

Fourth Edition

# BEHAVIOURAL ECOLOGY

An Evolutionary Approach

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## Chapter 2

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# Sensory Systems and Behaviour

Rüdiger Wehner

### 2.1 Introduction

Behavioural ecologists agree that if they metaphorically regard animals as 'decision-makers' (Krebs & Kacelnik, 1991), they do not imply that the animals decide on the basis of conscious choices or any appreciation of the computational structure underlying the problem to be solved. Instead, they assume that simple processes mediate apparently complex behavioural decisions. This assumption flies in the face of what the majority of neuroscientists have thought all along (e.g. Marr, 1982), namely that nervous systems form relatively complex internal representations of the outside world, and then use information derived from these global representations to accomplish any particular behavioural task that comes up. This conventional wisdom — the representational paradigm, supported also by cognitive scientists (Gallistel, 1990) — has been challenged recently by the notion that many behavioural tasks may not require elaborate representations of the external world. By exploiting constraints that are introduced when the animal interacts with its environment, special-purpose task-directed programmes may be able to solve a given behavioural problem more effectively (Ballard, 1991; Aloimonos, 1993; Churchland *et al.*, 1994). It is here that the ways of thinking of behavioural ecologists and physiologists converge.

This convergence, however, has not yet been put into action. Of course, the approaches of behavioural ecologists and physiologists differ in emphasis and focus. While the former — the functional or why-question approach — aims at an understanding of the fitness (and hence evolutionary) consequences of a particular mode of behaviour, the latter — the mechanistic or how-question approach — tries to understand the physiological machinery mediating that behaviour. Consider, for example, the case of a foraging honey bee, and in particular the question when the bee should stop collecting nectar and start to carry the load back to the hive. Functional analyses show that under a wide range of ecological conditions crop load can be predicted best by assuming that the bee maximizes energetic efficiency (energy gain per unit of metabolic cost) rather than net rate of gain (energy gain per unit of time), or any other more complex alternative (Schmid-Hempel *et al.*, 1985). However, economic models of this sort or another do not tell anything about how bees measure variables such as energy gain or foraging costs, and how they integrate these

measures in order to compute the amount of nectar they should extract from the flowers visited during individual foraging trips. It does not even prove that the 'currency', which describes the bee's behaviour in economic terms, is actually computed by the animal in the way proposed by the model. Only a physiological analysis can tell what sensory mechanisms a bee employs and what neural computations it performs in order to arrive at what the behavioural ecologist thinks is the currency used in a particular foraging task.

Although until recently mechanistic and functional approaches have been entertained by researchers of different camps, they are in no way mutually exclusive, but complementary. In the example mentioned above, knowing physiologically that worker honey bees are constrained by a limited amount of flight performance, or flight-cost budget (Neukirch, 1982), may emphasize the economist's finding that energetic efficiency rather than intake rate is the animal's decisive currency.

It is upon constraints imposed on behaviour by various sources that this chapter concentrates. One source is the animal's physical environment (see Section 2.2). Certain habitats on the surface of our planet favour particular sensory channels, and as sensory systems differ in their potential for, say, resolving spatial detail, certain behavioural tasks can be accomplished only in one type of habitat or another. When it comes to constraints set by the organism itself, body size is an important although widely neglected factor (see Section 2.3). The kind and amount of sensory information that can be handled and used by a nervous system depends more dramatically on the size rather than the particular design of the system. The latter is responsible for what could be called the fine tuning of behavioural performances (see Section 2.4) — and it is here that behavioural ecologists with their intrinsic interest in micro-evolutionary processes become most intrigued.

## **2.2 Constraints imposed on behaviour by the physical environment**

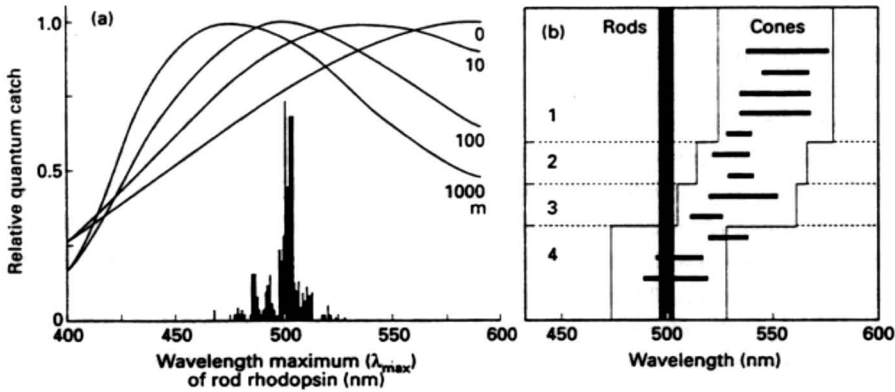
It goes without saying, but is not always fully appreciated, that the most fundamental functional characteristics of animal design have been shaped by very general properties of the physical world within which an animal lives, moves and behaves. For example, there are much larger fishes in water than there are birds in the air; the body of a fish is more perfectly streamlined than that of bird; for a fish it is more difficult to extract oxygen from its environment, but less costly to move through this environment than it is for a bird. A little exercise in physics and physiology will immediately show that all these functional differences between aquatic and terrestrial animals are due ultimately to the way in which water and air differ in such general properties like density, viscosity, oxygen content or gas diffusion rates.

Moreover, the fundamental physical properties of air and water are responsible not only for how animals gain and spend their energy, but also for

how they gain the information to move about, to detect, localize and recognize objects of interest — in short, to explore their environment (see Dusenbery, 1992, for a thorough treatment of such topics). One simple example might help to make the point. Above the water surface one can see even the islands furthest away on the horizon, but one will not receive any sounds from there. In contrast, under water the visual scene gets blurred and obscured even a few metres ahead of the observer, but one may readily pick up the sounds produced by the engine of a ship too far away to be seen. The reasons for these striking differences are simple and straightforward.

Owing to the physical properties of light, vision is the most accurate source of spatial information that an animal can gain about the world. In both air and water, absorption and scattering of light decrease the brightness and contrast of the image, respectively, but these effects are much stronger in water than in air (Lythgoe, 1988). Marine fishes, for example, have responded to the strong selection pressures of their dim-light environment by boosting the light sensitivities of their visual systems in various ways (Locket, 1977; Munz & McFarland, 1977; Douglas & Djamgoz, 1990). As depth increases, the spherical lenses of their eyes become more powerful, the photoreceptors increase in size, are arranged in multiple layers or are combined to functional multireceptor units; screening pigments usually shielding the photoreceptors are lost, and light reflectors underlying the receptor layer are formed — until, at depths of 800–1200 m, eyes disappear altogether (and prevail only in some bioluminescent species). At this 'faunal break' quantum capture rates have become so low that any visual signal gets buried in photon and receptor noise, and finally vanishes.

While this suite of adaptations to environmental constraints tells a clear-cut story, other seemingly similar specializations are more difficult to interpret in terms of the optimization towards which any adaptation works. Take, for example, the spectral absorption characteristics of the rhodopsin photopigments built into vertebrate photoreceptors. The maximal absorption rates of the high-sensitive, dim-light receptors, the rods, are tightly clustered around 500 nm (Goldsmith, 1991). This is a reasonably good adaptation to the spectral light conditions prevailing at depths of about 100 m, but at lower depths, as well as at and above the water surface, the photon flux is greatest at much longer wavelengths (Fig. 2.1a). Why have rod photopigments, which are trimmed for high quantum capture rates, not responded to these strong selection pressures and shifted their maximal spectral sensitivities (their  $\lambda_{\max}$ -values) to longer wavelengths? This question is all the more intriguing as the photopigments of the cone-type receptors containing the same chromophore (retinal-1) and the same opsin-type protein moiety as the rod-type receptors are usually well adapted to the colour of the water in which their owners live. This holds true even for closely related species inhabiting — like the snappers (genus *Lutjanus*) of the Australian Great Barrier Reef — different marine habitats, e.g. the clear blue water of the outer reef, the greener water of the inshore reefs or the more



**Fig. 2.1** (a) Histogram: absorption maxima ( $\lambda_{max}$ -values) of 274 photopigments (rhodopsins) of vertebrate rod photoreceptors. Curves: relative sensitivity (relative quantum catch) of rod rhodopsin as a function of  $\lambda_{max}$  (abscissa) calculated for various depths of water (0–1000 m). (Modified from Goldsmith, 1991.) (b) Absorption maxima ( $\lambda_{max}$ -values) of the photopigments of rods (dark grey area) and cones, i.e. double cones, (black bars) of 12 species of teleost fish belonging to the genus *Lutjanus* and inhabiting different marine habitats: 1, outer reef; 2, middle reef; 3, inner reef; 4, estuary. The left and right limitations of each bar mark the  $\lambda_{max}$  of the two members of the double cones present in the teleost retina. The light grey area represents the range of  $\lambda_{max}$ -values calculated, for each water type, to confer greater than 90% of the sensitivity of the most sensitive rhodopsin. (Modified from Lythgoe *et al.*, 1994.)

heavily stained mangrove and estuarine waters (Lythgoe *et al.*, 1994). Again, however, in all these species the absorption spectrum of the rod photopigment stays put (Fig. 2.1b).

Why does the family of rod pigments exhibit such evolutionary inertia, while that of the cone pigments does not? I ask this question, at this juncture, not in order to discuss hypotheses about the molecular biology of vision, but to caution against simplistic adaptational explanations. As this particular case shows, molecular constraints might be as significant as ecological ones. More generally, it is difficult to include in any hypothesis all the variables over which adaptation integrates. In the present context, the  $\lambda_{max}$ -value is certainly only one of many attributes of the rhodopsin molecule that is sensitive to natural selection. Note, for example, it might already be the high absolute sensitivity of the rods — higher by orders of magnitude than that of the cones — that limits any shift of  $\lambda_{max}$  to larger wavelengths. On the surface of the earth as well as in yellowish freshwater habitats, such shifts would indeed increase the number of quanta absorbed, but they would also increase the rate of dark-noise events and hence decrease the signal-to-noise ratio. In addition, rhodopsin is not only a receiver of light, but also a membrane-bound enzyme involved in the phototransduction cascade.

As mentioned before, due to the 'veil of scattered light' between the eye and the object, underwater vision is essentially a short-range affair. In contrast, underwater hearing extends into the far field. Hence, in aquatic as well as in

nocturnal animals acoustic (and especially sonar) systems of orientation are much more effective than visual guidance schemes. Dolphins and bats offer prime examples.

The propagation of sound pressure waves is almost five times faster in water than in air. Furthermore, the power of sound emission depends on the product of the velocity of propagation and the density of the medium. This product — the impedance of the medium (Michelsen, 1983) — is 3500 times larger for water than for air. Consequently, low-frequency sounds as produced by baleen whales (about  $20 \text{ s}^{-1}$ ) attenuate very little when travelling over large distances. Calculations of the transmission losses, which occur at various depths, especially in those layers in which sound is effectively trapped due to particular temperature conditions, show that fin whales, for instance, might hear each other over distances of several hundred kilometres (Payne & Webb, 1971). One only wonders how these whales could use an acoustic communication system in modern times, when the engines of ships produce powerful sounds exactly in the whales' frequency band.

Let us now turn to the special case of the sonar system. Whatever the medium within which such a system works, there must always be trade-off between the range and the accuracy of target detection: the higher the frequency of the emitted sound, the better the spatial resolution that can be achieved, but the stronger the attenuation of the signal as distance increases. In evolutionary terms, bats have responded to this trade-off situation by choosing their microhabitats and predatory life-styles correspondingly. For example, in comparisons across different species and genera of bats, the frequency of the echolocating sound (and, correspondingly, the best frequency of the auditory system) is inversely related to the height of the preferred foraging area (Neuweiler *et al.*, 1984). In other words, the frequency increases the closer the bats hunt to the ground or to the edges of vegetation (Fig. 2.2). Above the forest canopy, where potential prey (flying insects) are the only objects from which sounds can be reflected, a premium is paid for far-ranging (low-frequency) signals, while within cluttered environments the detection of targets against a noisy background becomes a more severe problem. In this case, high-accuracy (high-frequency) sounds are advantageous. What looks like the exception to the rule is *Megaderma lyra*, the false vampire (Fig. 2.2, M). However, this bat, which hunts close to the ground, detects its prey (beetles, birds, mice, etc.) not by using its sonar system but by listening to the sounds produced by the moving prey itself.

Due to the properties of sound transmission in air and water, some details of sonar systems should be different in aquatic and terrestrial animals. For example, sounds of constant frequency exhibit higher velocities and larger wavelengths in water than in air. Hence, the same accuracy of orientation (for data on toothed whales see Au, 1988; Würsig, 1989) requires that the echolocative sounds are of higher frequencies in aquatic than in terrestrial animals. This is indeed what occurs (Nachtigall & Moore, 1988).

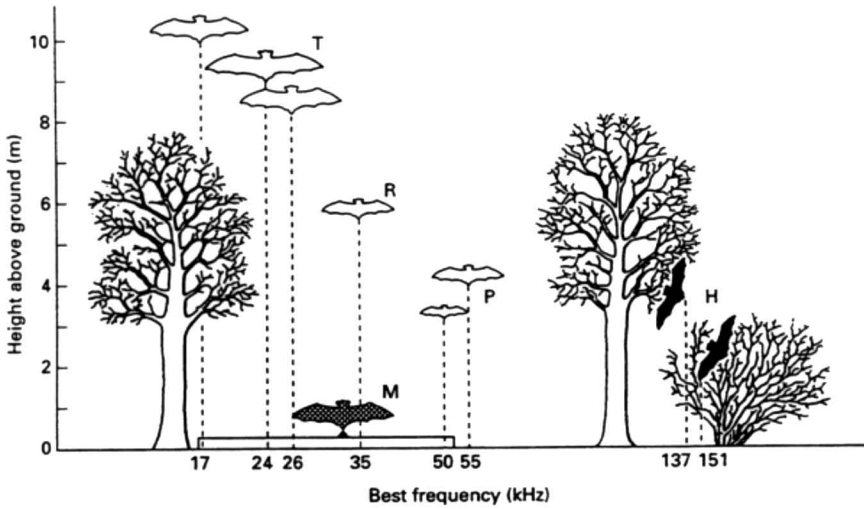
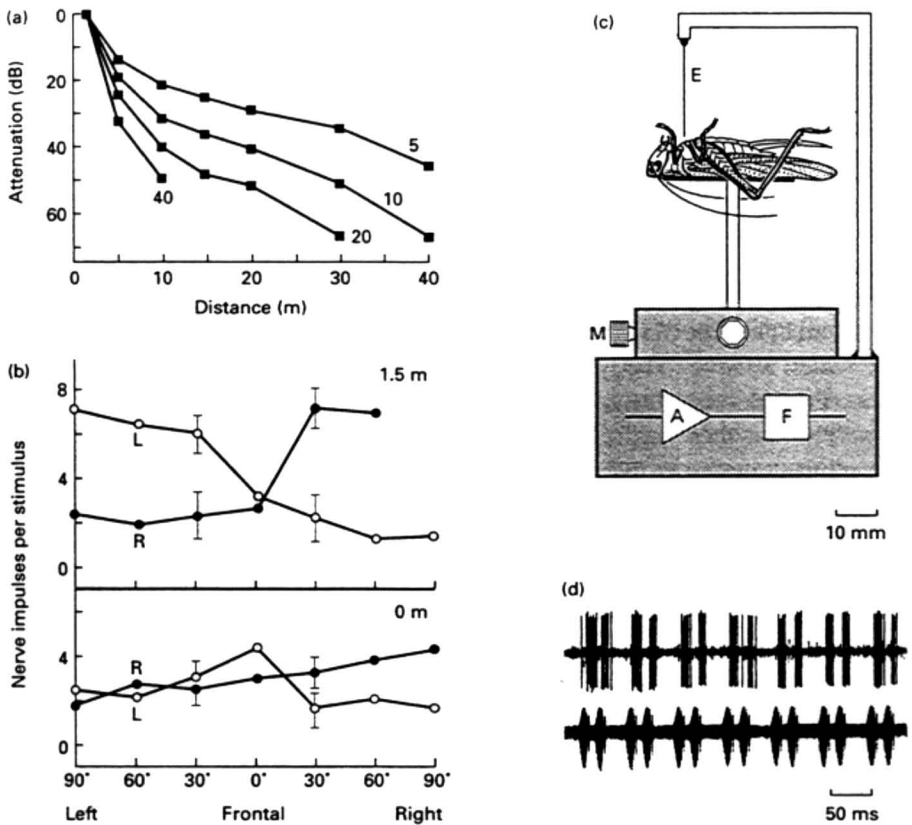


Fig. 2.2 Relationship between the best frequencies (of audiograms recorded in the dorsal midbrain) and the preferred foraging ranges of echolocating bats in southern India. The nine species of bats studied belong to the following genera: H, *Hipposideros*; M, *Megaderma*; P, *Pipistrellus*; R, *Rhinopoma*; T, *Tadarida*. (Modified from Neuweiler *et al.*, 1984.)

Similar environmental constraints apply to auditory communication, where they have been studied in both vertebrates (Wiley & Richards, 1978) and insects (Römer & Bailey, 1990). They are especially intriguing in the latter, because the frequencies of most insect songs lie in the high sonic or ultrasonic range, i.e. well above those of most vertebrates. The attenuation and degradation of these high-frequency sounds by vegetation poses intricate questions. For example, as insect habitats act as effective low-pass filters (Fig. 2.3a) and as all orthopterans studied so far have the potential for frequency analysis, the frequency-dependent attenuation of sound could be used as a means to estimate the distance between sender and receiver. However, as the amount of frequency filtering depends on the structure and density of vegetation, the frequency content of a signal does not provide an unambiguous cue. In fact, the spacing of calling bushcrickets in the field varies with the loudness of the calls (with larger animals producing more intense sounds) and the density of vegetation. As the calling males are not informed about either variable, they can maintain only acoustic rather than absolute distances to their neighbours. Males in which the sound output is experimentally reduced, or which live within denser vegetation, move closer together than the controls (Dadour & Bailey, 1990).

But, there is yet another and even more severe problem, namely to localize rather than only to detect the sound source. Due to multiple reflection and scattering of sound in vegetation, the sound field around a listening insect might become rather diffuse (Fig. 2.3b-d). Hence, nervous systems, especially



**Fig. 2.3** (a) Frequency-dependent sound attenuation in a bushcricket habitat. The four curves refer to sounds of 5, 10, 20 and 40 kHz. (Modified from Römer & Bailey, 1990.) (b) Directional selectivity of a pair of auditory interneurons (T-fibres) of the bushcricket *Tettigonia viridissima*. The recordings (see c and d) were taken in dense bushland at a distance of 10 m from the sound source either 1.5 m above the ground (upper figure) or on the ground (lower figure). The solid and open circles refer to the right (R) and left (L) interneuron, respectively. (c) Recording device: portable 'biological microphone'. The device enables long-term extracellular recordings from single identified interneurons in the prothoracic ganglion. The animal is mounted with the ventral side facing upwards. A glass-insulated tungsten electrode (E) is inserted in the ganglion with a microdrive (M). The socket of the recording contains an amplifier (A), a bandpass filter (F: 0.5–5.0 kHz) and the miniature microdrive (M) by which the preparation can be moved in three dimensions relative to the fixed electrode (E). The portable recording unit is placed within the habitat at various distances, heights and directions relative to the sound source. (d) Response of an auditory interneuron (upper trace) as monitored with the portable recording unit in the field. The sound stimulus (lower trace) is the conspecific male stridulatory song. (Modified from Rheinländer & Römer, 1986.)

of small animals, face the severe problem to extract information about sound-source directions from weak directional cues. The notion 'especially in small animals' brings us to our next topic: how body size influences the way animals behave.



### 2.3 Constraints due to one of the most fundamental biological characteristics: body size

Animals come in various forms, but functionally even more importantly, they also come in various sizes. From the smallest to the largest, they span a range of body masses that covers more than 10 orders of magnitude (Schmidt-Nielsen, 1984). Within this range, they are not isometric, even if the organization of their bodies follows the same general pattern (or *bauplan*). Nearly all morphological and physiological variables change in proportion to each other, as body size varies: relative to body size they are scaled in non-isometric (allometric) ways. Furthermore, the constraints that pertain to body size may become so severe that they can be overcome only by a novel design. For example, unicellular organisms move by using cilia or flagella, but if animals which are only one or two orders of magnitude larger (e.g. small crustaceans) were covered with cilia, they would get nowhere. As body size increases, a new design is needed — locomotion by movable body appendages. Or, to cite another example: diffusion is an adequate mechanism for supplying oxygen to all body parts of a small organism (less than about 1 mm in diameter), but it is too slow and hence completely inadequate for oxygen supply to larger animals. A novel mechanism — transport by convection — must be added to diffusion. As can be inferred already from these two examples, size dependencies in biological phenomena are anything but trivial. In fact, the appearance of the physical environment to an organism and the organism's evolutionary response depend most strongly not on whether the organism is a bee or a bird, a worm or a whale, but on how big it is (Schmidt-Nielsen, 1984; Vogel, 1988; Pennycuik, 1992).

How does this apply to an animal's behavioural ecology? One of the most fundamental interactions between an animal and its environment is the way in which it moves about within this environment. Here, it is already as simple an aspect of locomotion as tripping that scales dramatically with body size. The bigger an animal is the harder it falls. The momentum when a (large) organism hits the ground is proportional to the fourth power of its length (note that momentum is mass times velocity and that for short falls by large creatures drag is negligible). Hence, small animals can afford to stumble, but large ones cannot (Went, 1968). If this might seem to be too trivial an example, let us turn to a more intricate mode of behaviour: the throwing of projectiles like stones or rocks, as it is practised by apes but not by smaller (although manually dexterous) animals. One might surmise that the smaller animals lack the necessary sensorimotor skills. Be this as it may, the much more fundamental reason is that they just cannot impart enough momentum to a projectile to make it an effective weapon. The momentum of a projectile thrown by an animal of proportionate mass is again proportional to the fourth power of the animal's length. By the same token, kicking and hitting can be performed only by large animals, while biting, crushing and squeezing will work for small

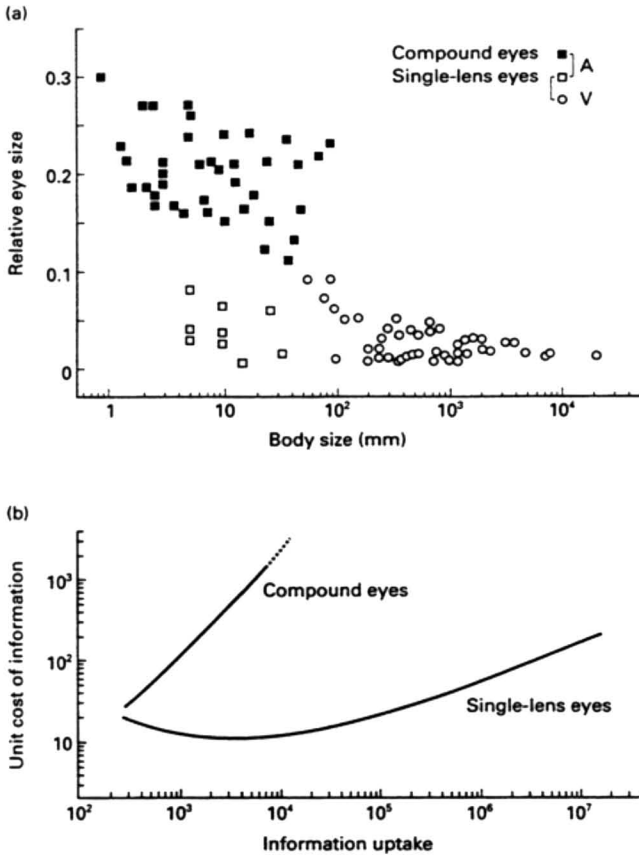
animals as well (Vogel, 1988). In conclusion, certain types of behaviour are beyond an animal's reach for reasons not (or not only) of neural performance but simply of body size.

### 2.3.1 Visual acuity

When it comes to behaviour that depends on the analysis of fine spatial detail, vision provides the most accurate source of information. In accord with this potential offered by the physics of light, simple eye-spots or more advanced types of eye have evolved independently 40–60 times in almost all major groups of animals (Salvini-Plawen & Mayr, 1977), and have led to at least 10 different biological solutions to the physical problem of forming an image (Land & Fernald, 1992). Among those animals which rely most heavily on vision, two types of eye prevail: single-lens eyes and compound eyes. The former occur in a wide variety of taxonomic groups (coelenterate medusae, annelid worms, gastropod and cephalopod molluscs, insect larvae and spiders), whereas the latter are restricted, almost exclusively, to the arthropods.

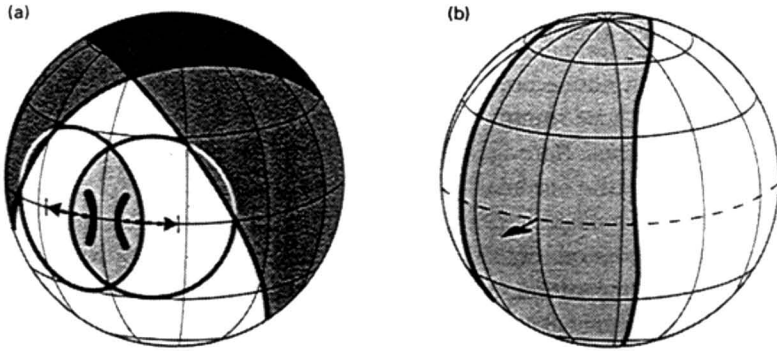
It is intuitively clear — but, can be derived from optical theory as well — that visual resolution decreases with eye (and body) size, but this size dependency varies dramatically between single-lens and compound eyes. In the former the radius of the eye increases linearly with resolution, while in the latter it is proportional to the square of resolution (Land, 1981; Wehner, 1981). This prediction derived from optical analyses is confirmed by the evolutionary result (Fig. 2.4a): compound eyes are rather large and restricted to small animals. Therefore, it is costly to support them and to carry them around (Laughlin, 1995). In order to acquire a unit of visual information (a pixel), the owner of compound eyes must invest more in terms of energy expenditure than an animal equipped with single-lens eyes (Fig. 2.4b). In other words, for a given size of eye single-lens eyes offer the potential of much better resolution than compound eyes. For example, in the principal (single-lens) eyes of jumping spiders the interreceptor angle can be as small as 2.4 arc min (Williams & McIntyre, 1980) and, hence, comes close to the one found in the human fovea (0.6 arc min). As a consequence, the spider can distinguish between conspecifics and similar-sized prey at distances as great as 30 body lengths away (Jackson & Blest, 1982). An insect of about the same body size but equipped with compound eyes must get one or two orders of magnitude closer to the object to resolve the same amount of spatial detail.

Why, then, are insects and crustaceans using such an inferior optical instrument? Why have they not replaced their compound type of eye with the single-lens type? Connecting a new set of eyes to an existing neural hardware might not have been a viable option (Laughlin, in press), so that insects might have got stuck with a type of eye that worked well at low resolution, but then could not be changed. However, as many insect larvae show, insects are, in fact, able to build high-performance single-lens eyes and to use them effectively in behaviour (Wehner, 1981).



**Fig. 2.4** (a) Relative size of compound eyes (filled symbols) and single-lens eyes (open symbols) in arthropods (A, squares) and vertebrates (V, circles). Body size is given in linear dimensions ('nominal length', i.e. the cube root of body mass), and so is eye size (the largest diameter of the eye). The relative size of the eye is defined as eye size divided by body size. (Modified from Wehner, 1981.) (b) The unit cost of visual information ( $10^3 \mu\text{m}^3$  transported retinal mass per pixel) plotted as a function of the total amount of information acquired (pixels per steradian of solid angle of visual space). The cost is defined in terms of the energy required to transport the volume of eye that subserves one pixel, since the metabolic cost of phototransduction is negligible if compared with the transportation costs. (From Laughlin, 1995; and personal communication.)

On the other hand, behaviour will certainly have exerted more selection pressures on eye design than merely the need for high visual acuity. For example, compound eyes may be the advantageous type of eye whenever panoramic vision becomes important. This is because compound eyes cover the surface of the head and hence create a convex — rather than concave — retina. The number of single-lens eyes a spider employs total up to eight, yet the spider cannot see all of its surroundings at once (Fig. 2.5a). On the other hand, many insects with only two compound eyes are able to view the entire visual world simultaneously, and at the same time may have at their disposal



**Fig. 2.5** (a) The visual field of a jumping spider, *Metaphidippus aeneolus*. The small visual fields of the anteromedian (principal) eyes shown in black can be moved over a horizontal range indicated by the heavy broken arrows. Light grey: monocular and binocular fields of view of the anterolateral eyes; dark grey: monocular and binocular fields of view of the posterolateral eyes. The visual fields of the tiny posteromedian eyes have been omitted. (From Wehner & Srinivasan, 1984; based on data from Homann, 1928; Land, 1969.) (b) Visual field of a praying mantis, *Tenodera australasiae*. Light and dark grey indicate the monocular and binocular fields of view, respectively. The arrow points forward. The dashed line marks the horizon. (From Wehner & Srinivasan, 1984; based on data from Rossel, 1979.)

a huge binocular field to which more than 70% of all ommatidia can contribute (Rossel, 1979; Fig. 2.5b). By monitoring the apparent motion of the environment and the objects within it as the animal moves, compound eyes provide useful information as to the animal's own motion and to the landmark skyline around the moving animal. Systems of navigation and course control in which such information is used do not necessarily demand high visual acuity. One can obtain sufficiently reliable information on movement by monitoring the low spatial-frequency content of the environment. Compound eyes, viewed in this light, 'creatively' destroy unwanted information at the very first stage of vision, by using their coarse-grain optics to filter out superfluous spatial detail.

In summary, the principal design features of compound eyes — relatively poor resolution and large fields of view — enable insects to perform well in dealing with *global* aspects of their visual world. Such aspects are used in course control and navigation; these types of behaviour might have been the ones for which compound eyes have evolved primarily. For performing detailed *local* analyses, i.e. detecting and identifying objects like conspecific mates, insects must employ complicated anatomical compromises to insert acute zones in their faceted eyes (Land, 1989) and must get rather close to the object under scrutiny. This may be the reason why in insect communication visual signals are usually restricted to short-range encounters. Over larger distances, species-specific messages are conveyed through other sensory channels — olfactory, acoustic, vibrational — which thus play a more significant role in insect communication.

### 2.3.2 Sound-source detection

The need to localize sounds becomes most apparent in acoustic communication. In this context, only those sounds are localized and recognized that can also be produced by the animal. Here again, physical limitations abound: the smaller the animal, the higher the minimal frequency that can be generated, and the lower the distance over which sounds can be received. This is because maximum efficiency of sound emission requires that the diameter of the sound source is of the same order or magnitude as the wavelength of sound. Consequently, insects with body lengths below 1 cm are restricted generally to ultrasound, but ultrasound is a useful means of communication only in free space or at short range (Michelsen, 1983). Yet, many small insects communicate over distances of many times their body lengths, even up to metres. For doing so, they must abandon the acoustic channel and switch to substrate-borne vibrations (Markl, 1983). Such signals can travel across the surface of an insect's host plant with rather little attenuation. In addition, the efficiency of converting muscle power into vibrational power is much higher than that of the conversion into acoustic power, so that it is not only functionally more effective but also energetically less costly for a small insect to communicate through solid substrates rather than through air.

If one is small, air offers yet another 'cheap' possibility: communication by near-field air oscillations rather than sound-pressure waves. Such oscillations as caused by wing vibrations are used by *Drosophila* flies to communicate with females (Bennett-Clark, 1971) and by dancing honey bees to convey their sound message to other workers (Michelsen *et al.*, 1987). At close range these oscillations are so intense (0.5–1.0 mm peak-to-peak amplitude, 1–3 mm s<sup>-1</sup>; Michelsen, 1983) that they are able to activate antennal mechanoreceptors of near-by conspecifics. As they decrease with the third power of the distance to the source, they are the signals of choice for 'private conversation'.

## 2.4 Constraints set by the animal's computational capabilities

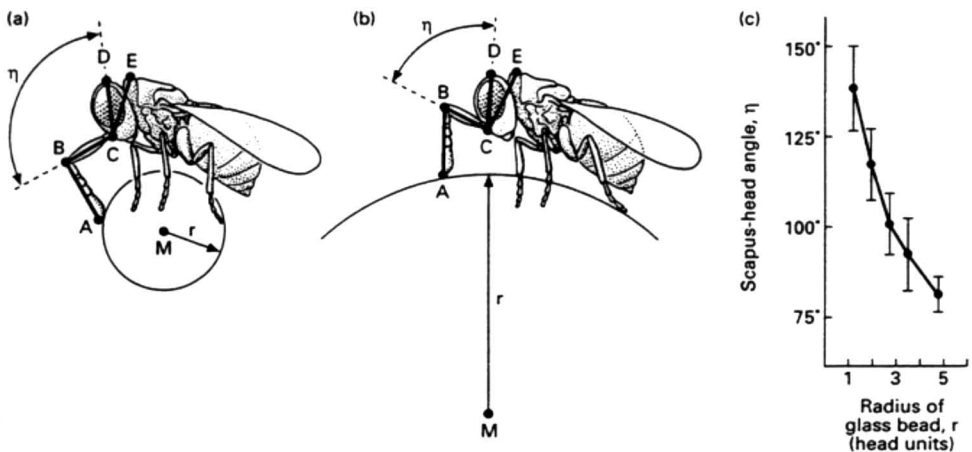
In trying to understand the computational software and physiological hardware of animal behaviour, neuroscientists have often been led astray by their ideal of general, all-purpose designs. The following section of this chapter shall remind us of what we have known all along, but not always fully appreciated, namely that an animal's solution reflects a unique nervous system with adaptive limitations and particular biases. Formally similar problems may be solved by different animals in different ways depending on the animal's evolutionary history and present-day ecology. Idiosyncrasies in neural circuitry may persist as long as they do their job and as long as the animal has managed to design its way around them. Just recall the example of compound-eye vision: as the need for higher resolution increases, insects squeeze high-acuity zones into

the low-acuity facet arrays of their eyes rather than exchange their type of eye for one that is intrinsically superior in terms of overall acuity.

### 2.4.1 Coping with spherical geometry: the egg and the globe

Ichneumonid wasps of the genus *Trichogramma* lay their eggs into the eggs of other insect species. The number of eggs which are deposited depends on the size of the host egg. In determining the volume of the spherical host, the wasp does not trace out spherical triangles and perform spherical trigonometry, but assumes a particular body posture, in which the angle between the head and the first segment of the antenna (the scapus) is related to the radius of the sphere (Fig. 2.6). This angle is probably monitored by the mechanosensory bristles located at the joint between head and scapus. Note, however, that this simple method, by which the volume of a sphere is 'computed' by relying on a simple angular measurement, works only if the wasp adjusts its body position so as to keep two other measures constant: (i) the height of the thorax above the surface; and (ii) the angle between thorax and head. Both conditions are met in the animal's behaviour.

While parasitic wasps must cope with the geometry of minute spheres, migrating birds must trace out navigational courses across the surface of the globe. On their spring and autumn migration even small birds — say, warblers and waders — can travel for several thousand kilometres non-stop over



**Fig. 2.6** Parasitoid wasps, *Trichogramma minutum* (Ichneumonidae), use the surface curvature of their host eggs to determine the number of progeny allocated to the host. (a, b) Female wasps examining glass-bead models of different sizes (radius  $r$ ). (c) Angles between head and scapus observed for different sizes of glass-bead models.  $\eta$ , scapus-head angle (angle BCD); M, centre of spherical glass bead. (From Wehner, 1987; based on data from Schmidt & Smith, 1986.)

potentially hostile territory like the vast expanses of sea or desert. What are the most convenient routes these migrants should take? With all other things being equal (which they never are on the surface of our planet), the energetically least demanding way of travelling is to follow the great-circle (orthodrome) route. This route (Fig. 2.7) defines the shortest distance between two points, but is cumbersome and difficult to compute, because it intersects successive lines of longitude at different angles. However, there is a short-cut way of travelling along the great-circle route: if the bird followed a sun-compass course, but did not reset its internal clock as it moved eastward or westward, i.e. crossed different time zones, it would automatically fly along that route without having to compute it by spherical trigonometry (Alerstam & Pettersson, 1991). Radar studies suggest that this mechanism is employed by Siberian waders crossing the Arctic Ocean.

In these polar regions, where there are no topographical and ecological barriers to cross, the great-circle route is the energetically most efficient one. On the other hand, if brent geese followed the great-circle route on their way from their spring stop-over sites in Iceland to their breeding grounds in northern Canada, they would have to cross the Greenland ice cap where it is steepest and widest. Instead, they take a more circuitous route following more or less a constant-angle (loxodrome) course from Iceland to the east coast of Greenland, turn south, stay for 2–7 days within a rather delimited area, and then continue across southern Greenland on a course nearly identical to the one taken at Iceland. It is fascinating to hypothesize that the geese use their temporary halt at east Greenland to reset their internal clock from local Icelandic to local Greenlandic time, and then continue on the same sun-compass course they have followed previously (Alerstam, 1996). We know from laboratory studies in other species of birds that under exposure to a new 24-h light/dark regimen



**Fig. 2.7** Orthodrome (great-circle) and loxodrome (constant-angle) courses drawn on the surface of the globe. Solid line, orthodrome; dotted line, loxodrome.

it usually takes 3–6 days to recalibrate the sun compass. In conclusion, depending on the ecological needs experienced during their evolutionary history, migrating birds might take orthodrome or loxodrome courses and select and maintain either course by rather simple computational means.

Moreover, modern large-scale satellite-based radiotelemetry reveals that long-distance migrants do not travel for very long distances on either orthodrome or loxodrome courses, but seem to employ a number of navigational subroutines rather than an all-purpose system of navigation. For example, North American warblers reach their South American wintering sites by following neither orthodrome nor loxodrome courses, but by taking a wide eastward sweep across the Atlantic. Surprisingly as it might appear at first sight, this vast detour is the energetically most economic route, because it allows the birds to exploit large-scale wind and barometric pressure patterns (Williams & Williams, 1978).

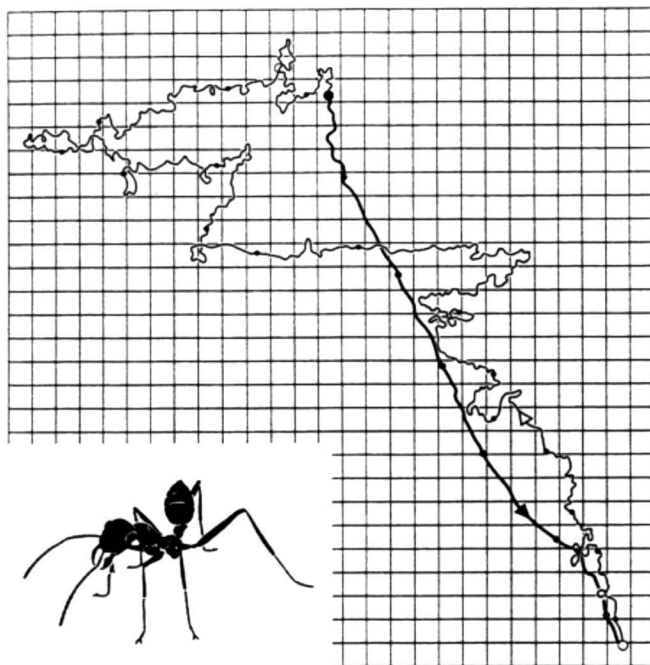
In conclusion, during evolutionary time the migration routes of birds have been shaped by a number of quite different selection pressures, e.g. by synoptic weather patterns, large-scale topography, suitability of celestial or magnetic cues, etc. As Alerstam (1996) has succinctly put it, birds travel without any idea in their minds that the earth is a globe. Instead, they have responded to the selection pressures mentioned above by developing a number of sophisticated tools of migration and ways to integrate and adapt these tools in intricate ways.

#### **2.4.2 Reading skylight patterns and landmark panoramas: the insect navigator**

Insect navigation, although less impressive than bird navigation in spatial scale, is just as intriguing in terms of behavioural sophistication — all the more as in insects some of the underlying mechanisms have recently been unravelled in unprecedented detail. The best studied and, in fact, most eminent insect navigators are eusocial hymenopterans like ants and bees. These central place foragers (Stephens & Krebs, 1986) continually move to and from their central place, the site of the colony, to retrieve widely scattered food particles from the colony's environs. It is during these foraging endeavours that the spatial coherence of the superorganism — the colony — is relaxed and is re-established only by the navigational performances of the individual colony members.

An example of this performance is given in Fig. 2.8. While foraging in a circuitous way over distances of more than 200 m, *Cataglyphis* ants of the Sahara desert navigate by path integration. They continually measure all angles steered and all distances covered, and integrate these angular and linear components of movement into a continually updated vector always pointing home. This is a computationally demanding task which *Cataglyphis* must solve with its small nervous system, and — as recent research has shown (e.g. Wehner *et al.*, 1996) — it does so by relying on a number of rather simple subroutines.

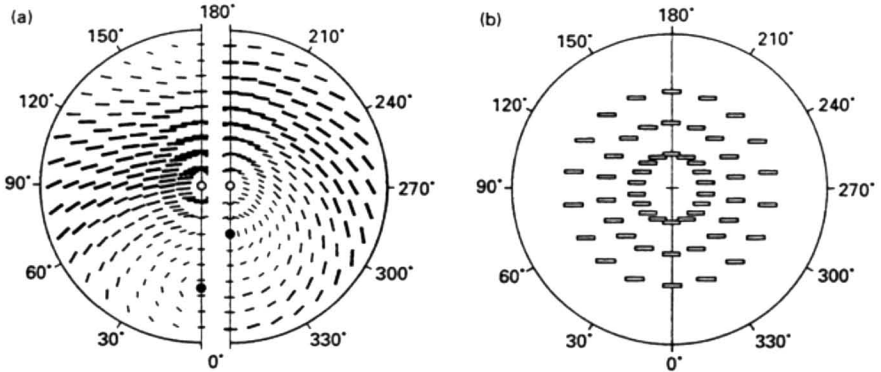




**Fig. 2.8** Outward and homeward paths of an individually foraging desert ant, *Cataglyphis fortis* (see inset). The start of the foraging excursion (nesting site) and the site of prey capture are indicated by the open and the large filled circle, respectively. Time marks (small filled circles) are given every 60 s. Grid width, 5 m; length of outward path (thin line), 592.1 m; length of return path (heavy line), 140.5 m. (Modified from Wehner & Wehner, 1990.)

In the present context, let me focus on the compass used by *Cataglyphis* to monitor the angular components of its movements. This compass is a skylight compass based primarily on a peculiar straylight pattern in the sky, the pattern of polarized light (or E-vector pattern; Fig. 2.9a). At this juncture, it is not important to understand this pattern in any physical detail. Suffice it to say that in any particular pixel of sky the electric (E) vector of light oscillates in a particular direction, and that the photoreceptors in a particular region of the ant's (and bee's) eye are sensitive to these oscillations.

But, there is more to it. The skylight pattern the insect experiences is not static, but changes with the elevation of the sun above the horizon (compare left and right half of Fig. 2.9a). These dynamics notwithstanding, *Cataglyphis* can infer any particular point of the compass — say,  $30^\circ$  to the left of the solar meridian — from any particular point in the sky. This task must be accomplished when, for example, under cloud cover or due to experimental tricks played by the human investigator, E-vector information can be obtained only from a small gap of clear sky. If a physicist tried to solve this navigational problem from first principles, he/she would have to run a rather sophisticated series

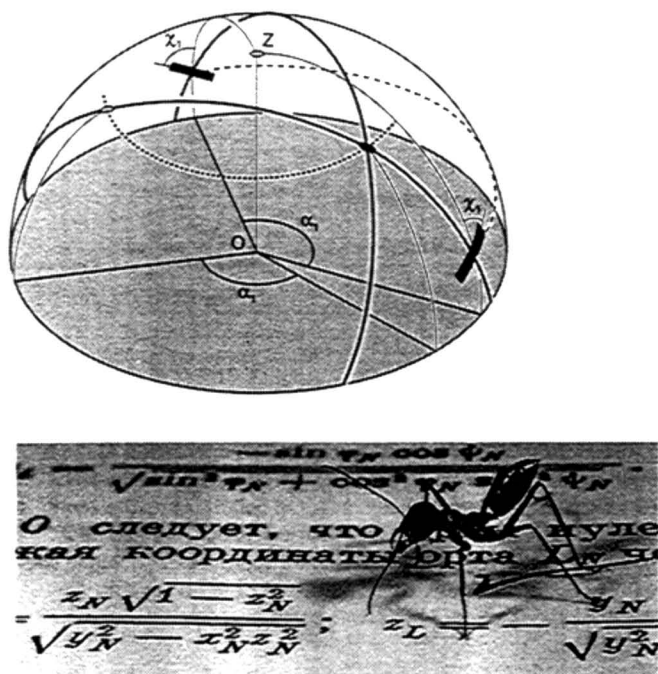


**Fig. 2.9** (a) Two-dimensional representation of the E-vector pattern in the sky shown for two elevations of the sun (black disc):  $25^\circ$  (left) and  $60^\circ$  (right). The orientation of the E-vectors (the directions of polarized light) are represented by the orientation of the black bars. The sizes of the black bars mark the degree (percentage) of polarization. The zenith is depicted by an open circle.  $0^\circ$ , solar meridian;  $180^\circ$ , anti-solar meridian. (b) The ant's internal representation of the sky as derived from behavioural experiments. The open bars indicate where in the sky the insect assumes any particular E-vector to occur. This 'template' is used invariably for all elevations of the sun (for details see Wehner, 1994).

of measurements and computations, and use spherical geometry to perform elaborate three-dimensional constructions (Fig. 2.10). The insect navigator, however, comes programmed with a strikingly simple internal representation — or 'template' — of the external E-vector patterns (Fig. 2.9b). This fixed neural template resembles the skylight pattern when the Sun is at the horizon, but differs from it for all other elevations (for a review of the behavioural and neurobiological analysis of the E-vector compass see Wehner, 1994).

The tantalizing question now is this: how can *Cataglyphis* navigate correctly by using an internal representation of the sky that is not a correct copy of the external world? In the full blue sky, with the entire E-vector pattern available, the best possible match between the external pattern and the internal template is achieved when the insect is aligned with the solar — or anti-solar — meridian, the zero-point of the compass. (The distinction between these two principal meridians can be made by other means.) The match decreases systematically, as the animal rotates about its vertical body axis, i.e. selects other compass directions.

Due to the discrepancy between the internal template and the external pattern, mismatches occur whenever only parts of the skylight pattern are available. For example, an individual E-vector is matched with its corresponding detector in the template only when the animal deviates by a certain angular amount from the solar meridian, so that the zero-point of its compass gets shifted. Consequently, navigational errors arise when the foraging animal experiencing, say, the entire skylight pattern, is suddenly presented with a small patch of sky. In fact, it was from these systematic errors observed in the



**Fig. 2.10** How a physicist could infer the position of the sun from viewing at least two small patches of skylight: First, determine the E-vector direction ( $\chi$ ) in the two patches of sky (this is a problem in itself, which is not discussed here). Then, construct the great circles that run at right angles through the E-vectors. The position of the sun (filled circle) is defined by the intersection of the two great circles. If only one E-vector is visible, the position of the sun cannot be determined unambiguously. Provided that the elevation of the sun is known at the particular time of day the (two) intersection points of the great circle and the parallel of altitude (dotted arc) defined by the elevation of the sun yield the correct position of the sun (filled circle) and a second one (open circle) that is separated by the azimuthal distance  $\alpha_1$  from the correct one. *Cataglyphis* does not perform such constructions but uses a generalized template of the sky (see Fig. 2.9b). (Modified from Wehner, 1981.) In the lower part of the figure *Cataglyphis* inspects a paper of Frantsevich (1982) outlining a model of E-vector navigation.

insect's behaviour under certain experimental conditions that evidence for the internal template could be derived in the first place. Note, however, that such errors do not occur when the animal is *continuously* presented with the same patch of sky. It then always uses the same reference direction, be this the actual solar meridian or any other celestial meridian that is characterized by the currently best match between the template and the outside world. For comparison, if a human navigator used a magnetic compass in which the needle erroneously but consistently pointed towards east rather than north, this 'defective' instrument would work as a reliable compass as well.

In conclusion, evolution has managed to build into the insect navigator a nervous system that includes only some general knowledge about the geometrical characteristics of the celestial world, but this partial knowledge

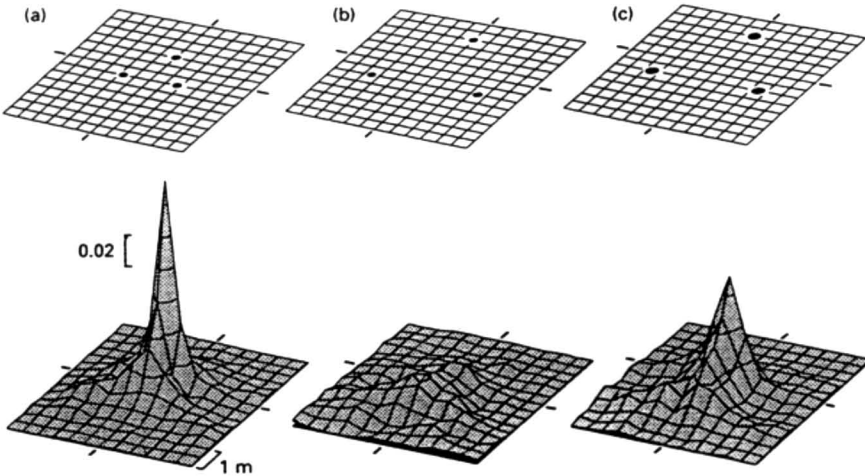
is sufficient if the navigator restricts its field trips to short periods of time. The insect assumes that the celestial hemisphere does not change during any of its particular foraging excursions. Given its short foraging times which lie in the range of tens of minutes rather than hours, this is generally a valid assumption.

Similarly, simplified solutions are employed by insect navigators when landmarks are used to back up the noisy path integration system. As shown in Fig. 2.8, in which an ant performed its foraging and return path within the expanses of a flat and featureless Saharan salt pan, the path-integration system worked without the aid of any landmark-based information. However, as this system is prone to cumulative errors, landmark guidance helps to reduce homing time, often substantially. The effective use bees and ants can make of landmarks as visual signposts (Wehner, 1981) has led to the assumption that insects are able to assemble map-like internal representations of the landmarks in their nest environs and then use such 'cognitive maps' to find their way to a familiar site, even from points at which they have never been before (Gould, 1986). Although this notion has generated a lot of excitement — and controversy — more recent research has shown that ants and bees are indeed able to make intensive use of landmark information in relocating nesting and feeding sites, but that they do not incorporate such sites into a map-like system of reference (Wehner & Menzel, 1990; Dyer, 1996). The strategies they employ are more straightforward, foolproof and largely sufficient for the task to be accomplished.

One task, for example, is to pinpoint the nesting site after the path integration system has led the animal into close proximity of the goal. As suggested by the experiments described in Fig. 2.11, ants seem to acquire a two-dimensional visual template — or 'snapshot' — of the three-dimensional landmark array around their nest, and later move so as to match this template as closely as possible with the current retinal image. This matching-to-memory routine can be studied best by distorting the training array of landmarks and recording the animal's responses to its altered visual world. In these experimental situations particular matching algorithms are able to indicate at which locations a better (partial) match is obtained than at any other location in their immediate neighbourhood, and it is at these locations that the local peaks in the insect's search density profile occur (Cartwright & Collett, 1983).

This snapshot-matching mechanism used in landmark guidance might have some fundamental neural traits in common with the template mechanism employed in skylight navigation. The obvious difference is that the skylight patterns are predictable, but the landmark configurations are not. Hence, the E-vector template can be hardwired, as it actually is, but the landmark snapshots must be acquired during the animal's individual foraging life.

In conclusion, the insect obtains landmark-based information not by taking a bird's eye — or a bee's eye — view of the terrain over which it travels, but gains this information successively and by egocentric perceptions during the process of path integration. This context-bound acquisition and retrieval of

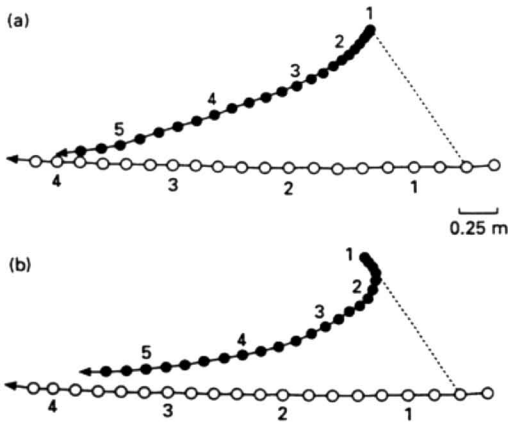


**Fig. 2.11** Search density profiles of desert ants, *Cataglyphis fortis*, trained to the centre of an array of three cylindrical landmarks. The test area containing three different landmark arrays is shown in the upper figures. (a) Landmarks in the training position. In the training area (not shown) the nest is positioned in the centre of an equidistant triangle formed by the three cylinders. (b) Landmarks separated by twice the training distance. The ants behave as though lost. (c) Landmarks twice the training size and separated by twice the training distance. Again, a match between the stored image ('snapshot') and the current retinal image can be achieved when the ants are in the centre of the landmark array. However, due to the larger distance of the landmarks from the goal (as compared to the training situation shown in (a)), motion parallax cues are weaker, and hence the search density profile is broader than in (a). The results in the three experiments are in full accord with the matching-to-memory hypothesis. (Modified from Wehner *et al.*, 1996.)

landmark information reduces the danger of getting inappropriately trapped by similar landmark configurations present elsewhere in the animal's environment. For example, the snapshot-matching mechanism, by which the ant finally pinpoints its nesting site, is activated only after the path-integration system has been reset to zero (Wehner *et al.*, 1996). In addition, the insect can take snapshots at various sites and from various vantage points, and can even align them as sequences of visual images like 'beans on a string' along frequently travelled routes. As such routes can be entered — and familiar sites can be approached — from various vantage points, landmark memories are retrieved and used in quite flexible ways. This flexible use of site-recognition and route-guidance mechanisms leads to navigational performances that might give the impression of map-based behaviour.

### 2.4.3 Computing interception courses: male pursuits and fly-ball catching

Another — and beautifully simple — example of how a difficult computational problem is turned into a tractable one is provided by male hoverflies pursuing and finally catching passing females. As Collett and Land (1978) have shown



**Fig. 2.12** (a) Film recording of a hoverfly male, *Volucella pellucens*, pursuing his quarry. Positions of male (filled symbols) and quarry (in this experimental case a black wooden block, 1.5 cm in diameter; open symbols) are given every 20 ms and numbered every 100 ms. The broken line indicates the line of sight between male and quarry 20 ms before the fly accelerates. As shown by the male's trajectory, the male sets out on the proper interception course. (b) Simulation of the male's behaviour on the assumption that he does not adopt an interception course but tracks his quarry, i.e. turns continuously towards it. This simulation does not describe the fly's real behaviour. (From Collett & Land, 1978.)

by filming hoverflies in the field, a male fly is able to foresee the female's flight path and to compute the proper interception course (Fig. 2.12a). The male initially does not turn towards his quarry, when the latter is first seen, but immediately sets out on an interception course. Theoretically, this task can be accomplished by a simple calculation only if the male 'knows' the absolute size and the absolute velocity of his female target (as well as his own acceleration when speeding up to catch the target) and incorporates these 'biological constants' into his neural computations. If these constants are given, the male can obey the simple rule that the size of the turn he makes ( $\Delta\phi$ ) depends on the initial position ( $\theta_t$ ) and velocity ( $\dot{\theta}_t$ ) of the target image within the male's visual field as follows:  $\Delta\phi = \theta_t - 0.1 \dot{\theta}_t \pm 180^\circ$ . The data indicate that the initial turns of the males obey this rule and lead to collisions between the male and the target, if — and only if — the target is a conspecific female. As in biological terms there is no need for a hoverfly male to chase anything other than a female, it is rather likely that natural selection has incorporated into the male's nervous system all the information about the female's flight behaviour that the chasing male needs to know.

It is not only a male hoverfly that must compute interception courses, but also a human fielder running to catch a cricket high-ball. In principle, the ball's path across the sky could be computed by a set of differential equations based on the observed curvature and acceleration. Obviously, fielders running for a high-ball do not get engaged in such intricate computations. Instead,

they seem to follow one or the other simple rule. One hypothesis holds that they select a running path that maintains a linear optical trajectory for the ball relative to the wicket and the background scenery. In short, a fielder is supposed to adjust his speed and direction so that the (apparent) trajectory of the ball looks straight (linear-trajectory hypothesis: McBeath *et al.*, 1995). If the ball is hit directly at the fielder rather than at an angle to either side, another simple rule might be used, namely to select a running path that keeps the apparent speed of the ball constant (zero-acceleration hypothesis: McLeod & Dienes, 1993). Both strategies, which receive support from video recordings of running paths, do not tell the fielder where or when the ball will land, and hence he does not run to the point where the ball will fall, and then wait for it. They simply set him on a course which will ensure interception — and this is all that matters.

## 2.5 Outlook

Behavioural ecologists and physiologists share a mutual interest in each other's efforts. In the case of the former, this interest is obvious, because behavioural ecologists are keen to learn how neural information-processing mechanisms might have constrained the functional design of the behaviour they analyse in economic terms. It is perhaps less obvious that physiologists should be interested in knowing why it is that a particular neural subsystem mediating a particular kind of behaviour has evolved in one way rather than another.

Until recently, behavioural scientists have been preoccupied with the belief that physiological mechanisms underlying behaviour have been designed from first principles (e.g. Mittelstaedt, 1985). They have usually aimed at outlining the complete algorithmic solution to a given behavioural problem, and then asked the physiologist to discover how this solution is implemented in the hardware of the nervous system. This is the classical approach 'neuroethologists' have entertained for decades. However, neurophysiological analysis is technically demanding, and exhaustive reconstructions of entire neural subsystems are even more so. All too easily does one get lost amidst the hurly-burly of the higher nervous centres. Are such herculean efforts worth it?

In this state of affairs, physiologists have learned an important lesson: that the mechanisms they study are adaptations tailored to particular ecological needs rather than general-purpose processing devices. It is these needs that the physiologist should be concerned with, in order to be able to formulate the right questions in the first place. Let me provide an example by going back to the safe ground of my favourite organism, the desert ant *Cataglyphis*. Only after we had realized that the awe-inspiring navigational performance of a homing ant could be dissected into a number of simpler special-purpose subroutines, each responsible for a particular aspect of the task, were we able to look properly at the underlying sensory and neural mechanisms. A system must be designed to solve the problem in question — but no more; or as

Diamond (1993), while discussing design limits of physiological systems, and especially the question of how physiological capacities are matched to their expected loads, has neatly put it: 'How much is enough but not too much?'

One day, historians of science might well come to the conclusion that the recent developments in behavioural ecology have had an impact on the way physiologists started to think in evolutionary terms and have caused them to promote what could be dubbed — analogous to Huxley's (1940) connotation of 'new systematics' — 'new physiology' (*sensu* evolutionary physiology). Hence, there is hope that these recent developments in conceptual approaches will help to bridge the gap in our understanding of what is economically desirable — in terms of the functional design of a given behavioural trait — and what is, after all, physiologically feasible.



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