disentangling information about distance and size, *Ocypode* solves the problem of *size constancy* in a most elegant way: Whenever a certain number of ommatidia positioned in vertical rows near the equator of the eye are stimulated, the crab 'knows' that an object of a given (absolute) size is ahead. Clearly, this simple mechanism of size constancy works only when the world within which the animal moves is projected onto the retina in a strongly predictable way as is the case in a flat environment viewed by a visually stabi-

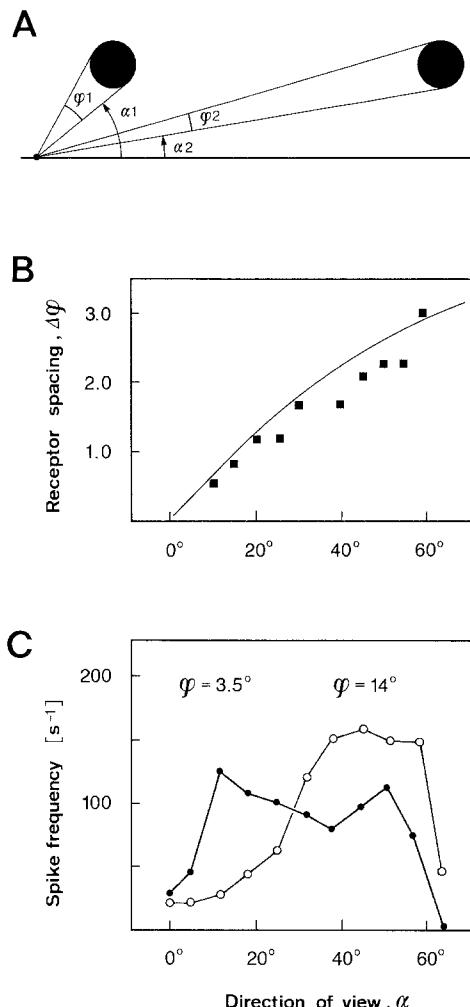


Fig. 3A–C. Size constancy in compound eye vision. **A** Schematic representation of the phenomenon of visual size constancy. Two black spheres of equal absolute size are presented at different distances from the eye and, thus, give rise to differently sized retinal images (angular widths φ_1 and φ_2). If the objects always occur at the same height above ground (e.g. the chela of a conspecific), the distance of the object from the eye is unequivocally correlated with the vertical position α of the retinal image. If, in addition, the vertical gradient of interommatidial angles φ is such that φ_1 and φ_2 include equal numbers of receptors, i.e. ommatidia, visual size constancy is achieved in a simple way (see text). **B** Vertical receptor gradient (vertical distribution of interommatidial angles, $\Delta\varphi$) in the crab *Ocypode ceratophthalmus*. Measured values of $\Delta\varphi$ are depicted by black squares; the curve describes the vertical distribution of $\Delta\varphi$ that would be expected if the eye were designed according to the rules outlined in A. Notice the fit between the data points and the theoretical function describing visual size constancy. Calculated from data in Zeil et al. (1986). **C** Responses of a visual interneuron of the waterbug *Notonecta glauca* (see Fig. 5C) to moving black squares of different sizes ($\varphi=3.5^\circ$, filled symbols, and 14° , open symbols). The responses are determined for different vertical positions of the targets within the insect's visual field. Redrawn and modified from Schwind (1978)

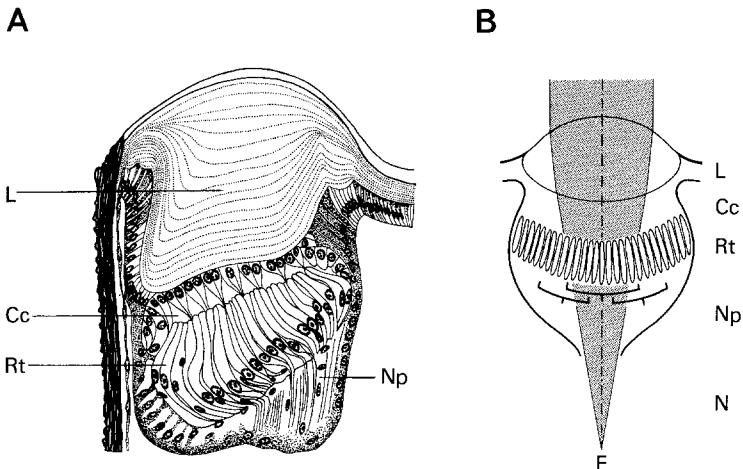


Fig. 4A, B. Insect ocelli. **A** Longitudinal section through a lateral ocellus of the dragonfly *Agrion* spec. Redrawn from Hesse (1901). **B** Schematic representation of an insect ocellus and its underfocussed optical system. The dashed and dotted line marks the optical axis of the ocellus. Light entering the ocellus from any particular direction (e.g. parallel to the optical axis as depicted in this figure by the grey area) is distributed over an extended part of the retina rather than focussed on a single retinal point. The highly convergent projection pattern of the photoreceptor axons is indicated by the three brackets underlying the retina and symbolizing three receptor populations which project onto three different interneurons. *Cc* Corneagen cells; *F* focal point; *L* lens; *Np* neuropil (first synaptic layer); *Rt* retina

lized eye. In humans, size constancy includes independent measurements of absolute distance and retinal image size, and thus requires more complicated neural circuitry than is necessary in crabs.

Of course, the evidence that the receptor gradient depicted in Fig. 3B provides the animal with size-constant information is suggestive rather than conclusive. More direct evidence comes from studies on water bugs, *Notonecta* (Schwind 1978, 1980). These predatory bugs hang upside down in the water with their feet in contact with the water surface. There they wait in ambush for insects moving in the surface film. In the optic lobes of the bugs, one type of visual interneuron responds maximally to moving dark objects of a certain (absolute) size, irrespective of the distance at which the object is presented in front of the eye. As shown in Fig. 3C, maximum responses are elicited by small spots projected onto those parts of the eye that look just above the horizon, but the size of the spots to which the interneuron is most sensitive increases as the position of the stimulus is shifted ventrally, that is to those parts of the eye that look at near-by rather than distant points on the water surface. In more quantitative terms, the neuron exhibits maximum responses when an object as large as about $1/4$ length of *Notonecta* moves somewhere along the water surface – and this is just the size of the insects *Notonecta* prefers to prey upon. 'Somewhere' along the water surface, however, is too vague a term. The neuron responds in the way described only for a limited range of distances covering a few centimetres in front of the insect. But it is only there that the bug's predatory behaviour is governed by vision. At larger distances, the localization of prey depends on vibratory stimuli (Wiese 1974).

To summarize, the band-like foveal regions ex-

tending across the eyes of *Ocypode*, *Cataglyphis* and *Notonecta* are specialized sets of receptors matched to the spatial peculiarities of the animals' essentially flat environment. They provide their owners with high-acuity and size-constant vision of objects appearing near the horizon, which is the most dominant feature within the visual world of these arthropods.

In flying insects, the horizon is important in yet another respect, but here a premium is paid for destroying rather than detecting fine spatial detail. As the horizon is the most ubiquitous visual cue indicating the horizontal, it can be used by the flying insect as an effective means for stabilizing the position of its body about the pitch and roll axes. Usually, a set of three tiny photoreceptor organs, the ocelli (Fig. 4A), fulfills this task. The ocelli have long been regarded as one of the most enigmatic sensory organs of insects, but it seems now clear that their prime function is to act as horizon detectors (for review see Wehner 1981). Whenever their directions of view have been recorded carefully enough, the ocelli have been found to look exactly at the horizon: the medial one in the animal's forward direction, the two lateral ones at 90° to the left and right of the forward direction.

Contrary to the visual streaks of compound eyes that detect *objects* at the horizon, the ocelli detect the *horizon* itself. However, as the horizon skyline might deviate locally from the horizontal, horizon detectors should be able to average out such disturbing irregularities and thus 'deliberately' destroy the unwanted information about structural details. The simplest way of furthering this end is to use a low acuity optical system. In fact, insect ocelli are characterized by highly underfocussed optics and high rates of receptor conver-

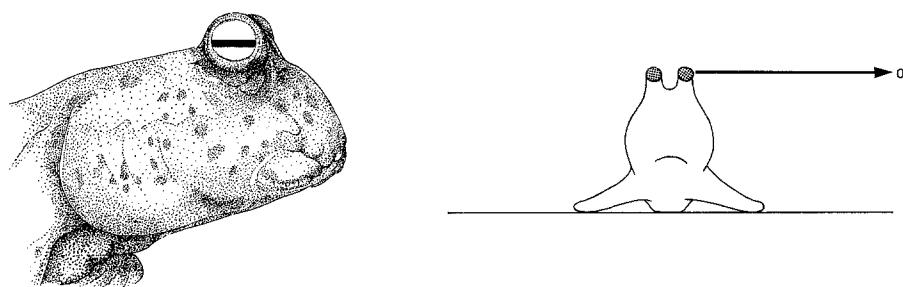
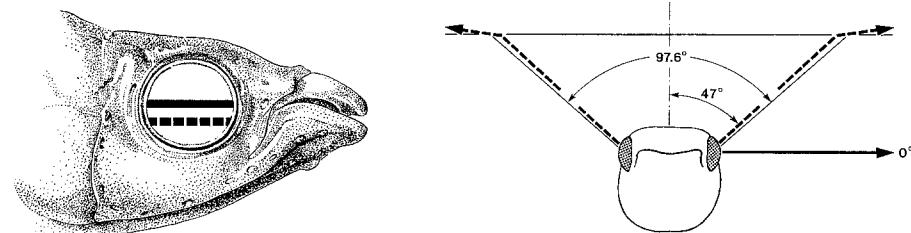
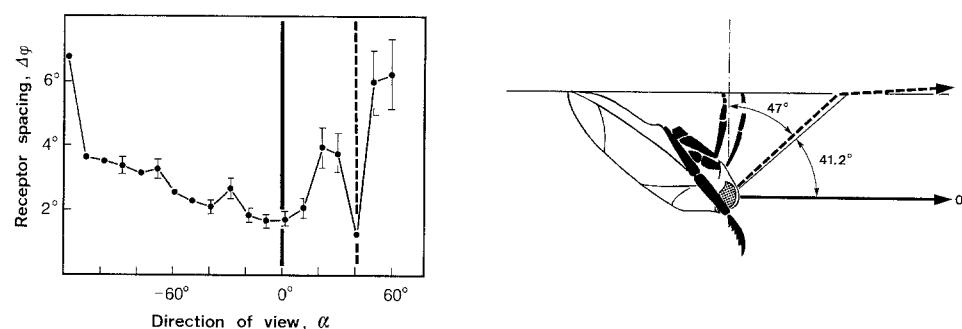
A**B****C**

Fig. 5A–C. Visual adaptations to living in a flat and optically split world. **A** The eye of the mainly terrestrial, shore-living teleost *Periophthalmus koelreuteri* (Gobiidae) is characterized by a conspicuous visual streak (band-shaped foveal area) looking laterally at the horizon. **B** The eyes of the surface-feeding fish *Aplocheilus lineatus* (Cyprinodontidae) are equipped with two horizontal band-shaped areas. Both 'visual streaks' look laterally at the horizon, but one below the water surface, and the other above it. Redrawn from Munk (1970). **C** Visual specializations similar to the ones depicted for *Aplocheilus* (**B**) are found in the compound eyes of the backswimmer, *Notonecta glauca*. The left figure presents the vertical distribution of interommatidial angles, $\Delta\phi$. Redrawn from Schwind (1980). 0° = horizontal direction of view. The plus and minus signs refer to the ventral and dorsal parts of the eye looking upwards and downwards, respectively. Notice that small values of $\Delta\phi$ correspond to high visual acuities. Notice further that in all figures A–C the heavy dashed lines and the heavy solid lines indicate corresponding directions of view

gence (Fig. 4B) providing the animal with heavily blurred neural images of the skyline. Apparently, the role of the ocelli is not to resolve images at all, but to detect rapid changes in overall intensity. A simple set of rules can suffice to inform the flying insect about inadvertent rolls and tilts of its body. Whenever the illumination of one lateral ocellus increases and, concomitantly, that of the other decreases (or vice versa), but that of the median ocellus does not change, the animal is rolling about its longitudinal body axis. On the other hand, when

the illumination of the median ocellus either increases or decreases, but that of the two lateral ocelli remains constant, the animal is pitching about its transverse body axis, either in the upward or in the downward direction, respectively. This hypothesis outlined by Wilson (1978) and put here in its simplest terms, has received support from behavioural work on dragonflies (Stange and Howard 1979) and locusts (Taylor 1981) and is therefore on a firm footing. Finally, however, in the present understanding of ocellar horizon detec-

tors, I cannot refrain from mentioning that Richard Hesse, Hansjochem Autrum's professor at the Humboldt University in Berlin, first developed this very argument and painstakingly predicted what neurophysiologists have discovered more than 70 years later (Hesse 1908).

3. Coping with a visually split world

The third case study keeps us within the flat visual world, but takes us under water. Immediately beneath the interface between air and water, some cyprinodontid fishes like *Aplocheilus* make their living by feeding on insects moving at the air/water interface. Their eyes are unique in that they possess two visual streaks rather than only one: a central streak positioned along the equator of the eye, and a ventral one looking upwards (Munk 1970). On closer scrutiny, this pair of band-shaped foveae reveals itself as a spatial filter matched to the curious optical properties of the world just below the water surface (Fig. 5B). Due to the reflection of light at the interface between air and water the aerial world comprising a solid angle of 180° is compressed into a solid angle of 97°, a circular image known as Snell's window. Consequently, *Aplocheilus* lives in an optically tripartite world: All objects within the hemisphere above the water surface appear inside Snell's window; underwater objects are seen either inverted or right way up depending on whether they lie just outside Snell's window, within the zone of total internal reflection, or further apart, downwards from the horizontal. This is demonstrated by the visual scene portrayed in Fig. 6, in which a sequence of letters extends into the water/air interface. The images of the aerial and underwater parts of the letters are separated by the zone of internal reflection within which the images of the underwater objects appear again, but this time inverted.

Now comes the fish's trick. Within its retina the two visual streaks are positioned exactly so as to re-unite neurally the optically split visual world. While the central streak looks laterally, below the water surface and parallel to it, the ventral streak looks upwards at an angle of 47° to the vertical, that is also parallel to the water surface, but above it. Between these two visual streaks the retina exhibits strikingly low densities of photoreceptors and visual interneurons, and structural peculiarities like "holes originated by disintegration of some of the neural elements" (Munk 1970) occur.

If further proof were needed that the retinal specializations of *Aplocheilus* subserved the func-



Fig. 6. The tripartite visual world of aquatic animals: I aerial (Snell's) window, II zone of total internal reflection, III zone of underwater vision extending downwards from the horizontal. A sequence of letters is positioned at the water/air interface. The images of the aerial and underwater parts of the letters are separated by zone II. Within this zone, mirror images of the underwater parts of the letters appear. The picture was taken with an underwater camera (Nikonos 5) equipped with a UW Nikkor lens 1:2.8, $f=15$ mm

tion proposed above, let us look at a fish living above rather than below the water surface – the mudskipper, *Periophthalmus* (Fig. 5A). This fish, certainly the most terrestrial of all teleosts (Stebbins and Kalk 1961), spends most of its time outside the water. Like *Ocypode*, it inhabits the intertidal mud and sand flats. Living in a flat visual world, but not disturbed, like *Aplocheilus*, by the oddities of the water/air interface, *Periophthalmus* has one – and only one – visual streak within its retina, and as to be expected this streak occupies a central rather than ventral position.

Further support for the double-streak hypothesis comes from the surface-feeding water insect already mentioned, the backswimmer *Notonecta* (Fig. 5C). Equipped with compound rather than single-lens eyes, it exhibits exactly the same retinal specializations found in *Aplocheilus*. At the proper angular separation of 42° two band-shaped areas of high visual acuity occur. Both look parallel to the water surface: one above it, the other below it (Schwind 1980).

4. Using the sky vault as a compass

The next example leads us back to the desert ants, *Cataglyphis*, and to the flat terrain they inhabit. Now, however, it is not the horizon skyline and the ant's visual streak I shall focus on, but the celestial hemisphere and the insect's way of using it as a compass. As celestial cues are effectively at infinity and thus not subject to the phenomenon of motion parallax, the retinal localization of any

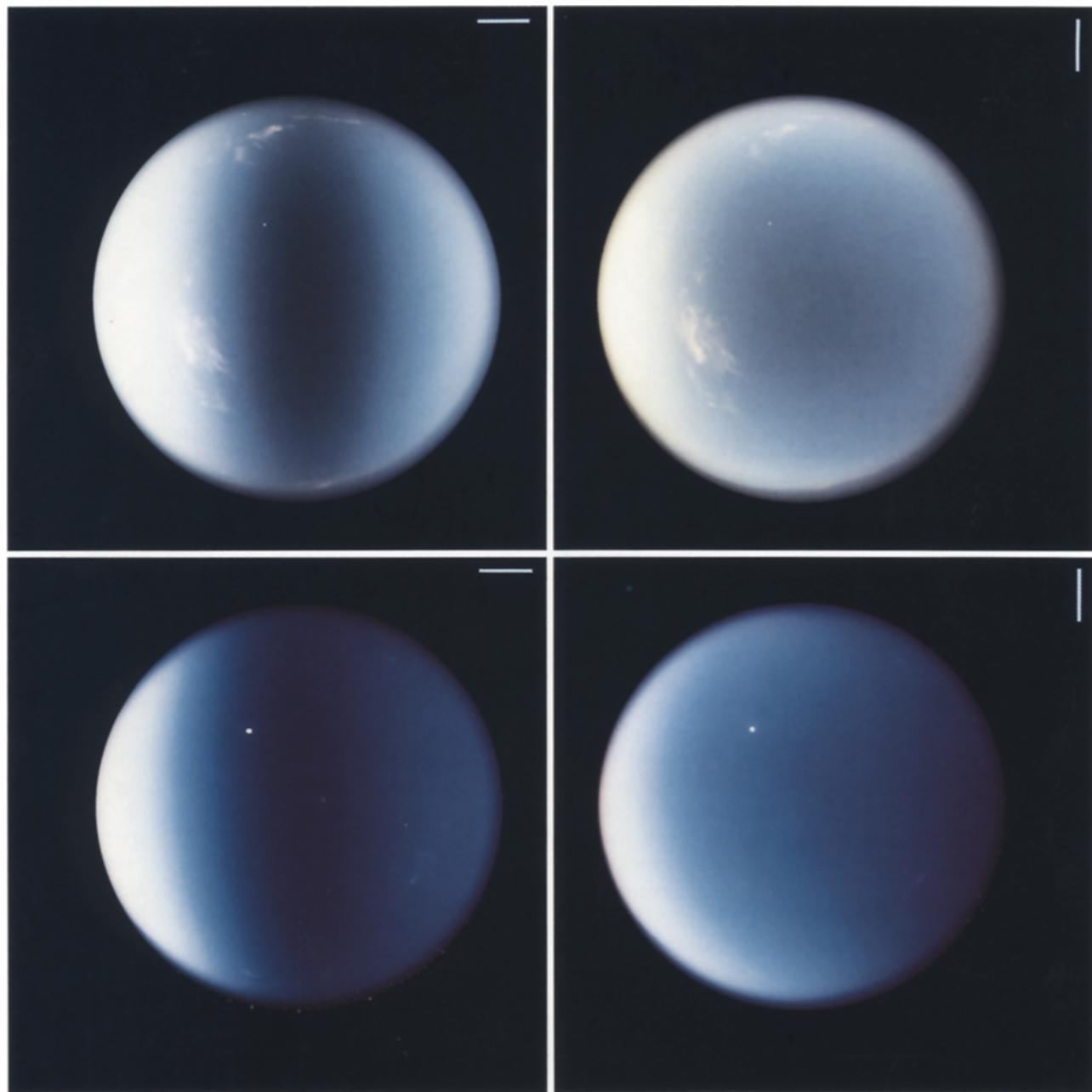


Plate I. Skylight polarization arising from the scattering of light by the earth's atmosphere. The pictures were taken with a 180° fisheye lens (Nikkor-Auto 1:2.8, $f=8$ mm) equipped with a linear polarizer (Polaroid HNP'B). The orientation of the polarizer is indicated by *white bars*. West is to the left. The upper figures were taken at sunset, the lower figures 30 min after sunset. The moon appears as a white disc

such cue changes only when the animal performs rotatory rather than translatory movements. For this reason, celestial cues provide powerful compass information.

There are several optical phenomena in the sky that, in principle, could be used as compass cues. First, there is the direct light from the sun (a point light source). In addition, the scattered light from

the sky (an extended source comprising the entire celestial hemisphere; Plate I) provides various kinds of information: intensity gradients, spectral gradients, and a striking pattern of linearly polarized light – striking at least to the eyes of insects which, unlike our own eyes, are equipped with photoreceptors sensitive to the plane of polarized light. In *Cataglyphis*, it is the latter cue, skylight

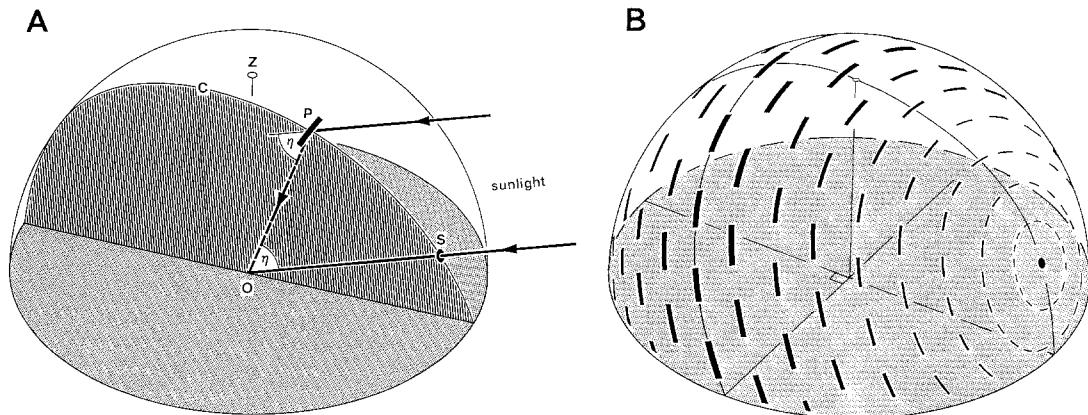


Fig. 7A, B. Skylight polarization. **A** The polarization of skylight arises from the scattering of sunlight by the air molecules within the earth's atmosphere. The celestial point P is characterized by the scattering angle η . Scattered skylight is partially linearly polarized with the direction of polarization (see black bar) extending at right angles to the plane of the scattering angle η (hatched plane). The latter plane includes the direct light from the sun (heavy solid lines), and the observer's line of sight, (heavy dashed line). **B** The entire pattern of polarization in the sky. The directions of polarization are indicated by the directions of the black bars. The sun is shown as a black disc positioned at an elevation of 24° above the horizon. C Circle in which the scattering plane intersects the celestial hemisphere; O observer; P point observed in the sky; S sun; Z zenith. From Wehner and Rossel (1985)

polarization, on which the compass system relies most heavily. But how is this pattern detected and used as a compass?

If one stops and thinks about it, this is a rather tricky problem. Almost forty years ago, von Frisch (1949) showed that bees can steer their proper compass courses even if they have access to only a small patch of blue sky. As each point in the sky is characterized by a particular direction of polarization (for details see Fig. 7B), the insect must somehow 'know' how these directions are distributed across the sky, and then determine, in the abstract, how the only patch it can see fits into the whole pattern. In more operational terms, one could say that the bee must infer the position of a reference cue (say, the sun) from any particular patch of sky. This takes the insect – and the investigator – into difficult ground.

In theory, the insect could perform something analogous to a geometrical construction (Fig. 8). Due to the laws of light scattering, the sun can be located from any point in the sky following a great circle which passes through that point in a direction perpendicular to the local direction of polarization (see also Fig. 7A). Armed with this knowledge, the insect could compute the position of the sun by using at least two points in the sky, tracing out the relevant great circles, and then defining the position of the sun as the point at which the great circles intersect.

Are we really to assume that the insect's brain comes programmed with the ability to perform such three-dimensional constructions in the sky,

let alone to acquire, by either evolutionary or individual experience, the underlying knowledge about skylight optics? I doubt it – all the more, as the computational difficulties are even more formidable than the preceding discussion might let one assume. In the first place, the insect must be able to determine the direction of polarization at any particular point in the sky. Given the fact that insect photoreceptors are polarization analyzers, each being maximally sensitive to a specific direction of polarization (rev. Wehner 1983a), this seems to be an easy task, but it is not. At least it is not easy enough to be explained here in detail. So I would just like the reader to feel the grip of the problem: Each pixel of the celestial pattern of polarized light is characterized not only by its specific direction of polarization, but also by its specific intensity, spectral composition, and degree (percentage) of polarization. As information theory tells us, under these conditions multiple measurements are required – performed either simultaneously by several receptors or successively by one receptor – to determine the direction of polarization unambiguously, i.e. independently of the other optical parameters. For a skylight compass, such unambiguity is absolutely necessary, as intensity, spectral content, and degree of polarization may vary dramatically in the sky due to haze, clouds, or other atmospheric disturbances, and thus provide unwanted information.

Even if we assume for a while that the insect is equipped with the neural machinery to determine individual directions of polarization unambiguously,

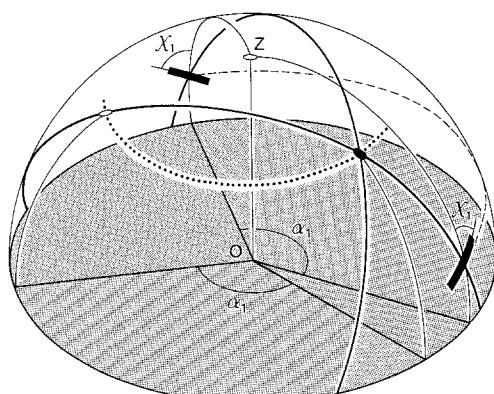


Fig. 8. The physicist's way of solving the compass problem. First, the direction of polarization χ is determined in at least two points in the sky (black bars). Second, the position of the sun (black disc) is computed as the point at which the two circles running at right angles to the local directions of polarization intersect. If only one direction of polarization were available and if, in addition, the insect knew the elevation of the sun at the particular time of day, two possible positions of the sun could be inferred. These positions are marked by the black and white discs separated by the azimuthal distance α_1 . (As in this figure the two local directions of polarization are assumed to be identical, χ_1 , the azimuthal distance between the two points in the sky is α_1) Modified from Wehner (1983a)

ly, a further problem immediately arises. As mentioned above, one direction of polarization determined in one pixel of sky is not sufficient to solve the compass problem. At least two such directions are needed. But bees and ants are able to select their proper compass courses even if they are presented with no more than a single direction of polarization, irrespective of whether this is displayed in the natural sky or in an artificial set-up.¹

This finding was more than mildly surprising, but was confirmed repeatedly in more than ten thousand measurements in both bees and ants. It presented a real challenge. Why did the proposed mechanism not work in theory, but in practice? A dead-end!

The only way out of this impasse was to assume that we all had been looking at the problem the wrong way round, and that the insect had found a simpler solution than met the physicist's eye. Obviously, this assumption seemed so unlikely that sensory physiologists trying to solve the riddle of the insect's polarization compass had never considered it seriously. But it was exactly this idea that led us to the answer.

¹ Experiments performed on honey bees, *Apis mellifera*, and desert ants, *Cataglyphis bicolor*, have led essentially to the same conclusions about the insect's polarization compass (for bees see: Wehner and Rossel 1985; Rossel and Wehner 1986, 1987; for ants see: Wehner 1982; Fent 1985)

The answer is as follows: Like the surface-feeding fish whose retina is equipped with a spatial filter that *automatically* solves the optical problems arising from the reflection of light at the water/air interface, the navigating insect employs a retinal filter that is matched, in its spatial properties, to the pattern of polarized light in the sky. This filter consists of an array of analyzers (polarization sensitive photoreceptors), whose analyzer directions (microvillar directions) are arranged similarly to the distribution of polarization planes across the sky. I say 'similarly', because the retinal array of analyzers is a simplified and stereotyped rather than exact image of the skylight pattern. Whereas the latter changes with the height of the sun, the former, of course, is hard-wired and stays in place.

The retinal filter – a *compound polarization filter*, so to speak – resides at the uppermost dorsal margin of the bee's and ant's eye. We have called this specialized part of the eye the insect's *POL area* (Wehner and Strasser 1985), because this area is necessary and sufficient for the detection of polarized skylight. Equipped with its compound polarization filter so miraculously matched to the polarization pattern in the sky, the insect can solve the compass problem, or at least the decisive part of it, more or less *automatically*. It must do nothing but scan the sky, i.e. rotate about its vertical body axis. Whenever an optimal match between the receptor array and the celestial pattern is achieved, the summed output from all polarization analyzers of the POL area reaches a maximum value. This is the case when the animal has aligned its longitudinal body axis with the symmetry plane of the sky (Fig. 9A). As this symmetry plane includes two compass cues, the solar and the anti-solar meridian, the insect must (in a second step) discriminate between the two, and then (in a third step) set its compass course relative to one of them. As far as we know, polarized skylight is necessary only for the first step, in which the animal determines when it is aligned with the symmetry plane of the sky. Hence, let us examine how this is achieved.

As we have seen, the match between the receptor array and the celestial pattern of polarization is, by necessity, incomplete, because the static receptor array cannot match all possible versions of the dynamic skylight pattern. This has important consequences. Navigational errors must necessarily occur when the insect can see only small patches of sky. Take, for example, the extreme case as depicted in Fig. 9B, in which only one direction of polarization ($\chi = -70^\circ$) is displayed. At the time of day at which the experiment is performed, and at the elevation at which the patch of polarized

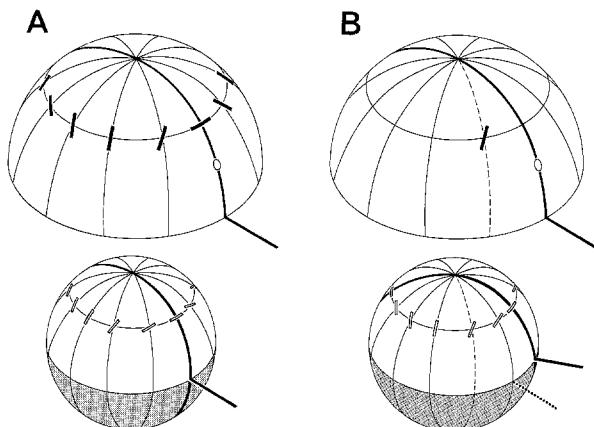


Fig. 9A, B. How insects use the polarized light in the sky as a compass. The upper graphs depict the celestial hemisphere in which the entire pattern of polarization (shown in A for a particular elevation above the horizon) or a single patch of skylight (B) is available to the insect. The directions of polarization are indicated by the directions of the *black bars*. In the lower graphs the insect's compound polarization filter is shown. This 'matched filter' residing in the POL area at the dorsal margin of the eye consists of an array of ultraviolet receptors, in which the microvillar directions (*white bars*) mimic, on the average, the pattern of polarized light in the sky. The retinal array of receptors is displayed for the same parallel of altitude as is the celestial array of directions of polarization. In the upper and lower graphs, the *heavy black line* marks the symmetry plane of the skylight pattern and the symmetry plane of the animal, respectively. In A an optimal match between the compound polarization filter and the skylight pattern is achieved when the animal's symmetry plane coincides with the symmetry plane of the skylight pattern. In B, in which only a single pixel of sky is available, the animal must deviate – in this case, by 30° to the left – from the celestial symmetry plane in order to reach a match between its compound polarization filter and the only direction of polarization available in the sky

light is presented, this particular direction of polarization ($\chi = -70^\circ$) occurs 30° to the right of the solar meridian, but in the insect's compound polarization filter the corresponding analyzer direction (-70°) is located at 60° to the right of the insect's forward direction. Thus, a match is achieved when the insect deviates by 30° to the left of the solar meridian rather than coincides with it. This false localisation of the celestial symmetry plane must lead to navigational errors when the insect finally sets its compass course, and these errors are indeed observed. Actually, it was from these navigational errors, and their systematic relation to the polarization patterns of skylight, that we first proposed the hypothesis of the insect's celestial 'map' (Rosselet and Wehner 1982), and it was only later that we found this 'map' laid down at the level of the receptor layer. At this point, the results of our behavioural and neurophysiological studies clicked into place.

Now we are prepared to turn to some supplementary details, which are not absolutely necessary for understanding the insect's way of using its compound polarization filter, but tell us a bit more about how this filter is designed.

First, the polarization analyzers are *ultraviolet receptors*. In evolutionary terms, this makes a lot of sense, because the shortest wavelengths are most strongly scattered and polarized. As ultraviolet receptors are used to detect skylight polarization, and as the ultraviolet receptors of the ant's and bee's POL area are more highly sensitive to polarized light than any other type of photoreceptor within the same eye, a fundamental aspect of Rayleigh scattering has been incorporated into the insect's matched filter. Let me go even one step further and assume that ultraviolet receptors have evolved originally as a means of detecting skylight – the ubiquitous source of ultraviolet radiation an insect encounters within its world. Ultraviolet light is absorbed by most terrestrial objects more or less indiscriminately, so that for vision on earth ultraviolet receptors are of relatively little help. However, there is one obvious exception to what I have just said: the detection of ultraviolet reflecting patterns as displayed by the petals of angiosperm plants. It is well known (rev. Menzel 1979) that in bees, butterflies, and many other insects ultraviolet receptors are part of a colour coding system capable of detecting such terrestrial ultraviolet cues. Angiosperms, however, evolved rather late in evolutionary history, not before mid-cretaceous times. Therefore, it is a likely hypothesis that the plants exploited the pre-existing ultraviolet receptors of insects, developed ultraviolet floral patterns, and caused their pollinators, the bees, to incorporate their ultraviolet receptors into a colour coding system. Clearly, evidence on this point is hard to obtain, but nevertheless, nothing beats an innocent speculation.

Second, the intrinsically high polarization sensitivity of the retinal analyzers is further enhanced by *local inhibitory circuits*. Within each ommatidium of the bee's and ant's POL area, two sets of ultraviolet receptors occur which share a common field of view, but differ in their (mutually perpendicular) analyzer directions. As one set (type-I receptors) is inhibited by the other (type-II receptors), the polarization sensitivity of the former is increased (Labhart 1985). It is the retinal distribution of these type-I receptors that matches the skylight pattern (Wehner 1982).

Third, in the scanning model sketched out above I have tacitly assumed that the outputs of all retinal analyzers (type-I receptors) are summed

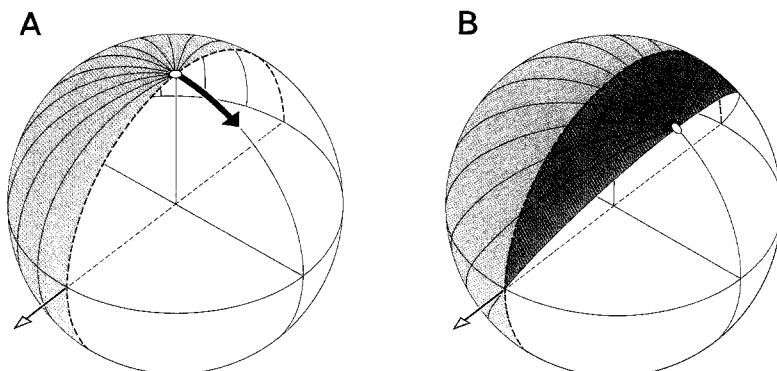


Fig. 10A, B. Geometrical design of the analyzer directions within the bee's and ant's compound eye. The analyzer directions (the microvillar directions of the type-I ultraviolet receptors) run parallel to the meridians of the compound eye. In figures A and B these meridians are projected out into visual space, i.e. onto the surface of a sphere. The white arrow marks the animal's forward direction, the white disc the pole of the retinal array of receptors. In A the visual field of the right eye is restricted to the ipsilateral side (light grey shading), in B it extends to the contralateral side (see heavy black arrow in A and dark grey shading in B). The dark area shown in B corresponds to the visual field of the insect's POL area

indiscriminately. The circuitry might indeed be as simple as that, but behavioural data indicate that at least the anterior and posterior parts of the POL area converge on different interneurons. For the sake of perspective, let us assume that a small number of such interneurons each picking up its information from a separate part of the POL area really exists. Then, a little clever wiring between these interneurons would provide the insect's POL system with a *global inhibitory network* which could further enhance the contrast seen by the system while the insect scans the sky. But this is speculation and not yet built on fact, and so let us leave this digression on the functional anatomy of the compound polarization filter, and return to the main story.

The scanning hypothesis as outlined above implies that while scanning the sky the insect translates the spatial information inherent in the skylight pattern into temporal modulations of summed receptor responses. All the insect derives from these responses is *when* it is aligned with the celestial symmetry plane. If the system were indeed that simple, one should be able to deceive the insect by presenting it with unpolarized, but temporally modulated beams of ultraviolet light. Such an experiment is difficult to design and perform, but once designed works exactly as the scanning hypothesis predicts. Whenever the unpolarized light reaches its peak intensity, the insect 'thinks' that it is aligned with the celestial symmetry plane, and orients correspondingly (Rossel and Wehner 1986).

The most striking feature of the insect's celestial compass is its simplicity, but the compass owes its simplicity to its limitations. Early investigators (e.g. Stockhammer 1959) have frequently

tried to train bees to distinguish between different directions of polarization – all to no purpose. The answer is now clear: The insect's compass system is designed to detect the symmetry plane of celestial polarization patterns, and nothing else. To fulfil this task, it employs a retinal filter matched exquisitely to the skylight pattern.

At least two questions remain: one dealing with developmental biology, the other with economics. First, how is the compound polarization filter established during the ontogenetic development of the insect's retina? As it appears, the task is a formidable one: Each of the about 70 (*Cataglyphis*) or 150 (*Apis*) retinal analyzers must be spatially adjusted in a way that more or less mimics the external polarization pattern. However, the general geometry of compound eye design goes part of the way toward explaining how this is achieved. All retinal analyzers – or to be more precise: the microvillar directions of the type-I ultraviolet receptors of all ommatidia – run parallel to the meridians of the compound eye, and all meridians originate from the pole of the retinal system of coordinates that is located at the uppermost dorsal margin of the eye. In bees and ants this pole does not look at the zenith, as one might assume if the visual field of each compound eye covered just the ipsilateral side of the visual sphere (Fig. 10A), but looks contralaterally – and so does the entire POL area (Fig. 10B). The optical displacement of the POL area and its fan of meridians to the contralateral field of view automatically ensures that a (partial) match between celestial and retinal patterns is achieved. The reason is that the celestial pattern of polarization is geometrically related to its pole, the position of the sun, much in the same way



Plate II. Polarized light arising from the reflection of light by water surfaces (upper figures) and glossy foliage (lower figures; leaves of ivy, *Hedera helix*). The pictures were taken with a UV Nikkor lens 1:4.0, $f=105$ mm, equipped with a linear polarizer (Polaroid HNP'B). The orientation of the polarizer is indicated by white bars. In the lower figures, leaves that are oriented more or less horizontally exhibit the strongest polarization of reflected light (see white arrows)

as the retinal analyzers are related to their pole, the uppermost dorsal ommatidium of the compound eye. For the match to be as complete as possible, the dorsal pole of the compound eye must look contralaterally. Some time or other in their evolutionary history, insects must have 'discovered' that drawing their dorsal arrays of photoreceptors to the contralateral field of view creates

a situation in which remarkable skylight patterns show up. This discovery might well have been the starting point for the POL area to develop the functional specializations we have mentioned.

Second, how can the insect afford to use an array of photoreceptors that allows for nothing but a partial match with the outside world, and thus inevitably creates navigational errors? The

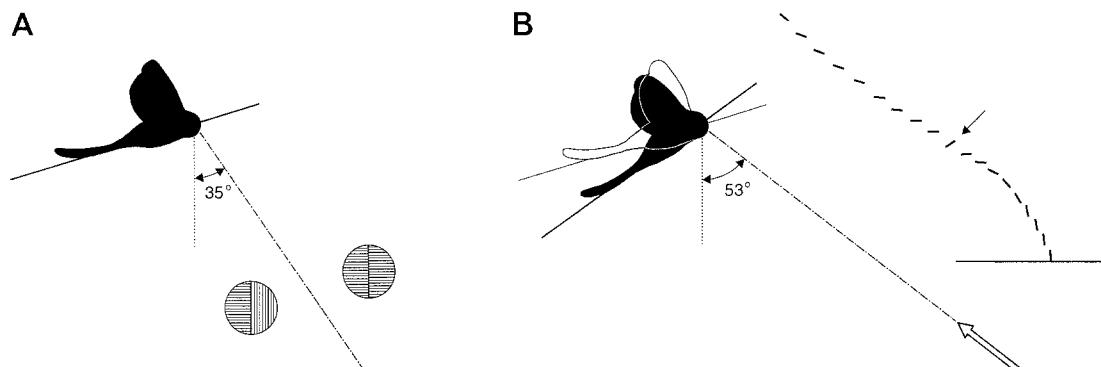


Fig. 11A, B. The plunge reaction of flying water bugs, *Notonecta glauca*. **A** Profile of a water bug cruising above a polarizing surface (horizontal line). The inset figures depict the microvillar directions of the ultraviolet receptors within individual ommatidia. Orthogonally arranged microvillar directions (left figure) occur in those parts of the eye that look down to the water surface (POL area). **B** Shortly before diving into the water, *Notonecta* raises its body axis up to an angle of 53° (Brewster's angle, white arrow), and then tilts down and dives into the polarizing surface – be it a water surface or a sheet of artificial polarizer. In the inset the whole sequence of events occurring during the descending flight of *Notonecta* is filmed at 80 frames/s. The length of the animal indicated by the black bars is 1.5 cm. The small black arrow marks the position at which *Notonecta*'s POL area looks down at an angle of 53° to the vertical. Redrawn and combined from Schwind (1983, 1984)

situation is not all that bad. Needless to say, no navigational errors, or only very small ones, occur when the spatial distribution of blue patches in the sky does not change dramatically between the ant's foraging and homing trip. Such is usually the case. If it is not, the navigational errors are the smaller, the larger a part of the skylight pattern is available, at any one time, about the symmetry plane of the sky; and there are no errors at all, when the entire pattern of polarization is displayed. Finally, the insect has a number of efficient back-up systems at its disposal that keep the overall navigational errors to a minimum (Wehner 1983 b).

5. Detecting water surfaces

Linearly polarized light arises from either scattering or reflection of light. Consequently, there are two main sources of polarized light on our planet: sunlight scattered by the air molecules within the earth's atmosphere (Plate I), and light reflected from water surfaces (Plate II, upper figures). As shown in the preceding section, the former source forms the basis of the insect's celestial compass, and as will be shown now, the latter source provides flying insects with reliable cues for detecting bodies of water. Whereas the polarized patterns of skylight are complicated in so far as they comprise all possible directions of polarization arranged in a particular geometrical way that changes with the position of the sun, the geometry of reflected polarized light is simple: the latter is always polarized horizontally – that is parallel to the horizon.

The very water bugs to which we have alluded already twice when discussing under-water vision (pp. 516, 518) make use of the second source of polarized light. On dispersal, they leave their aquatic environment and search for new bodies of water. For this they must fly, and do so at crepuscular times when spatial vision is impaired because of the reduced contrast sensitivity of the eye. Even at such low levels of light intensity, however, water surfaces stand out from the remainder of the insect's environment by the polarized light reflected from them. In that context, Schwind (1983) has shown that within the ventral part of the *Notonecta* compound eye the analyzer (microvillar) directions of the ultraviolet receptors are arranged so as to pick up horizontally polarized light most effectively. The ultraviolet receptors of each ommatidium form a pair of 'crossed analyzers' (see inset in Fig. 11 A) much in the same way as I have described it for the dorsal POL areas of ants and bees. In the ventral 'POL area' of *Notonecta*, however, these pairs of mutually perpendicular analyzers are arranged so that one analyzer direction is always horizontal and thus most sensitive to light reflected from water surfaces. Most probably, polarization contrast is enhanced by inhibitory inputs from the other (vertical) type of analyzer, but this has not been shown yet in *Notonecta*.

Provided with these neuroanatomical data one can easily conceive of a simple mechanism to explain how *Notonecta* makes use of its ventral POL area (Fig. 11). Most probably, *Notonecta* 'assumes' that it is flying over a body of water whenever the summed output of all horizontally arranged retinal analyzers reaches maximum values.

By filming flying water bugs, Schwind (1984) was able to show that under the conditions mentioned above *Notonecta* indeed starts its descending flight and finally dives into the water surface – or an artificial polarizer laid down on the ground by the experimenter. Before the water bug goes into its final dive, it rears up so as to form an angle of 53° to the vertical (Fig. 11B), as if to make sure that the surface underneath has really the right polarization properties. Notice that at an angle of 53°, the so-called Brewster angle, reflected light is polarized maximally.

As an interesting side line it might be mentioned that in some insects all analyzer directions of the ventral photoreceptors are arranged vertically rather than horizontally (Bohn and Täuber 1971; Trujillo-Cenoz and Bernard 1972). This arrangement makes the insects almost blind to polarized surface glare. The effect is analogous to what humans achieve by wearing polaroid sunglasses. The insects in which the vertical analyzers occur, gerrid bugs and dolichopodid flies, are predators living on or near to the water surface. Unlike *Notonecta*, they have no need to detect water surfaces, but to detect prey objects against the water surface or any other glossy background such as leaves (Plate II, lower figures) or mud.

Finally, one may wonder why *Notonecta* uses its ultraviolet rather than its long-wavelength receptors for detecting reflections from water surfaces. During the course of evolution, the insect might have 'discovered' that reflected light is polarized most strongly in the ultraviolet range of the spectrum, even though the wavelength dependency of polarization by reflection on water surfaces is rather small (Chen and Rao 1968). Alternatively, the fact that ultraviolet receptors were already used by insects in navigation by polarized skylight could be regarded as a preadaptation to employ them in other navigational tasks that depend on the exploitation of polarized light.

6. Exploiting the earth's magnetic field

How animals, especially birds, use the earth's magnetic field to navigate is the subject of much wonderment, confusion and disagreement among biologists. The fact that migratory birds and homing pigeons do use the magnetic field as at least one source of navigational information seems to be firmly established (Wiltschko 1968; Keeton 1971; Walcott and Green 1974), but hypotheses about how birds and other vertebrates proceed in handling this information range from the eminently plausible (Wiltschko 1972) to the completely

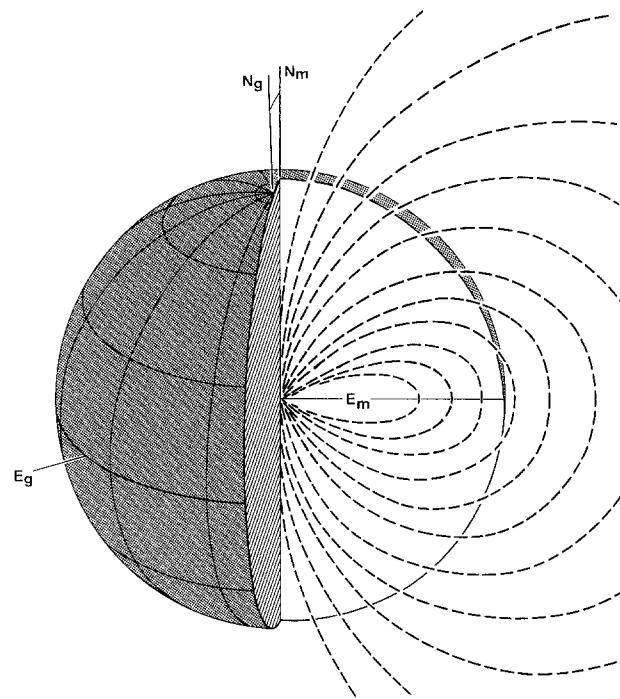


Fig. 12. The earth's magnetic field. E_g , E_m geographic and magnetic equator; N_g , N_m directions of geographic and magnetic north. At present, the axis of the magnetic field deviates by 11.5° from the earth's axis of rotation. The dashed lines mark the lines of magnetic force. The angle of dip (γ , see Fig. 13) is the angle at which the lines of force and the surface of the earth intersect

speculative (Gould 1982) and absurdly ad hoc (Baker 1985). At least to me, the most thought provoking hypothesis is the one recently put forward by Kiepenheuer (1984). Surprisingly, it has gained little following among other workers in the field, but this is certainly due to difficulties in acknowledging its elegance and simplicity rather than to contradicting experimental evidence.

The hypothesis states that migratory birds use the earth's magnetic field merely as a compass, and that this compass employs something akin to a 'matched filter'. At the heart of the hypothesis is the assumption that the bird when flying along its innate migratory route simply tries to keep the apparent angle of inclination of the magnetic field at a constant value. What does this mean in detail? As already shown experimentally (Wiltschko 1972), the bird's magnetic compass – unlike the magnetic compass used by human navigators – is a 'dip compass' relying on the inclination (vertical angle, direction of dip, γ) rather than the polarity of the earth's magnetic field. For a bird on the northern hemisphere, north is in the direction of $\gamma < 90^\circ$ (Fig. 12). The conventional wisdom now

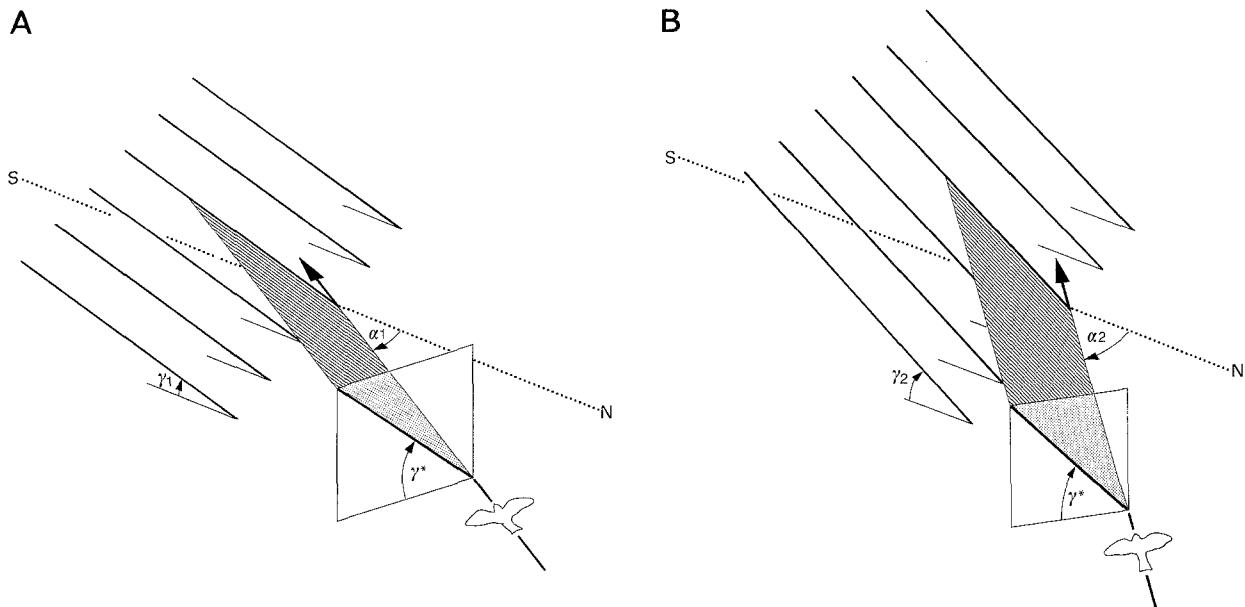


Fig. 13A, B. Kiepenheuer's model of how migratory birds use the earth's magnetic field as a compass. In **A** and **B** two parts of the surface of the earth are shown which differ in geographical latitude and, as a consequence, in the angle of magnetic dip (γ_1 and γ_2). The bird is assumed to adjust its migratory direction, α , so as to maintain a constant apparent angle of dip, γ^* . For this, the bird must change α (compare α_1 and α_2) whenever it encounters a change in γ (γ_1 and γ_2 in **A** and **B**, respectively). N-S Magnetic north-south direction. Designed according to the hypothesis of Kiepenheuer (1984)

holds that the bird having established the direction of dip (say, north) sets its actual compass course relative to that direction – possibly by employing other, e.g. astronomical cues (Wiltschko and Wiltschko 1976) – and does so repeatedly for all different compass courses it must steer to reach its final geographical destination. According to Kiepenheuer's new model, however, there is no need for the bird to come programmed with a whole catalogue of steering directions which all must be set relative to an independently determined reference direction (e.g. north). Instead, the bird is assumed merely to try to match an apparent angle of dip (γ^*) with an inner reference (γ_r^*). When the match is achieved, the bird is on its migratory route.

For the model to work it is crucial to select the proper γ^* . Depending on the direction of view, there are many possible angles that could be measured between the magnetic vector and the surface of the earth. The hypothesis assumes that the angle γ^* measured by the bird is the projection of the magnetic vector onto the animal's transverse body plane (Fig. 13). When the inclination γ of the magnetic vector changes (it varies with geographical latitude, see Fig. 12), the angle γ^* changes concomitantly. As a consequence, the bird equipped with a constant reference angle γ^* , must change its heading α so as to match its γ_r^* with the γ^* it

encounters when reaching other latitudes (compare Figs. 13A and B). Although this hypothesis may be hard to prove directly, it does make testable predictions. For example, a migrant flying, say, south to its wintering grounds should continually change its migratory direction α , and should do so in a predictable way depending on its starting direction α_0 and the range of geographical latitudes it passes on its way south. In fact, Kiepenheuer (1984) has computed theoretical migratory paths for many species of birds, and found them to agree amazingly well with the paths actually taken by the birds.

Magnetic material (magnetite) is now found in nearly all animals examined, at least in one kind of tissue or another (Kirschvink et al. 1985) – and the latest craze, magnetoreceptor madness, is spreading like an epidemic. Nevertheless, we have not the slightest idea of what the sensor within the bird's transverse body plane might look like. But this is a problem with which all hypotheses about the bird's magnetic compass must contend, and should not distract from the charming simplicity of Kiepenheuer's idea.

To bring this idea into still closer alignment with the remainder of this chapter, let me point at some striking similarities between the magnetic compass proposed for birds and the polarization compass found in insects. In both cases, the com-

pass works by establishing a match between a pre-ordained spatial filter – a particular array of photoreceptors (POL array) or a particular projection pattern of the magnetic vector (angle γ_r^*) – and the outside world. In both cases, the match is achieved by a temporal scanning procedure that translates spatial information about the external stimuli into temporal fluctuations of summed receptor responses. Whenever these fluctuations reach a peak value, the difference between the expected and the observed is minimized, and the animal is properly aligned either with the symmetry plane of the sky or with its species-specific migratory direction. Thus, both compasses rely on self-induced intensity fluctuations occurring within properly matched spatial filters. Both compasses measure relative rather than absolute intensities. This allows for quick and accurate measurements, and leaves the system unaffected by accidental intensity fluctuations within the external fields of stimuli.

C. Conclusions and speculations

As animals are heterotrophic organisms which, unlike the autotrophic plants, must move about to search for food, the ability to orient themselves within their three-dimensional world is one of their prime characteristics. The preceding sections have dealt at some length with several of the more advanced systems of spatial orientation which have evolved in the higher forms of animal life, the arthropods and vertebrates. In all these case studies there are still loose ends and unresolved details, but I hope to have made at least one major point: to persuade us that our own formulations of the problems discussed are not at all representative of how the animals tackle their tasks. The upshot of the preceding discussions, I believe, is to remind us of something that we have known all along, but not always fully appreciated, namely that an animal's solution reflects a unique nervous system with adaptive limitations, biases, and distortions. Similar problems may be solved by different animals in different ways depending on the animal's evolutionary past. Anachronisms in neural circuitry may persist as long as they do their job or, as one of my colleagues has nicely put it, as long as the animal has managed to 'design its way around them'. All too often old neurons and circuits have been incorporated into – rather than been replaced by – new and more appropriate ones (e.g. Dumont and Robertson 1986). As we have said before, natural selection favours whatever works, however short the final solution may fall

of the investigator's optimal design criteria. As it appears, neurobiologists and their fellow cyberneticists have often been led astray by their ideal of optimal design.

First, the animal's solution is often restricted to a narrow range of stimuli and situations. For example, the parasitoid wasp's way of measuring the size of a sphere applies only to a limited range of sizes (Section B1), and so does the insect's and crab's way of perceiving visual objects size-constantly (Section B2).

Second, the animal's solution mostly covers only a partial aspect of the problem the human investigator has in mind. For example, the insect's system of detecting polarized light in the sky is aimed merely at determining the symmetry plane of the skylight pattern rather than measuring individual directions of polarization, but it was the latter ability that most investigators have tried to explain (Section B4). Similarly, the magnetic compass of a migratory bird might well be nothing but a device by which the bird achieves a match between a certain projection of the earth's magnetic vector and a preordained, built-in value of that quality – or in other words: a device by which the bird merely maintains a balance between a specific parameter of the earth's magnetic field and the orientation of its body (Section B6). The fact that, in spite of numerous attempts, no one has succeeded yet in training an insect to a specific direction of polarization, or a bird to a specific direction of the magnetic field, lends support to the assumption that both compasses – the insect's polarization compass and the bird's magnetic compass – have not been designed to measure such qualities, but to accomplish the more limited tasks mentioned above. Even in fulfilling these limited needs either compass provides the animal with an approximate rather than precise way of determining a navigational course. As is apparent from the preceding descriptions, such approximate solutions sacrifice absolute precision for workable neural strategies. The results are exciting because they give us hope that other still unresolved systems of orientation are mediated by similar neural strategies.

Third, the simple solutions described in this chapter are basically geometrical solutions rather than solutions depending on complicated computations and manipulations of symbols. Speaking of geometry reminds us of 'maps'. It has long been known that the external world is mapped onto the brain not only once, but several times over; and with the advent of voltage-sensitive dyes (e.g. Blasdel and Salama 1986) and positron-emis-

sion tomography (e.g. Fox et al. 1986), beautiful pictures of the spatial organization of neuronal responses are at hand. One of the knottier puzzles, however, is to understand how the brain interprets such images. An intuitively attractive idea holds that all incoming information is mapped in the brain onto some kind of 'inner screen' from which the brain can later retrieve all kinds of spatial information needed for whatever particular task the animal must solve. However, the neural maps are often distorted in the extreme, and often pay attention only to certain aspects of the outside world. Concomitantly, different aspects of the same information are processed in parallel and represented in different areas of the brain. The oddities of such mapping might give any die-hard inner screen theorist pause for thought. But they are less surprising when one realizes that the brain is designed to steer the animal's actions within the outside world rather than to portray this world as completely as possible. Sensory maps are not neutral photographic images cast on some kind of inner neural screen, but devices shaped by particular selection pressures to preprocess sensory information in a way readily translatable into the necessary motor commands.

In that sense, the particular receptor arrays discussed in this chapter are the most peripheral maps of the brain. They are matched, in their spatial design, to very specific spatial aspects of the external world, and it is for that reason that I have dubbed them 'matched filters'. Insects are particularly noteworthy in this regard, as in them much of the processing of information occurs at rather peripheral neural levels, at both the sensory and the motor side. Of course, such 'peripheralisation' of the insect's nervous system limits the versatility with which information can be handled and used, but eases the way the information can be processed. These potentialities and constraints inherent in the design of the insect's nervous system are certainly related to the small body sizes and narrow ecological niches characterizing all insect species.

And what can be said in this context about the higher vertebrates? Early comparative anatomists (e.g. Elliot-Smith 1924) have claimed that animals with a well-developed cortex exhibited greater flexibility of behavioural responses and were able to modify genetically determined behavioural patterns under different circumstances more readily than animals with less developed cortices. Nowadays many neurobiologists agree that the cortex is designed to detect an abundance of local properties of the animal's world, and to mediate behav-

iour that requires extensive knowledge of this world (e.g. Rose and Dobson 1985). Both views can be reconciled by assuming that the cortex builds up a detailed working model of the environment the animal lives in, and continually tests and modifies this model.

In humans, one of the models underlying our spatial conceptions and mental images is the abstract notion of Newtonian space. This is the space of man's cognitive ecological niche. Within this space we feel free to perform whatever esoteric geometrical construction we can think of. Nevertheless, in coping with the more mundane kinds of spatial orientation such as moving about in our immediate environment, trying to avoid an obstacle, etc. we certainly rely on more direct and approximate ways of sensorimotor coordination than we usually appreciate when imagining the geometrical complexities of the tasks. Even philosophers have noted that in many deeply rooted spatial perceptions we do not resort to our cognitive models of the world (Schmitz 1967), and that "for a great many absolutely fundamental spatial abilities there may not be any theoretical mental level underlying those abilities: the brain just does them" (Searle 1984). Given the multiple representations of sensory surfaces within the brain, and especially within the visual system, the brain just does them by employing different links between the sensory input and the motor output, each having evolved to accomplish its private particular task (Creutzfeld 1981). In solving such particular tasks, the primate's brain and its sensorimotor links may well adopt strategies reminiscent of the ones described in this chapter. Similarities to 'matched neural filters' might emerge in the end, even though 'in the end' may be some time off.

However far-fetched the previous notion might appear, it should not distract from the general conclusion. The brain, especially that of a small insect, was forced by evolution to rely on tricks. The trick I have focussed on in this chapter was to incorporate the fundamental spatial aspects of a navigational problem into the spatial design of the sensory surface, and then to rely on rather simple circuitry to process the outputs of such a 'matched filter'. Clearly, the 'matched filters' cannot include all spatial idiosyncrasies of the animal's world. Nor can they foresee all temporal variations that might occur. Hence, navigational errors and noise are inevitable. The systems are not perfect, but they work sufficiently well not to be pared down by natural selection. When there is no need for a more perfect solution, why bother with it? This is certainly the elegant way of solving a problem – and

the brain depends on elegance to compensate for its small size and short lifetime.

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