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14 Colour Vision in Insects

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Introduction

No other group of animals is represented by such a vast number of species and lives in such different habitats and ecological niches than the insects. The degree to which insects have been forced to adapt to such varying environmental situations is admirably illustrated when one considers the enormous differences in insect eye structure in response to varying light conditions. For example, the light conditions experienced by a millimetre sized *Collembola* in the dark caves of the underground and a large fast flying dragonfly are indeed extremely different, both with respect to absolute light flux and spectral distribution.

The optimal compromise between absolute sensitivity (quantum catch) and spatial resolution favours compound eyes rather than lens eyes in small animals (Barlow, 1952, 1965; Kirschfeld, 1974, 1976; Snyder, 1979). Consequently, spatial resolution is poor due to the diffraction limitation of the tiny lenses (20 μm or less in diameter), but the absolute sensitivity for extended visual objects is in the same range as that of the vertebrate lens eye, since each facet lens has a very short focal length and a correspondingly large effective aperture. Compound eyes are often spherical in shape and this provides the animal with a simultaneous vision in virtually all directions. Furthermore, compound eyes have a high temporal resolution (up to 300 Hz) and this is particularly important for fast flying, diurnal insects (Autrum, 1958; Laughlin, 1981).

Colour vision is a receptor-neural strategy which enables an animal to detect and recognize objects of differing spectral reflection or emission properties, and irrespective of differences in light intensity. The capacity of colour vision is not unusual in insects (Menzel, 1979) and appears to be even more complex in some species than in primates, with the potential of tetrachromatic or even pentachromatic colour vision. However, conclusive behavioural evidence exists only for trichromatic colour vision in a small number of species, and higher order colour vision phenomena such as colour constancy, colour contrast and luminance dependence of colour discrimination have so far been demonstrated in only one species of insect, the honey bee *Apis mellifera*. Therefore, many aspects of colour vision in insects will be discussed with respect to the honey bee.

A prerequisite for the collection of behavioural data on colour vision is that the animal can be trained to a chromatic stimulus and tested for discrimination between chromatic contrasts independent of effective intensity contrasts. Flower visiting Hymenopterans, such as the social bees or wasps, have been carefully studied since von Frisch's (1914 a,b) first unequivocal demonstration of colour vision in honey bees. Flies and butterflies are much harder to train to chromatic stimuli, and thus evidence for colour vision is less conclusive in these species. Other insects, such as locusts, cockroaches, dragonflies, beetles, bugs (e.g. the water bug *Notonecta*), and moths probably have the ability of colour vision since they have different spectral classes of receptors, but conclusive behavioural evidence is either weak or non-existent. However, the existence of different spectral receptor types is not necessarily an indication of colour vision since spectral inputs may also be used to control specific behaviours. Insects often respond to a particular wavelength band with a specific behaviour and to another wavelength band with a different behaviour. Such 'wavelength-selective behaviour' may also include aspects of colour vision, e.g. the categorical separation along the wavelength scale. However, since wavelength-selective behaviour is highly dependent on intensity within each wavelength band, and since different behaviours are involved, this infringes upn an important criterion of colour vision, the sensation of chromatic contrast independent of intensity contrast within on perceptual task. We shall see that both wavelength selective behaviour and colour vision are inextricably involved in the control of certain visually guided behaviours in insects, and that it is extremely difficult to separate the role of each parameter particularly if the animal in question is difficult to train. However, those species which can be

trained to colour stimuli possess phenomena of colour vision such as spectral antagonism, colour contrast, colour constancy, and unique perceptual dimensions of colour vision like hue and saturation.

This review is a condensed discussion of the existing literature on colour vision in insects with a strong emphasis on colour vision in the honey bee, *Apis mellifera*. In the first section, the spectral input systems of several insect species are compared and the data used to construct receptor models of colour vision. Data from the honey bee is used to test the predictions of these model calculations and, as we shall see, the outcome of similarity judgments and discrimination values can be quantified by the receptor model. A later Section summarizes the evidence for spectral opponency as a major component in the neural coding of colour and the appearance of colour. The neural mechanisms of colour coding resemble many features of those in the vertebrate nervous system such as spectral opponency and combinations of spatial, temporal, and spectral opponencies. Colour constancy is also considered, and has so far only been demonstrated in one insect, the honey bee, but it is likely that colour constancy is a general phenomenon of insects with colour vision. Specific adaptations of spectral receptor-neural mechanisms are discussed in the Section on Colour Vision and Wavelength-Selective Behaviour. The evolution of colour vision is discussed at the end of this Chapter, and the honey bee is once again used as an example to illustrate the specific adaptations of flower visiting insects.

The Input System: Spectral Receptor Types

Constraints of Spectral Sensitivities

Natural light stimulates photoreceptors in a wavelength range of 300–720 nm, whereby the short-wavelength limit is defined by the high absorption of the atmosphere for wavelengths shorter than 300 nm. The long wavelength cut-off results from the minimal amount of energy provided by a single light quantum that is sufficient to initiate the phototransduction process (40 kcal equivalent to 1 Einstein of 720 nm). Since photopigments have a half-bandwidth of spectral absorption of approximately 100 nm or 150 THz, one might expect that four pigments evenly spaced throughout the spectrum between 300 and 720 nm would be sufficient if a visual system seeks to optimize total quantum catch over the whole spectrum range, combined with best differential coding of smoothly changing spectral reflectancies. The packing of the receptors into a retinal locus for high spatial resolution is of less importance, since many compound eyes, e.g. those of Hymenoptera, Lepidoptera and Orthoptera, have seven to nine receptors that are optically connected by their fused rhabdomeres. Lens eyes in vertebrates have the physical imperfection of strong chromatic aberration, which compresses the spectral range over which the high resolving power of the lens and retina can effectively be used (Wald and Brown, 1965). Compound eyes are not affected by either of these problems because their spatial resolution is low as a consequence of the small diameter of their lenses, and the receptors packed into groups behind this lens have the same direction of view. Furthermore, these small lenses do not suffer from chromatic aberration (McIntyre and Kirschfeld, 1982). Therefore, one would expect that insect eyes take the full advantage of the spectral sampling and assemble as many different spectral receptor types into one ommatidium as possible. Typically seven or nine receptor cells have the same optical axis, since their rhabdomeres are either fused in an optically homogeneous light guiding rhabdomere (e.g. in apposition eyes of bees and moths, Fig. 14. 1(b),(c)), or the rhabdomeres are separated (as in the fly, Fig. 14.1a) and the axons of the retinula cells with the same view are joined together neurally (neural superposition). Thus, each functional ommatidium could have seven to nine different receptor types which would provide the nervous system with seven to nine independent samples of the spectral reflection if the action spectra of each channel would be accordingly narrow (about 40 nm). Small differences in spectral reflectancy would be highly resolvable with such an input system. However, this is not the strategy insect eyes apply. As Fig. 14.1 shows, each functional ommatidium contains several receptors of the same spectral type as opposed to an increasing number of spectral sampling points. The most likely reason for this is that the effective quantum flux in eyes with such small apertures and the noise properties of the receptor transducer mechanism are prominent limiting factors (Laughlin, 1975; Snyder *et al.*, 1977), even if nearly 100% of the light travelling in the light guiding rhabdomeres is absorbed, as is the case in the long rhabdomeres. The nature of the photopigment, with its intrinsic half-bandwidth at around 100 nm, would require additional filters to narrow the bandwidth to an optimal relationship between spectral peak separation and spectral half-bandwidth according to Shannon's sampling theorem (Shannon and Weaver, 1949). Such a narrowing, if it were possible, would result in a strong reduction of the effective light flux in each receptor. A compromise within these constraints seems to be a multiple replication of a small number, which in most cases is three receptor types (see Fig. 14.1(a)–(c)) within one ommatidium. Each receptor retains, via mutual screening between the combined receptors, the bandwidth of its photopigment and this counteracts self-screening in an absorbing system of high efficiency. Since natural objects tend to have smooth

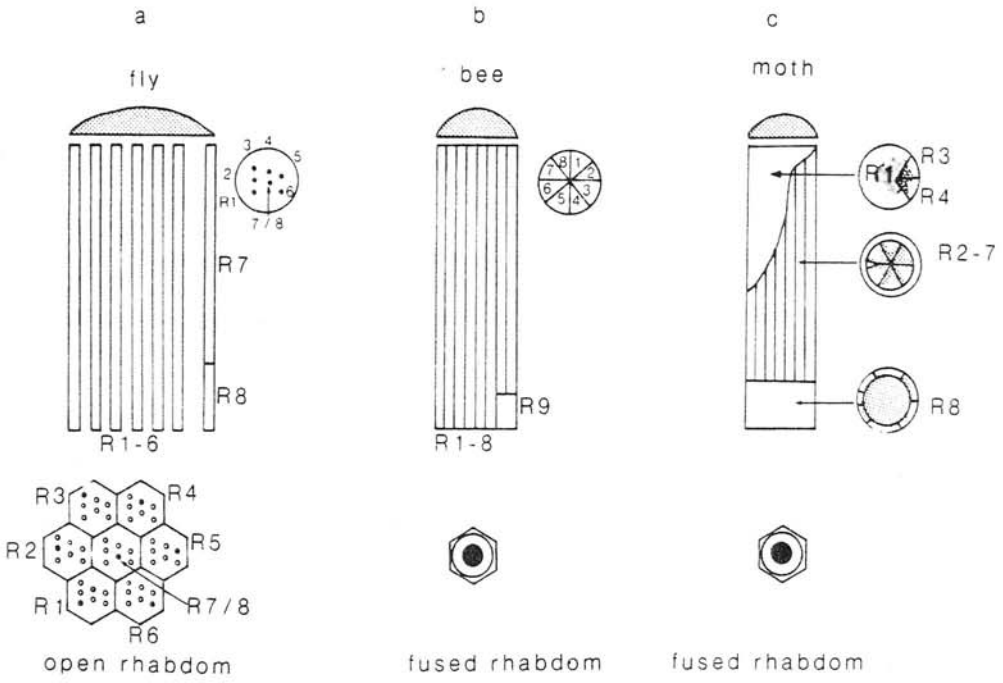

Fig. 14.1 *Three examples for the composition of single ommatidia in the compound eye of insects. In the fly (a) each of the eight photoreceptors (retinula cells R1–R8) have their own light guiding and absorbing structure, the rhabdomere. This arrangement is called an open rhabdomere. The pattern of rhabdomeres is very regular (see upper cross-section) and identical in neighbouring ommatidia apart from a transition into a mirror image at a horizontal line in the middle of the compound eye. The optical axes of the retinula cells in neighbouring ommatidia are arranged in such a way that eight different retinula cells point in the same direction (see cross-section R7/8 – the two tiered cells are taken as the centre and R1 and R8 in the neighbouring ommatidia are marked which point in the same direction). The axons of these retinula cells project to the same set of second order neurone (neural superposition principle, Kirschfeld, 1967, 1972). The bee and moth compound eye is composed of ommatidia with a fused rhabdom. The rhabdomeres of the nine or eight retinula cells are optically coupled but electrically more or less separated. In the bee (b) the ninth cell (R9) is a short proximal cell in most parts of the eye. In the dorsal eye region, R9 stratches also over the whole length of the ommatidium. Retinula cells R1 and R5 are S receptors, R2 and R6 M receptors, and R3, R4, R7, and R8 are L receptors (Menzel and Blakers, 1976). The short ninth cell is likely to be an S receptor (Menzel and Snyder, 1974) although confirmation by intracellular marking is still lacking. In the moth (c) lateral and tiered compositions act together in a complicated fashion (see also cross-sections at different levels of the ommatidium). The distal cell R1 is either an S receptor or an M receptor. The receptors R2–7 are L receptors and R8 is a VL receptor (Langer* et al., *1979). In both bees and moths, as in other insect species, the axons of the retinula cells within one ommatidium project to the same unit of the first visual ganglion, the lamina cartridge.*

and broad reflection functions, with less than three optima of spectral reflection, not more than three receptor types are needed to unambiguously resolve the chromatic differences whilst also ensuring that the system is minimally sensitive to metameric effects (Gouras and Zrenner, 1981; Gouras, 1985). Conversely, in cases where the pigmentation of the objects are selected in a co-evolutionary fashion (e.g. flower colours, coloration of conspecifics, mimicry of plants), along with the eyes designed to detect them, reflection functions with less than three spectral reflection optima should be favoured (see Section on Ecology and Evolution of Photopigments and Colour Vision).

Comparison of Photoreceptor Action Spectra

A considerable number of insect species have been studied with respect to the spectral properties of their photoreceptors (Review: Goldsmith and Bernard, 1974; Menzel, 1979; Burkhardt, 1983; Stavenga and Schwemer, 1984; Tsuda, 1987). Fig. 14.2 gives a frequency histogram of the λ_{max} values. Each spectral receptor type of a particular species is represented by a box with a number so that the species can be traced in the frequency histogram. Let us first consider the general distribution of the λ_{max} values

and deal with specific cases later. Four groups of spectral receptor types with average λ_{max} values at around 350, 440, 530, and 600 nm cover the whole potential visual range between 300 and 720 nm. One might ask why the visual pigments are not evenly spaced over the entire spectral range but appear in these four distinct groups, and this point is discussed by Goldsmith in Chapter 5. Since the photopigment in insects is either a rhodopsin with retinal as a chromophore (in the orders of Caelifera, Heteroptera, Coleoptera and Hymenoptera), or a xanthopsin with 3-hydroxyretinal as the chromophore (as in Lepidoptera and Diptera) (Vogt, 1983; Kirschfield, 1986), one might expect that the spectral groups are related to the chromophore. However, if one compares the values for the Hymenoptera and Diptera it is obvious that this is not the case. Instead, it is solely the protein moiety which determines the λ_{max}. Whether inherent molecular constraints restrict the pigments to certain spectral regions is at present unknown. We shall outline arguments in favour of ecological adaptations (see Section on Ecology and Evolution of Photopigments and Colour Vision) although additional factors cannot be ruled out.

Accessory pigments may co-exist with the photopigment in the same light guiding and light absorbing structure, the rhabdomer, and have a strong influence on the effective action spectrum. Sensitizing pigments may enhance the UV-sensitivity by a radiation-less energy transfer to the primary photopigment (Kirschfeld *et al.*, 1977; Minke and Kirschfeld, 1979). The fly *Musca domestica* is a most interesting example for a highly complex arrangement of spectral receptor types (Fig. 14.3) (Review: Hardie, 1986; Kirschfeld, 1986; Kirschfeld *et al.*, 1988). Six out of eight receptors in each ommatidium, the retinula cells R1–6, are equipped with the same mixture of a xanthopsin and a UV-sensitizing antennal pigment (3-hydroretinol) and appear identical all over the eye. The receptors represent the broad band, high sensitivity system which is certainly not involved in colour vision (see Fig. 14.2, Nos. 55 and 58 for *Calliphora* and *Musca*, and Nos. 50, 54 for *Drosophila*). The two remaining receptors (R7 and R8) may appear as one of eight different spectral types depending on the eye region. In the dorsal margin, a specialized region for polarized light vision, R7 and 8 are UV-receptors with λ_{max} at 335 nm (No. 11 in Fig. 14.2), while in the region of the 'love spot' or male fovea, a specialized dorsal frontal region in male flies for tracking female flies, R7r and 8r are equipped with the same pigments as R1–6 with λ_{max} at 490 nm and 350 nm (Nos. 10, 49, 55). Over most of the frontal and ventral eye, there exist two populations of ommatidia, a larger population (70%) with R7y (y, yellow refers to the colour of flourescence under shortwave illumination) ($\lambda_{max} = 360$ nm, No. 22) and R8y ($\lambda_{max} = 560$ nm, No. 78) and a smaller population (30%) with R7p (p, pale, no fluorescence) ($\lambda_{max} = 335$ nm, No. 11) and R8p ($\lambda_{max} = 460$ nm, No. 47). The action spectra of R7y and R8y are the most peculiar ever described (Kirschfeld *et al.*, 1988). R7y, for example, contains a xanthopsin (430 nm) whose direct absorption is blocked by a blue carotenoid (zeaxanthin and/or lutein) screening pigment. However, since it contains a UV-sensitizing pigment (3-hydroxyretinol), radiation-less energy is transferred to the xanthopsin and the cell is excited with a spectrum that is highly dominated by the sensitizing pigment ($\lambda_{max} = 335$ nm). R8y, the retinula cell beneath R7y, receives light which is filtered through R7y. Thus, UV-sensitivity is highly reduced and the longwave sensitivity is shifted bathochromatically. In higher Diptera, the sensitizing pigment is 3-hydroxyretinol, whilst in the lower Diptera (Simuliida) it appears to be retinol (Review: Kirschfeld, 1986).

Various mechanisms alter the action spectra via screening of the pigments. For example, the thermostable metapigments (metarhodopsin, metaxanthopsin) absorb in the blue or in the orange and may change the effective light flux accordingly. It has been calculated, however, that this effect is small for natural illuminations in eyes where the adaptation mechanism functions via moving granules of screening pigments (Schlecht, 1979). Furthermore, the light absorbing structures of different spectral receptors are combined in one light guiding structure, either in a parallel side-by-side or tiered arrangement (Fig. 14.1(b), (c)). In this case, the various photopigments screen each other counteracting the flattening of the action spectra by self-absorption in the long rhabdomers (Synder *et al.*, 1973). The refraction, reflection and light guiding properties of the rhabdom can also cause considerable wavelength dependencies and electrical interactions between photoreceptors may shape the effective action spectra (Review: Menzel, 1979; Snyder, 1979; Stavenga and Schwemer, 1984).

Determination of the Spectral Sensitivity of Single Photoreceptors

It is obvious that multiple factors can alter and shape the action spectrum of the receptors. In order to determine the spectral input to the neural colour processing, it is necessary to obtain accurate measurements of the spectral sensitivity of single photoreceptors. Since pigment extractions and electroretinograms are of little help, great efforts have been put into electrically measuring the spectral sensitivities of single photoreceptors, and under conditions which leave the photoreceptors as undisturbed as possible. The first recordings of the intracellular action spectra of an eye were successfully completed by Burkhardt and Autrum in 1960, and were measured from the fly *Calliphora*. Electrophysiological measurements of the $S(\lambda)$

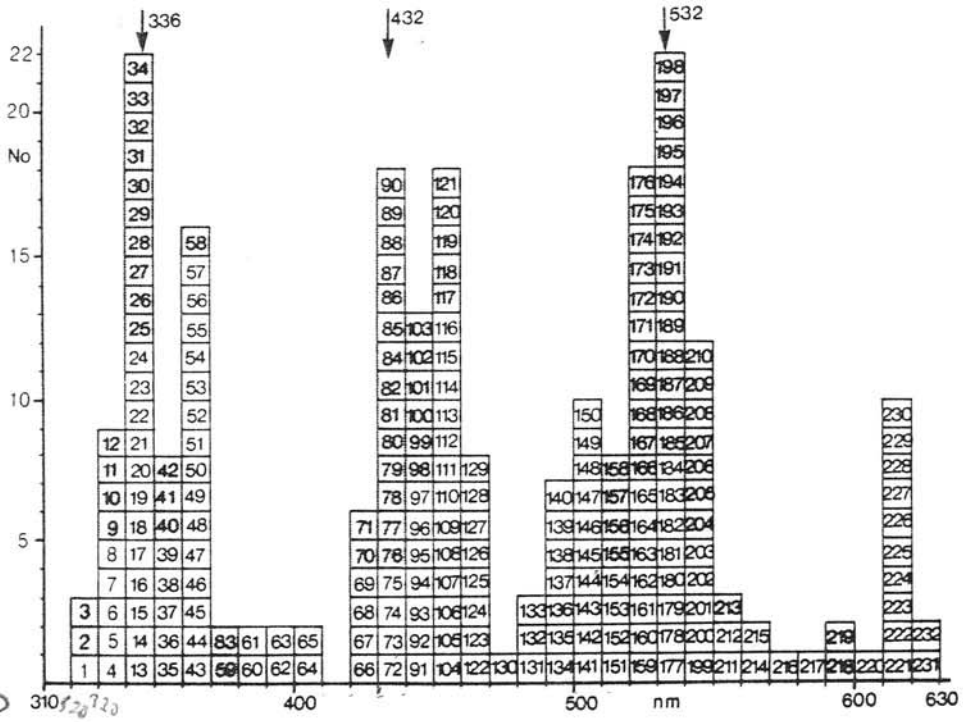

Fig. 14.2 *Frequency distribution of λ_{max} values of photoreceptors in insects. The grey squares are from recent measurements of the S (λ) -function of the photoreceptors in* Hymenoptera *with the spectral scan method (Menzel* et al., *1986). Abbreviations: numbers (1 to 232) refer to the respective fields in the histogram. Methods: intr. cell.: intracellular recording; ERG; electroretinogram, recording of the light induced mass potential (only those papers are used for the figure here, in which ERG measurements are used in connection with spectral adaptation experiments, and thus give information on the spectral sensitivity of the subsystems); micr. spect.: microspectrophotometry; pigm. spectr.: spectrophotometry of extracted pigment(s); spectr. pup.: spectrophotometry of the pupillary response. The three arrows (above) indicate the λ_{max} of the three spectral receptor types in the eye of the worker honey bee* Apis mellifera carnica.

Orthoptera: Locusta migratoria, *intr. cell.:* 73, 145 *(Bennett* et al., *1967), intr. cell:* 51, 74, 179, *(Vishnevskaya* et al. *1986). intr. cell. (bumps):* 112, 147 *(Lilliwhite, 1978), intr. cell. (long visual fibres):* 50 *(Osorio, 1986).* Gryllus campestris, *intr. cell. (spectral scan method):* 7, 116, 165 *(Zufall* et al., *1989).*

Hemiptera, Plannipennia, Coleoptera: Notonecta glauca, *ERG (Bennett and Ruck, 1979), intr. cell. (Bruckmoser, 1968):* 48, 67, 122, 159. Ascalaphus *ERG:* 1 *(Gogala, 1967), ERG:*61, 148 *Paul* et al., *1986);* Carabus auratus, *ERG (Hasselmann, 1962):* 14, 75. Photurus lucicrescens, *ERG:* 52, 68, 212 *(Lall* et al., *1982),* Photurus pyralis, *ERG:* 63, 216 *(Lall* et al., *1980a).*

Odonata: Anax junius, Ocellus, *intr. cell.:* 43, 141 *(Chappell and DeVoe, 1975). Compound eye intr. cell.:* 144 *(Horridge, 1969).* Aeschna *several species, intr. cell.:* 44 (Ocellus), 4, 46, 72, 104, 143, 134, 151, 135 *(Chappell and DeVoe, 1975; Autrum and Kolb, 1968, Eguchi, 1971).* Libellula *several species, intr. cell.:* 45, 66, 142, 177 *(Chappell and DeVoe, 1975; Horridge, 1969).* Hemicordula, *intr. cell.:* 35, 91, 152 *(Laughlin, 1975).* Sympetrum rubicundulum, *intr. cell.:* 19, 64, 146, 232 *(Meinertzhagen* et al., *1983).*

Blattoptera: Periplaneta americana, *intr. cell.:* 47, 153 *(Mote and Goldsmith, 1970; Butler, 1971; Butler and Horridge, 1973).*

Diptera: Calliphora erythrocephala, *intr. cell. R1–6 (two peaks):* 137, 140 *(Burkhardt, 1962; Meffert and Smola, 1976), spectr. pup. (Bernard and Stavenga, 1979).* Drosophila melanogaster *R1–6 ERG with mutants, two peaks:* 135, 136, *(Harris* et al., *1976).* Musca domestica, *intr. cell. R1–6:* 137, 140, *R7, 8 dorsal margin* 6; *R7r, R8r love spot* 5, 131, 137; *R7y 49; R8y* 214; *R7p* 6; *R8p* 126 *(Rev. Hardie, 1984, 1986; Kirschfeld, 1986).* Eristalis tenax, *intr. cell.:* 16, 125 *(Bishop, 1974),* 37, 111, 160 *(Horridge* et al., *1975), R1–6 spectr. pup.* 109 *(Bernard and Stavenga, 1979).* Eristalis arbustorum, *R1–6, spectr. pup.:* 94 *(Bernard and Stavenga, 1979).* Syrphus *spec. R1–6, spectr. pup.:* 93 *(Bernard and Stavenga, 1979).* Allograpta obliqua, *R1–6, spectr. pup.:* 107 *(Bernard and Stavenga, 1979).* Toxomerus marginatus *R1–6 spectr. pup.:* 115 *(Bernard and Stavenga, 1979),* Chlorops *spec. R1–6, spectr. pup.:* 130 *(Bernard and Stavenga, 1979).* Simulidae *three species, dorsal eye, ERG:* 21 *(Kirschfeld, 1986),* Bibio *spec. white eye, ERG:* 22 *(Kirschfeld, 1986).* Haemotopata *white eye, ERG:* 182 *(Kirschfeld, 1986).*

Lepidoptera: Heliconius numata, *intr. cell.:* 62, 123, 199 *(Struwe, 1972).* Macroglossum stellatorum, *ERG:* 13 *(Hasselmann, 1962).* Papilio aegeus, *intr. cell.:* 60, 106, 211, 221 *(Matic, 1983; Horridge* et al., *1983, 1984).* Papilio xuthus, *intr.:* 54, 65, 129, 163, 220 *(Arikawa* et al., *1987).* Aglais urticae, *ERG:* 53, 127, 180 *(Kolb, 1985; Steiner* et al., *1987).* Pieris brassicae, *ERG:* 55,

113 *(dorsal eye)*, 56, 114, 215, 231 *(medio ventral eye) (Steiner* et al., *1987; Paul* et al., *1986). Several species measured with spectr. pup.:* Anartia amathea, A. fatima 222, Polygonia interrogationis 223, Eurema mexicana 224, Eurema nicippe. 225, Phobis sennae 226, Pieris rapae 227. Apodema mormo 229, Everes comyntas 230 *(Bernard, 1979)*. Vanessa cardue *(and several other species), spectr. pup.:* 181 *(Bernard, 1979, 1983)*. Anthereae polyphenus, *pigm. spectr.:* 8, 128, 164 *(Langer* et al., *1986)*. Spodoptera exempta, *micr. spectr.:* 39, 129, 154, 217 *(Langer* et al., *1986)*. Manduca *spec., intr. cell.:* 20, 95, 161 *(White* et al., *1983)*. Deilephila elpenor, *micr. spectr.:* 38, 96, 162 *(Höglund* et al., *1973)*.

Hymenoptera: Apis mellifera *worker, intr. cell.:* 17, 92, 200 *(Autrum and v. Zwehl, 1964; Menzel and Blakers, 1976). Drone, intr. cell.:* 18, 105, 201 *(Autrum and v. Zwehl, 1963). Drone, spectr. pigm.:* 24, 97 *(Muri and Jones, 1983)*. Bombus *spec., intr. cell.:* 178, 184 *(Burkhardt, 1983)*. Bombus *spec., spectr. pup.:* 36, 110, 202 *(Bernard and Stavenga, 1978)*. Formica polyctena, *ERG:* 57, 150 *(Menzel, 1973)*. Cataglyphis bicolor, *intr. cell.:* 23, 149 *(Mote and Wehner, 1980); ERG: Paul* et al., *1986)*. Myrmecia gulosa, *intr. cell., bumps:* 69, 203 *(Lieke, 1981)*. Vespa rufa, *intr. cell.:* 183 *(Burkhardt, 1983)*.

The following species of Hymenoptera *were measured with intracellular recordings using the fast spectral scan method. The results are unpublished (Menzel, Peitsch, Fietz) if no authors are indicated.*

Apis mellifera *worker* 9, 76, 185 *(Backhaus* et al., *1987) Drone* 2, 77, 166; Bombus lapidarius 10, 78, 186; B. terrestris 11, 79, 187; B. jonellus 12, 80, 204; B. monticola 25, 98, 205; B. mori 40, 70, 188; B. hypnorum 220, Anthidium manicatum 3, 99, 169; Anthophora acervorum 41, 81, 168; Melecta punctata 26, 82, 189; Xylocopa brasilianorum 83, 84, 206 *(Hertel, personal communication)*; Schwarziana *spec.* 27, 100, 169 *(Hertel, personal communication)*; Nomada albogutata 71, 155; Melipona quadrifasciata 28, 117, 207 *(Backhaus* et al., *1987; Hertel and Ventura, 1985)*; M.margianata 29, 118, 208 *(Hertel and Ventura, 1985)*; Trigona spinipes 30, 85, 190 *(Hertel and Ventura, 1985)*; Polistes gallicus 42, 119, 170; Paravespula germanica 32, 87, 192; P. vulgaris 31, 86, 191; Vespa grabro 193 *(Hertel, personal communication)*; Dolichovespula norvegica 101, 171; Philanthus triangulum 33, 102, 172; Cerceris rybynensis 88, 156, 173; Lasioglossum malachurum 103, 174; L. albipes 157; Osmia rufa 34, 89, 213, 120, 194; Ichneumon *spec.* 175; J. stramentarius 176; Tenthredo campestris 121, 195, 218; T. scrophulariae 196, 219; T. *spec.* 159; Oxala flavescens 59, 90, 197 *(Hertel, personal communication)*; Lestrimelitta limao 198 *(Hertel, personal communication)*; Urocerus gigas 210 *(Hertel, personal communication)*.

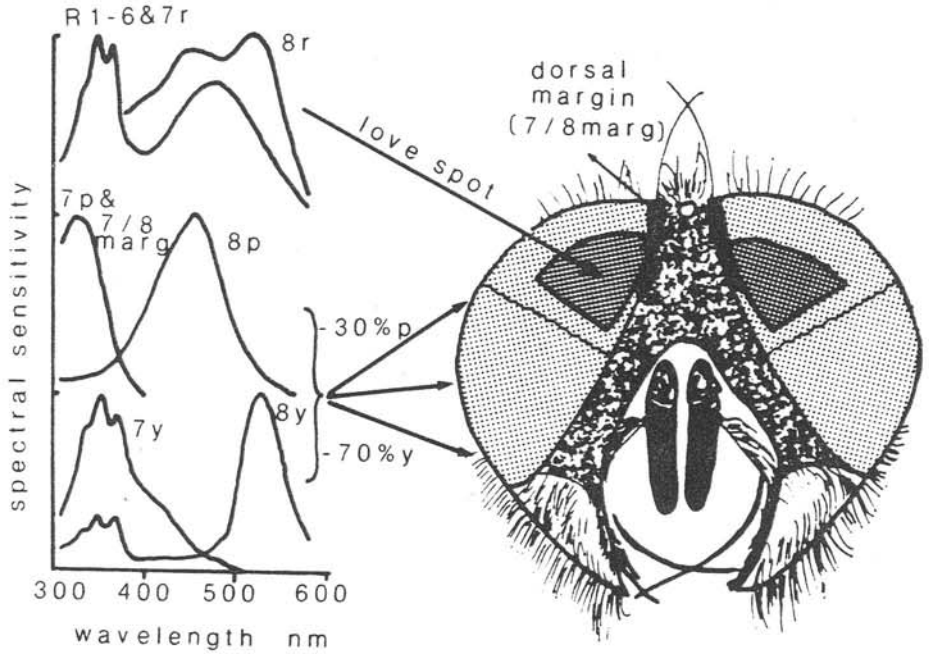

Fig. 14.3 *Arrangement of spectral receptor types in the compound eye of the fly,* Musca domestica *(Hardie, 1986). Receptors R1–6 (see also Fig. 14.1) appear all over the eye with the same spectral properties. The receptors R7 and R8 differ considerably in their spectral properties depending on their location within the eye. R7r (R7 in the male 'love spot') has the same visual pigments as R1–6. R8r also has the same pigments but a distorted action spectrum due to the filtering effect of the overlying R7r. R7 and R8 in the dorsal margin (R7/8 margin) are pure UV receptors, and are sensitive to the E-vector direction of polarized light. Over the rest of the eye R7 and R8 appear in two different spectral classes (7/8y, 7/8p).*

function of receptors in insects are often complicated by the fact that the penetrating electrode artificially couples neighbouring receptors together or connects the extracellular space with the interior of the recording cell. Indeed, in some instances complete theories of colour vision in insects have been based on such unreliable recordings (Horridge *et al.*, 1983, 1984). For example, it has been claimed that depolarizing and hyperpolarizing receptor potentials appear in one photoreceptor of the butterfly *Papilio*, depending on the wavelength of light, and such a spectral opponent receptor has even been described in the honey bee (Menzel and Blakers, 1976). Other examples, although less dramatic, can be found in nearly all papers dealing with the intracellular recording of insect photoreceptors and spectral sensitivity measurements (for discussion see Menzel, 1979; Meinertzhagen *et al.*, 1983; Menzel *et al.*, 1986). The apparent violations of the univariance principal in insect photoreceptors are more than likely an indication of methodological failures rather than a discovery of new principles, as is demonstrated by the history of receptor recordings in the honey bee eye. When Autrum and von Zwehl (1964) succeeded for the first time in measuring different S(λ)-functions in different receptors, practically none of the functions corresponded to a clean one-pigment system. They interpreted these results as imperfections in their methods, and this turned out to be a wise and far-sighted interpretation as we now know after 20 years of intensive studies (Menzel *et al.*, 1986).

Although the data shown in Fig. 14.2 are collected from studies using less reliable methods (see legend to Fig. 14.2), the general picture is well supported by results from more appropriate studies (e.g. the grey fields which give the results from Hymenopteran species). The two shorter wavelength populations (which we shall term S and M receptors respectively) are well represented in all insect species so far studied. The population of receptors with λ_{max} around 520 nm (L receptors) clearly separate into two subpopulations, if the insect orders are considered individually. The population around 500 nm is mainly from dragonflies, butterflies and Orthopterans, whereas the population around 540 nm is predominantly from Hymenopterans such as bees and wasps. The very long wavelength (VL) receptor population (λ_{max} = 600 nm) appears small, but this may be due to the great difficulties involved in the recording from photoreceptors in butterflies, which are the major group of insects that have such very longwave-sensitive cells. The λ_{max} of 610 nm is one of the longest λ_{max} found so far in the animal kingdom. The long-wavelength peak does not result from a screening pigment at shorter wavelengths.

Not all the VL receptors have photopigments with corresponding λ_{max} values, since screening pigments may shift the absorption to a longer wavelength by selective transmission above 590 nm. Such a screening pigment may be the photopigment of the L receptors or an additional passive pigment as is the case in pierid butterflies (Ribi, 1979). A consequence of this screening at the shortwave end of the action spectrum is a narrowing of the half-bandwidth by approximately 70 nm. A similar shift to long wavelength with a reduction in the half-bandwidth has been described for several species of fire flies (Lall *et al.*, 1988), where a rhodopsin with λ_{max} at 550 nm probably exists. This shift is caused by a screening pigment which is packed into granules in the close vicinity of the rhabdom. The sharp transmission cut-off is at slightly different wavelengths (between 520 and 540 nm) for different species, and this results in a species-specific difference in the effective λ_{max} of the L receptor. Since the pigment granules in the retinula cells are part of a pupil mechanism, their filtering effect is stronger and spectrally more selective in the light adapted state. In house flies, the closing of the pupil reduces sensitivity in the blue-green region more strongly than in the UV, and shifts the longwave sensitivity to longer wavelengths (Vogt *et al.*, 1982). There is, however, no evidence that such shifts effect the behaviourally measured spectral sensitivity in the sense of a 'Purkinje-shift', or that these shifts may be used to create spectrally different receptor types that are used in colour discrimination. Experiments designed to study a 'Purkinje-phenomenon' in honey bees did not give consistent results (Thomas and Autrum, 1965), and the claim that grasshoppers may use different coloured filters for colour discrimination is not supported by experimental evidence (Kong *et al.*, 1980). It has recently been claimed (Gribakin, in press), that the L receptors in the honey bee are also shifted to long wavelength by screening pigment granules in the receptors. Experimental evidence comes from white eye mutants whose receptors peak at 526 nm as opposed to 549 nm for wild type eyes. The scatter of the λ_{max} of single L receptor recordings (Menzel and Blakers, 1976) may be related to this effect, and variations in the screening strength may be a consequence of the different states of adaptation.

Apart from the main photopigment, we have so far only mentioned the following mechanisms as influencing the spectral sensitivity of single insect photoreceptors: self-screening in the highly absorbing rhabdom, antennal or sensitizing pigments, filtering by metarhodopsin, and filtering by a screening pigment. Although other factors such as waveguide modes, corneal filters and tapetum may also be important, they shall not be discussed in any great detail here. Waveguide modes (Snyder, 1979) probably have only a slight influence on the cell's spectral sensitivity, even for very narrow rhabdomeres where the effect would be strongest (see Stavenga and Van Barneveld, 1975), and whether corneal interference filters, which appear so colourful in tabanid and dolichopodid flies (Review: Miller, 1979), change the spectral sensitivity of

the receptors is at present unknown. In most butterflies, the tracheoles at the proximal end of the rhabdomes form interference reflection filters (Miller and Bernard, 1968), and it is often assumed that these filters should improve absolute sensitivity and also affect spectral sensitivity. But once again, conclusive experimental evidence is still lacking. The above is also true for other reflecting layers in the retina, which frequently appear not only in insect eyes but also those of other animals (Review: Miller, 1979; Land, 1981).

Number of Spectral Inputs

The spectral input system of insects varies between monovariant and pentavariant forms (see legend to Fig. 14.2). Monovariant systems are often restricted to specialized eye regions, such as the dorsal eye regions of several species which have been found to be exclusively composed of S receptors, e.g. in *Ascalaphus* (Fig. 14.2, No. 1), *Musca*(Fig. 14.2, No. 11) or M receptors as in *Gryllus* (Labhart *et al.*, 1984; Zufall *et al.*, in press). Some insect species, e.g. the backswimmer *Notonecta gluaca* possess two types of ommatidia in the dorsal eye region, one of which is monovariant UV-sensitive, the other trivariant (Schwind, 1985). Since the monovariant S or M systems are often highly sensitive to the direction of the e-vector of light, they appear as specialized polarized light detectors in the dorsal eye region which avoid signal confusion by restriction to a narrow spectral window. High sensitivity to short-wavelength light also optimizes the detection of very small objects, such as conspecific animals, against the bright background of the sky. This is because the already small acceptance angle of the large lenses in the dorsal eye region is even smaller for shorter wavelengths, and contrast is greatest at short wavelength (Kirschfeld and Wenk, 1976). In some species, the lateral and ventral eye regions (e.g. lateral eye in honey bees, ventral eye of *Aeschnia*, ventral eye of the cricket) may contain only or predominantly L receptors, but experimental evidence for monovariant longwave-sensitive eye parts is less conclusive.

Divariant systems are more frequently found, e.g. in the ants *Formica polyctena* (Fig. 14.2, Nos. 57, 150) and *Cataglyphis bicolor* (Fig. 14.2, Nos. 23, 149), the cockroach *Periplaneta americana* (Fig. 14.2, Nos. 20, 67) and in the ventral eye of *Ascalaphus* (Fig. 14.2, Nos. 61, 148). In all these species, S receptors are combined with L receptors. In the drone bee S and M receptors have been found to cover most of the eye (Autrum and von Zwehl, 1963). However, since drone bees discriminate bluish-green pigment colours very well with their frontal eye (Menzel *et al.*, 1988a), the L receptors, which have so far only been recorded in the extreme ventral part of the eye, have probably escaped detection. In *Notonecta* (Fig. 14.2, Nos. 122, 159; also Schwind 1985) M and L receptors cover the ventral part of the eye. The male fly (in *Musca*, but probably not in *Drosophila* and *Calliphora*) is equipped with a special divariant region of its dorsal front eye, the 'love spot' (see above and Fig. 14.3). However, the very broad action spectra of both of these receptor classes make any chromatic computations very unlikely, and it would seem that they are more concerned with neural pooling in a high sensitivity system.

Trivariant eyes are the regular case in insects as they are in other classes of the animal kingdom. Typically the VL receptor is lacking (Fig. 14.2). Tetravariant systems were predominantly found in Lepidoptera (see Fig. 14.2, *Papilio argus*, *Pieris brassicae*: medio ventral eye, and probably nine other species for which a VL receptor was detected, e.g. *Spodoptera exempta*, a noctoid butterfly, Fig. 14.2, Nos. 39, 129, 154, 217) and in the dragonfly *Sympetrum* (Fig. 14.2, Nos. 9, 25, 64, 81). Two species of primitive wasps (*Tenthredo*) were found to contain four spectral receptor types (Peitsch and Menzel, 1988; Fig. 14.2 does not show the S receptor because it was only just recently recorded, Nos. 124, 195, 218, 196, 219 in Fig. 14.2). Another Hymenopteran, the solitary bee *Callonychium*, also possesses a tetravariant input system with λ_{max} at 363, 404, 553 and 600 nm. We shall analyse a tetrachromatic colour vision system using *Callonychium* as an example (see below). One species of the Papilionaceae, *P. xuthus*, is claimed to be pentavariant with λ_{max} at 360, 400, 460, 520, and 600 nm (Fig. 14.2, Nos. 54, 65, 129, 163, 220). It is very likely, although not yet verified, that tetra- and pentavariant eyes are divided into regions with different combinations of the receptor types, and thus *P. xuthus* may not have the capacity of tetra- or pentachromatic colour vision. Evidence comes from ERG recordings in different parts of the eye.

Multiple spectral input does not necessarily mean a colour vision system of corresponding dimensionality. This is why the terms mono- to pentavariance were used, rather than mono- to pentachromaticity. We shall come back to this problem in the Section on Colour Vision and Wavelength-Selective Behaviour.

Receptor Models

Any receptor model of colour vision may start with the assumption that each spectral receptor type provides the nervous system with an independent signal of the effective photon flux in the wavelength band described by the receptor's action spectrum. Such an assumption allows for the construction of a physiological colour stimulus space (tristimulus space) very similar to a colour mixture space (Le Grand, 1948; Cornsweet, 1970; Rushton, 1972; Rodieck, 1973), where the primaries correspond to the photon fluxes absorbed by each of the spectral receptor

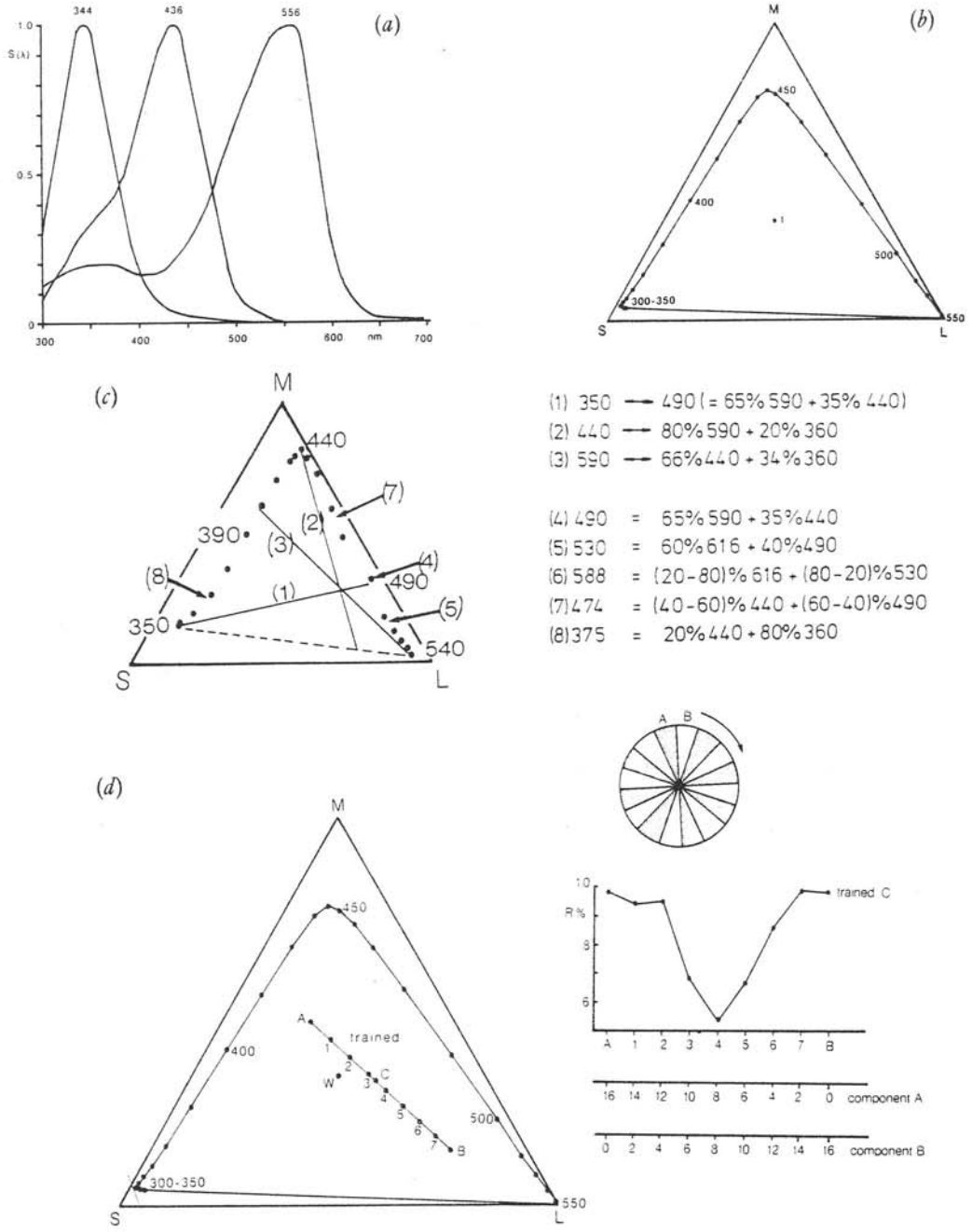

Fig. 14.4 *A receptor model of colour vision in the honey bee,* Apis mellifera. *(a) Spectral sensitivity functions as they were used for all the model calculations. These functions are the best estimate of all measurements collected so far with various methods (see also Fig. 14.5 for actual measurements). (b) The chromaticity diagram plotted from calculations described in the text. (c) Results of mixture experiments carried out by Daumer (1956) and the predictions of the receptor model. The colour matching loci are constructed from the mixture fractions of the behavioural experiments and are compared with the corresponding loci in the chromatic diagram. The table gives the average proportions of spectral lights as determined by Daumer for complementary colour stimuli (1–3) and non-complementary stimuli (4–8). (d) Results of mixture experiments with rotating sectors. The colour stimuli A and B correspond to a blue (A) and a yellow (B) cardboard. The bee has been trained to a stationary homogeneous stimulus C. If the arrangement of sectors (see inset) is rotated with a speed that results in more than 150 Hz local flicker frequency, then the colour appearance fuses for the bee with the consequence that the bee confuses the mixed stimuli as if they were of equal proportions (A:B = 8:8 – colour locus 4). For other pretrained colour stimuli other proportions of confusion are reached. The result of the mixture experiment is well predicted by the receptor model. (W = White background).*

types (tristimulus values). Let us again apply this procedure to the honey bee principally because the action spectrum have been relatively accurately determined. Nevertheless, further assumptions are necessary. In the model presented in Fig. 14.4, we assume that 'bee-luminance' is proportional to the sum of the tristimulus values and that the 'bee-brightness' of any spectral mixture is only dependent on the spectral sensitivities of the receptors. Therefore, the colour stimulus space corresponds to the colour luminance space in our model calculation. The corresponding physiological chromaticity diagram (Fig. 14.4(b)) represents a plane of constant 'bee-brightness' (equivalent to constant total absorbed quanta) (see Backhaus and Menzel, 1987, for details).

If the Grassmannian mixture rules hold for the bee, as they do for man, the outcome of mixture experiments should be predicted by our model, and this is indeed the case as Fig. 14.4(c) shows. A different kind of colour mixture experiment is depicted in Fig. 14.4(d). Here sectors of pigment colours on a circular disc are mixed by fast rotation. If the local flicker frequency, i.e. the flicker frequency at any small field within the target resulting from the rotaton, exceeds 200 Hz then the bee chooses the rotating sectors as if they were an evenly coloured, stationary target. As Fig. 14.4(d) shows, the colour mixing by rotation is also well predicted by the application of Grassmann's rules to the physiological chromaticity diagram.

The concept of perceptual distance between two colour signals can also be applied to the tristimulus space if we assume that the uncertainty of the receptor voltage signal determines the smallest just noticeable distance (jnd-step) in perception. Schrödinger's (1920) line element is thus traced back to the voltage noise components of the receptor (Backhaus and Menzel, 1987). Voltage noise originates from the statistical nature of photon absorption and fluctuations in the latency and the amount of current after each quantal absorption. The photon absorption processes and transducer processes are responsible for fluctuations in the receptor potential (shot noise and transducer noise) (Laughlin, 1981). We estimated a maximum fluctuation amplitude of $\pm 1.2\%$ of the maximal receptor potential and noticed that to a first approximation these fluctuations are independent of the magnitude of the potential. The fluctuation amplitude can be converted into a perceptual jnd-step by assuming that one jnd is reached if the variation in intensity, wavelength and white-light proportion, with respect to a reference light, causes a just significant change ($P = 0.5$) in at least one of the three receptor types in one ommatidium. The total perceptual distance is assumed to be equivalent to the smallest number of receptor based jnd-steps. The receptor based jnd-steps are determined by the smallest number of noise steps in all three receptors. When the jnd-scale is compared with the behaviourally determined discrimination functions, a very good agreement is found for both spectral stimuli and

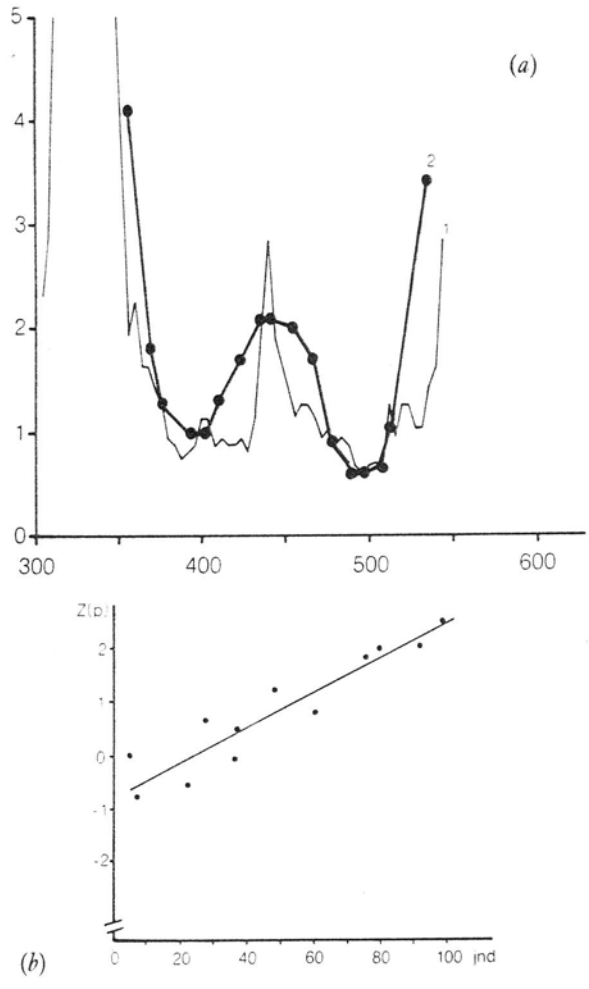

Fig. 14.5 *(a) Spectral discrimination as predicted by the receptor model (curve 1) and as determined in behavioural experiments (curve 2, v Helversen, 1972a). The two functions are nomalized at 490 nm: The unit of the ordinate corresponds to 8 nm of v. Helverson's $\Delta\lambda$-function, and to the reciprocal value of 40 jnd steps per 10 nm in the model calculation (see text and Backhaus and Menzel, 1987). (b) Comparison of the probability transformed choice frequencies* z(p) *(ordinate) from dual choice discrimination tests of pigment colours with the corresponding perceptual distance as derived from the jnd-measure of the receptor model (abscissa). A full explanation of the figure is given in Backhaus and Menzel (1987). Many different colour stimuli were used in the training. The total number of choices in 210 discrimination tests is 4622.*

pigment colours (Fig. 14.5). Discrimination of monochromatic stimuli can be best described by the $\Delta\lambda/\lambda$-function. Such an experiment was carried out with honey bees by von Helversen (1972a), who found the expected optima of discrimination at around 400 and 490 nm. The model calculation predicts, in addition to these optima, an improved spectral discrimination in the far-UV region. The receptor

based jnd-model also reliably predicts the discrimination between broad band colour plates. Since such colour plates differ in intensity and chromaticness (hue, saturation), we analysed whether intensity difference contributes to discrimination. The correlation between the jnd-scale and the choice proportion is optimal if any differences in intensity are ignored and the number of jnd-steps is calculated for the chromaticity plane of equal brightness. Experiments showed that bees ignore brightness differences if they are not particularly trained to signals that differ only or predominantly in brightness. That bees are extremely insensitive to brightness differences when trained to colour signals was already observed by Daumer (1956) and von Helversen (1972a), and was recently confirmed by Backhaus *et al.* (1988).

How strong is the predictive power of such model calculations, and more specifically, how sensitive are the predictions with respect to the action spectra of the receptors? This question is particularly relevant for a comparison between species. Spectral sensitivity measurements of single receptors are relatively easy to collect and this facilitates the comparative approach to colour vision. Never-

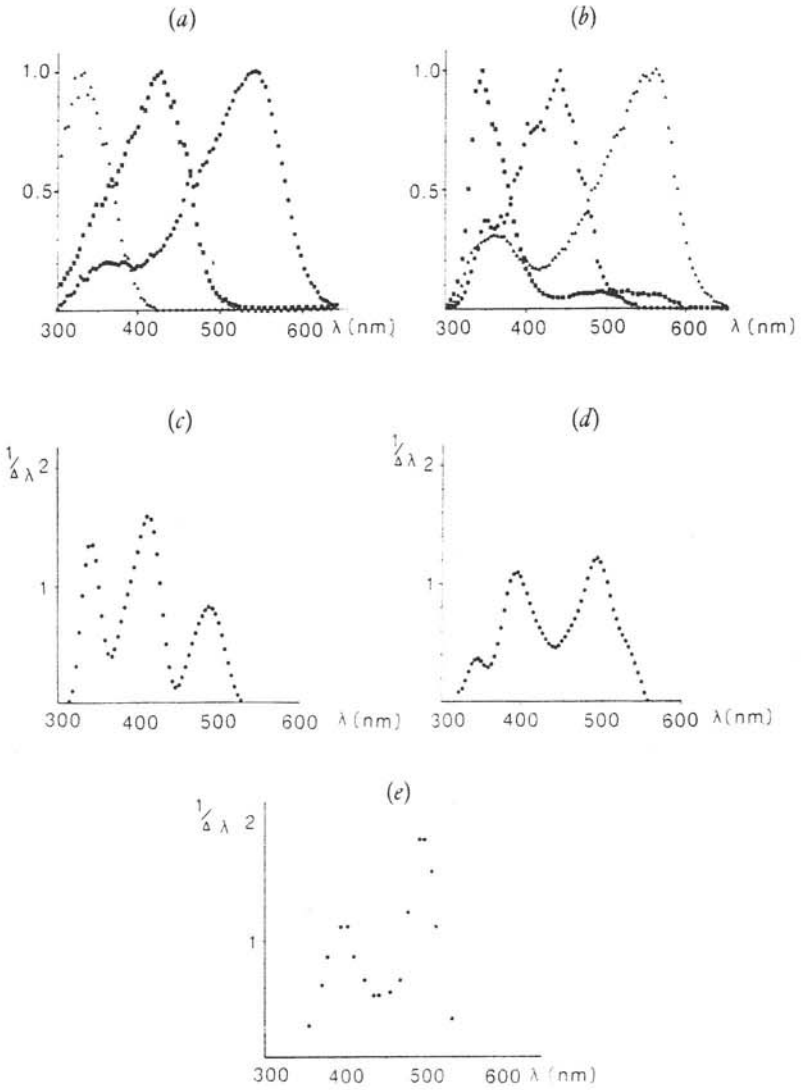

Fig. 14.6 *A test of the predictability of the receptor model. As described in the text, two sets of $S(\lambda)$ functions were used which were collected by two experimentors, (a) Fietz (1986) and (b) J. de Souza (see Menzel* et al., *1986). The corresponding $\Delta\lambda/\lambda$-functions as calculated by the receptor model are shown in (c) and (d) respectively. (e) Gives the result of behavioural experiments of spectral discrimination by v. Helversen (1972a). The unit of the vertical scales in (c) and (d) correspond to 14 jnds. In (e) the unit of the vertical scale is 0.9, which means that, for example, wavelengths separated by 6 nm (at 490 nm) or 9 nm (at 400 nm) are discriminated (see text for further explanation and Fig. 14.5).*

theless, receptor measurements may suffer from methodological imperfections (see above). For example, we routinely use the fast on-line computation of $S(\lambda)$ during recording experiments, and this stimulates the rejection of $S(\lambda)$ measurements which deviate from a clean one-pigment function. The averaging of such recordings results in a different set of spectral input data from those obtained by averaging all recordings, which only meet criteria of the quality of recording (Fig. 14.6(a),(b)). The corresponding $\Delta\lambda/\lambda$-functions (Fig. 14.6(c),(d)) calculated by the procedure described above, indicate that the set of the total averages of $S(\lambda)$ are indeed the better input set than the preselected averages. This result does not rule out the possibility that the photoreceptors in the honey bee eye have clean single pigment-based $S(\lambda)$-functions, but it does indicate that if such functions exist on the receptor level, then neuronal processing is likely to alter them in such a way that the S and M receptors are somewhat more sensitive at longer wavelengths than one would expect from the absorbance spectrum of the corresponding pigment. The predictive power of the model calculation is also demonstrated in an experiment with the solitary bee *Osmia rufa*. Although only five narrow band colour signals were tested in behavioural discrimination tests, the receptor model describes the hue discrimination very well (Menzel *et al.*, 1988b).

With this in mind, it is worthwhile comparing the colour vision systems of different species of flower-visiting Hymenoptera, for which only the receptor $S(\lambda)$ functions have been determined but where behavioural data are lacking (Fig. 14.7). Although all species discriminate best in the violet and bluish-green region, as one would expect from the position of their respective λ_{max} values (see also Fig. 14.2). The various species differ considerably in the relative height of the optima and in the absolute number of jnd-steps, as well as the shape of the $\Delta\lambda/\lambda$-function. This is in accordance with species-specific adaptations of colour vision systems (see Section on Ecology and Evolution of Photopigments and Colour Vision).

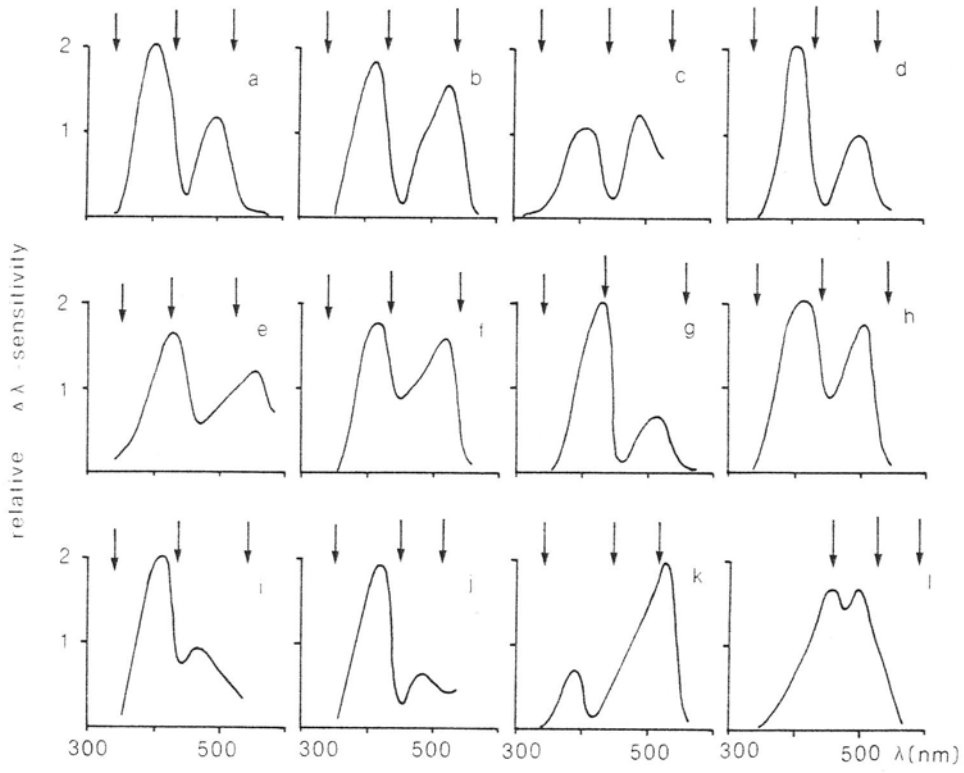

Fig. 14.7 *Spectral discrimination functions for 12 different species of* Hymenoptera *calculated by a receptor model of colour vision (see Figs. 14.4, 14.5 and text). The respective ordinates give the number of jnd-steps in relative units (relative $\Delta\lambda$-sensitivity). The scale is not the same for all species, and is therefore given in brackets after each species name. a – d = bumble bees: a*—Bumbus terrestris *(scale 1 corresponds to 11 jnd steps), b*—Bombus jonellus *(25), c*—Bombus monticolla *(6), d*—Bombus lapidarius *(13); e–h = solitary bees: e* — Anthophora acervorum *(19), f* — Melecta spec *(25), g* — Osmia vulgaris *(27), h* — Trigona spinipes *(7), i–l = wasps: I* — Paravespula germanica *(8) j* — Paravespula vulgaris *(4)* Polistes gallicus *(14), l* — Philanthus triangulum *(4). The arrows in each figure mark the λ_{max} of the photoreceptor of the corresponding species (see also Fig. 14.2).*

Poly-Dimensional Colour Vision Systems

Many species of insects have more than three receptor types, and in such cases neuronal processing of the receptor potentials may lead to a more-dimensional colour representation. In this chapter we shall outline the general properties of a poly-dimensional colour vision system, and then give a quantitative description of two selected examples.

Lower colormetrics investigates colours that match in all colour attributes such as brightness, hue and saturation (strong metameric colours) or colours which match only in one or two colour attributes (partial metameric colours). In the case of strong metamerism, different spectral light distributions cause identical colours because the photon fluxes absorbed by each of the receptors are identical. Thus, the values of the colour coding system and, therefore, the corresponding colours are the same (small-field colour vision, lateral effects neglected). This should also be the case for colour vision with more than three dimensions. The linear Grassmannian rules for colour mixture hold exact because of the linear superposition law of photon absorption.

Colour matches in chromaticness (hue and saturation) where brightness is neglected are only approximately described by the Grassmannian mixture rules. In general, hue shifts occur when colours vary in brightness or saturation (Bezold-Brücke and Bezold-Abney phenomena). If brightness differences are not too large, and not too different from the brightness of the adapting (background) light, chromaticness of a colour is well represented in the chromaticity diagram by the chromaticity coordinates, which are the absorbed photon fluxes normalized to the total sum of the photon fluxes absorbed by the receptors (see below). The calculation of the chromaticity coordinates is simply extended to more than three dimensions (von Helversen, 1972b):

$$p_i = P_i / \sum_{j=1}^{n} P_j \qquad (14.1)$$

where P is the polystimulus values equivalent to the effective photonflux in each of the photoreceptors, p is the chromaticity coordinates, and i denotes the different spectral receptor types (e.g. S, M. L, VL,. . .).

The loci of the colour mixtures are calculated by the centre-of-gravity construction as in the three-dimensional case (see above). Since by equation 14.1 the dimensionality is reduced by one, a geometrical representation is also available for e.g. the four-dimensional case. From equation 14.1 the three two-dimensional sub-cases with zero contribution of one of the four receptors may be represented as three dependent colour triangles, so that the representation of four-dimensional colours by three chromaticity coordinates builds up an equally sided tetraeder (see also Neumeyer, 1988). For two-dimensional chromaticity diagrams (colour plane), the three orthonormals from each of the edges to the respective opposite triangle side represent the chromaticity coordinates with maximum length of unity. However, with respect to equation 14.1, only two of them are independent. In the case of four-dimensional colour vision, the four chromaticity coordinates are orthonormals from one edge of the tetraeder to the opposite colour plane also with maximum length of unity. Only three of them are independent. Colours are represented by the crossing points of the four planes perpendicular to the four chromaticity coordinates (parallel to the outer planes of the tetraeder) intersecting

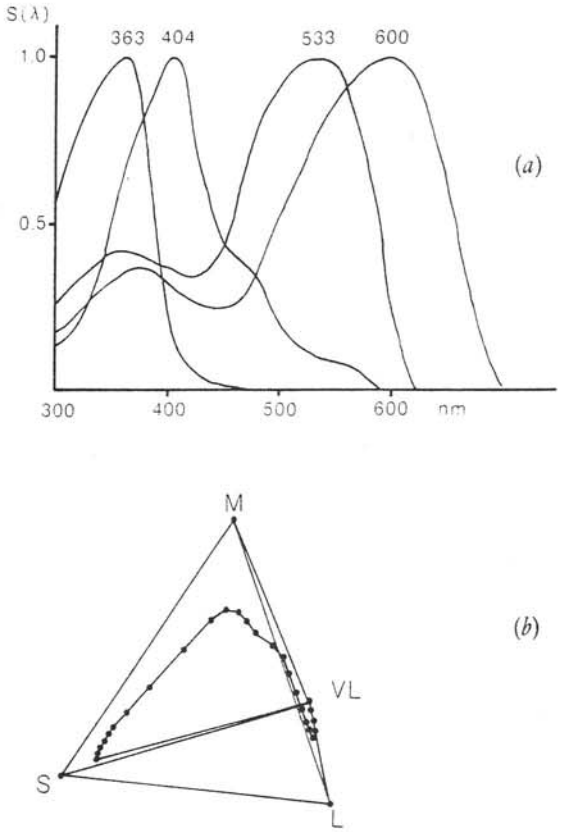

Fig. 14.8 *Model calculation for a tetrachromatic colour vision system in the solitary bee* Callonychium petuniae. *The spectral sensitivities (a) were recorded by intracellular electrodess (courtesy Dr D. Fix-Ventura). Since only few cells were found so far for the M and VL receptor the scatter of the sensitivity values were slightly smoothed. (b) A three-dimensional chromaticity diagram for the tetrachromatic colour space of* Callonychium *(see text). The spectral line together with the 'purple mixture line' is indicated with a thick line, and spectral lights between 300–600 nm are indicated in 10 nm by dots.*

the coordinates at the points of the calculated chromaticity values. As derived above, the three dependent chromaticity coordinates are transformed to two orthogonal (Cartesian) coordinates x and y:

$$x = p_3/\sin(60°) + p_2/\tan(60°)$$
$$y = p_2 \qquad (14.2)$$

the transformation from four dependent chromaticity coordinates to three orthogonal (Cartesian) coordinates is similarly:

$$x = 1.224744 - ((p_1/\sin(\alpha) + p_2/\tan(\alpha))/(\sin(60°) + y/\tan(60°))$$
$$y = p_4/\sin(\alpha) + p_2/\tan(\alpha)$$
$$z = p_2$$
$$\text{with } \cos(\alpha) = 1/3 \qquad (14.3)$$

The linearity of the Grassmannian mixture rules allows for brightness to be expressed as a factor normalized to the chromaticity coordinates which results in different volumes of the tetraeder. As an example, we calculated the chromaticity coordinates of the spectral lights from 300–600 nm for the spectral sensitivities of the solitary bee *Callonychia*. Fig. 14.8 shows the chromaticity coordinates transformed according to equation 14.3 plotted in a Cartesian coordinate system.

Lower colormetrics (identity judgements) fails in answering the question of colour discrimination and colour similarity. In general, the loci of colour stimuli surrounding a reference stimulus in the colour plane do not lie on a circle but, as in the case of human colour vision, on asymmetric ellipses. Thus, the chromaticity diagram is not a representation for subjective discrimination values. In three-dimensional colour vision, colour differences cannot be read from the chromaticity diagram, and in four-dimensional colour vision, colour differences cannot be read from the three-dimensional Cartesian plot.

By applying the concept of receptor-based just noticeable difference steps (jnd) as the limiting factors in perceptual discrimination one can calculate spectral discrimination functions for the tetrachromatic or even pentachromatic case similarly as described for the trichromatic case (see above). Perceived colour differences are interpreted as being a linear function of the number of jnds. If one assumes that only the spectral sensitivities differ from species to species, and that noise and adaptation properties are nearly the same, then the model can be used to calculate colour differences for different species. The calculations for two different species are shown in Fig. 14.9.

The predictions of these model calculations are of course then subjected to experimental verification. For example, *Callonychia* was tested for discrimination to pigment colours, and discrimination was found to exist for orange and red colours (Wittmann, personal communication). This confirms that a VL receptor must be involved in colour discrimination but does not test the existence of a tetrachromatic colour space. The butterfly *Papilio* is known to perform wavelength-selective behaviours (see Section on Colour Vision and Wavelength-Selective Behaviour), but colour discrimination tests based on colour training experiments have yet to be carried out. One insect, the desert ant *Cataglyphus bicolour*, was claimed to have tetrachromatic colour vision (Kretz, 1979), but the behavioural evidence is not convincing and is partially in contradiction to an earlier publication (Wehner and Toggweiler, 1972) where only two optima of

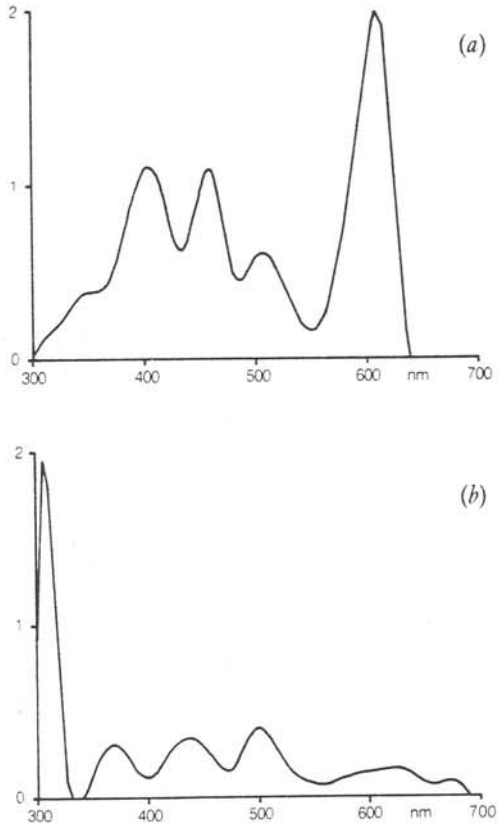

Fig. 14.9 *Spectral discrimination functions for tetra- and pentachromatic colour vision system as revealed by model calculations (see text). (a)* Callonychium petuniae, *an example for a tetrachromatic colour vision system (see Fig. 14.8). The unit at the ordinate corresponds to 12 jnds. (b)* Papilio xuthus, *an example for a pentachromatic colour vision system. The unit at the ordinate corresponds to 70 jnds. The spectral input functions were taken from Arikawa* et al. *(1987) (see also Fig. 14.2, Nos. 54, 65, 129, 163, 220). The peak at very short UV wavelengths results from the steep $S(\lambda)$-function of the S receptor at these wavelengths.*

spectral discrimination were found. Furthermore, only two spectral receptor types have so far been recorded in the eye of *Cataglyphus* (Mote and Wehner, 1980, see Fig. 14.2 Nos. 23, 149).

Spectral Opponency

Spectral opponency is the neural mechanism that codes for hue contrast in the insect brain. Evidence comes from three independent sources: (a) neurophysiology of visual neurones, (b) behavioural colour contrast phenomena, and (c) dimensionality of colour vision as derived from multidimensional scaling procedures of colour discrimination experiments.

Neurophysiology of Visual Neurones

Recordings from visual neurones in the insect brain revealed spectral opponent neurones as early as 1968, and Swihart (1968, 1970, 1972a,b) found a variety of such neurones in the visual ganglia and the brain (protocerebrum) of the butterflies *Heliconius, Papilio, Epargyreus*, e.g. neurones with excitatory ($^+$) and inhibitory ($^-$) response patterns of the following kind: B^+G^-, $G^+B^-R^-$, $R^+G^-O^-$, $B^+G^-R^-$ (B for wavelengths 430–480 nm, G for 490–560 nm, O for 560–620 nm, R for $\geq$ 620 nm). Unfortunately, Swihart did not test UV light and the experiments have not been repeated in the meantime. Horridge *et al.* (1984) also recorded from butterfly visual interneurones, but did not find any spectrally opponent responses. Since butterflies have UV receptors (Fig. 14.2) and respond to UV selectivity in behavioural tests (see later), one would expect even more combinations of spectrally opponent responses. Several other insect species have also been studied, and spectral opponency was established in all cases (locust: Osorio, 1986, 1987b; cockroach: Edwards, 1982; Mote and Rubin, 1981; Mote *et al.*, 1981). The most thoroughly investigated species is once again *Apis mellifera*, and we shall use the honey bee to illustrate a few principles.

The three spectral inputs from each of the 5400 ommatidia in each compound eye are interconnected in the first visual ganglion, the lamina, and in such a way that separate pathways for achromatic (black/white) contrast and spectral coding are already formed at the first level of synaptic interaction. Spectral coding in the lamina (not shown in Fig. 14.10) is represented by a large monopolar cell (LMC) which responds with depolarization to S receptor and hyperpolarization to M and L receptor inputs. Another LMC is dominated by inputs from the M receptors and receives only weak inputs from the S and L receptors, and a further LMC receives only L receptor input. The fourth LMC sums all three receptor inputs and may represent the first neurone of a high sensitive, achromatic system (see below) (Menzel, 1974; Hertel and Maronde, 1987b; de Souza, personal communication.). The outputs of these LMCs are combined with those of the S receptors in the distal layer of the next visual neuropile, the medulla, where the S receptors project with their long axons. Processing of spectral information in the distal medulla is not yet understood, but neurones in the proximal medulla already respond with the whole set of spectral opponency found in the visual system of the bee (Fig. 14.10).

Spectral opponency of neurones in the proximal medulla and lobula appears in two forms, tonic opponency and ON/OFF (phasic) opponency. In the first case the neurones are excited or inhibited by a flash of monochromatic light in their sustained response (Fig. 14.10, see inset left upper side). Typically the sustained response follows an ON excitation or inhibition which is broad band sensitive and dominated by the L receptors (examples in Kien and Menzel, 1977b). Thus, the spectral opponent response needs time to develop, about 30–50 ms for the latency plus 50–80 ms for the non-colour coded ON component. Four types of sustained opponency were found: $S^+M^-L^-$, $S^-M^+L^+$, $S^+M^-L^+$, $S^-M^+L^-$. The reversed combinations of the two pairs seem to be realized, at least sometimes, in closely attached neurones, and extracellular recordings have revealed mirror-like spectral response patterns in two simultaneously recorded neurones. Phasic spectrally opponent neurones were found less frequently and with only two response patterns: S-OFF, M-ON, L-OFF or S-ON and OFF, L-OFF (M unknown, see Fig. 14.10, inset right side) (Hertel, 1980). Phasic opponency seems to be restricted to local neurones in the medulla, whereas tonic opponency has been recorded in the medulla, lobula, and mid-protocerebrum (Kien and Menzel, 1977b; Hertel, 1980; Riehle, 1981; Hertel *et al.*, 1987; Hertel and Maronde, 1987b).

Intracellular markings have also revealed a functional organization of the projecting pathways in the brain (see Fig. 14.10). Only two of the many nerve tracts and commissures contain spectrally opponent neurones, and these are the posterior optic commissure (POC) and the anterior optic commissure (AOC). The POC is comprised of medulla extrinsic neurones with or without tonic spectral opponency. These neurones are sensitive to stationary flashes and have large receptive fields. Since the POC is a fast direct pathway between the right and left visual system, it is likely that neurones running in the POC are involved in a fast comparison between the two visual systems, namely the achromatic neurones with high spatial resolution and the colour coded neurones with low spatial resolution (Hertel and Maronde, 1987a,b; Hertel *et al.*, 1987). The AOC incorporates spectral opponent neurones and motion sensitive neurones, which either connect the two lobulae and/or medullae, or which project from one

visual system to the ipsi- or contralateral median protocerebrum. Here they terminate in the mushroom bodies and in the output region of the brain, the lateral protocerebrum. Since the mushroom bodies are considered to be the high order multisensory integration centres of the insect brain, coding of hue contrast serves two important functions – object alignment by fast comparison between the two visual systems (POC fibres) and object identification by multisensory comparison in the mid-protocerebrum (AOC fibres).

The receptive fields of the spectral opponent neurones range from simple small fields to large complex fields which may cover the entire visual fields of both eyes (Fig. 14.11). The smallest receptive fields without obvious

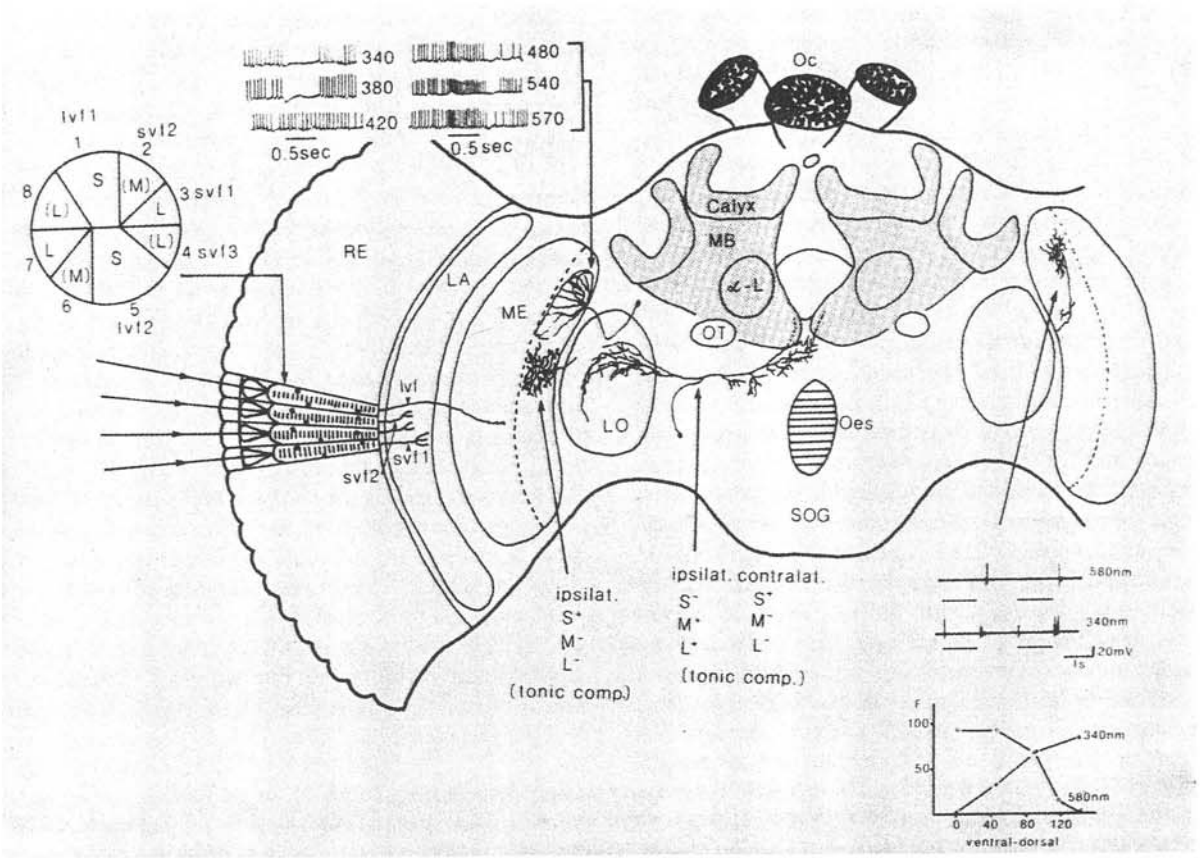

Fig. 14.10 *A diagram of the pathways in the visual system of the honey bee that are related to chromatic coding. The retina (RE) of each compound eye consists of 5400 optically and physiologically isolated units, the ommatidia, each of which contains nine retinula cells with four L receptors, two M receptors and three S receptors (one of the three S receptors is not shown in the schematic cross-section of the upper left inset, because it is a short proximal cell, see Fig. 14.1). The L and M receptors project to the first visual neuropile, the lamina (LA), with short visual fibres (svf 1, 3 and svf 2 respectively). The S receptors project through the lamina into the second visual neuropile, the medulla (ME), with long visual fibres (lvf 1, 2). Very little is known about colour processing in the lamina and the distal medulla (see text). Colour coded neurones were recorded and intracellularly marked in the proximal medulla and the third visual neuropile, the lobula (LO): The spike traces in the upper left inset shows an example of a tonic spectral opponent neurone recorded in the proximal medulla (see single cell marking in the upper proximal medulla, Schäfer 1984). Another example is shown in the marking just below (Hertel, 1980, his Fig. 6). This neurone responds to inputs from the ipsilateral eye and is tonically excited by UV light (S^-) and inhibited by long wavelength light (M^-, L^-). The neurone marked in the lobula represesnts a class of neurones which respond to stimulation of both eyes. In this case (Hertel and Maronde, 1987b, their Fig. 6) the spike trains reveal spectrally opponent responses in their sustained components with different receptive field organization for the two sides (ipsilat. contralat.: stimulation of the ipsilateral or contralateral eye respectively with flashes of monochromatic light). The single cell marking shown for the proximal medulla on the right side of the figure gives an example for a neurone, which responds with short, phasic bursts of spikes to spectral flashes. The ON and OFF components differ in their spectral sensitivities (Hertel, 1980, his Fig. 8). This neurone stretches from dorsal to median-ventral. Stimulation of the dorsal part of the eye reveals high UV-sensitivity (ON and OFF excitation), stimulation of the ventral eye, high green sensitivity (OFF excitation). Further abbreviations: Oc: ocelli; MB: mushroom bodies with α−lobe (α−L) and calyx, OT: optic tubercle, Oes: oesophagus; SOG: suboesophageal ganglion.*

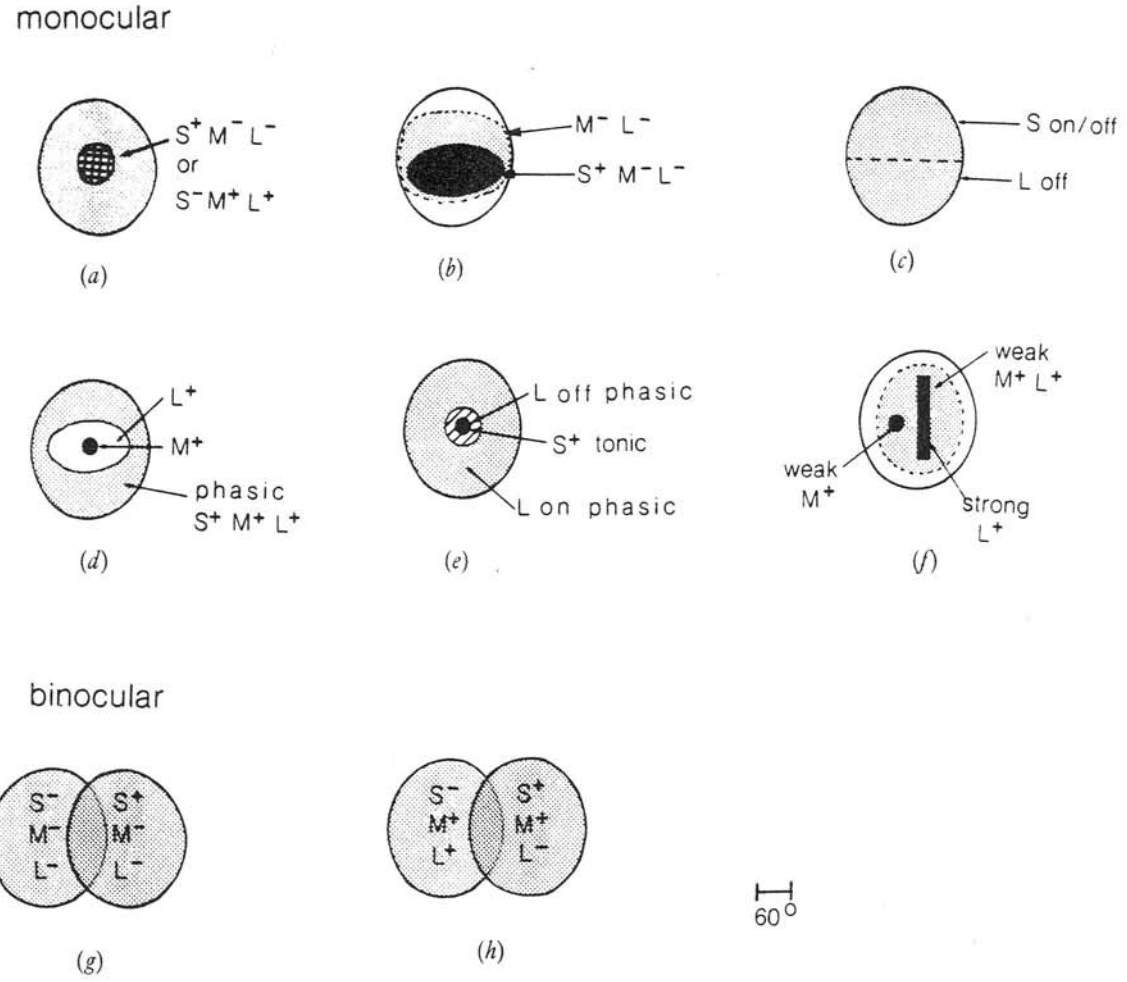

Fig. 14.11 *Examples of receptive field structures of neurones recorded in the medulla and lobulla of the bee brain. Monocular receptive fields (a–f): (a) A neurone recorded in the medulla with a median size (60° visual angle) receptive field with coextensive spectral components (Kien and Menzel, 1977b, their Fig. 3). (b) A medullary extrinsic neurone which responds with strong sustained excitation (S^-) and inhibition (M^-, L^-) in a median size receptive field (dark area) which is surrounded by a large receptive field with weak inhibitory responses only to long wavelength light (Kien and Menzel, 1977b, their Fig. 11). (c) A neurone of the proximal medulla with a receptive field occupying the whole ipsilateral eye. The receptive field is split into a dorsal part with phasic ON and OFF responses to UV and ventral part with phasic OFF responses to long-wavelength light (Hertel, 1980, his Fig. 8; see also Fig. 14.10, right side). (d) A spectral opponent neurone recorded in the lobula with small receptive field (10°) which responds only to blue light stimulation with strong excitation (M^-) and a medium sized surround which is dominated by excitation to long-wavelength light (L^-). The remaining visual field of the whole eye gives phasic ON responses over the whole spectrum (Kien and Menzel, 1977a, their Fig. 10E). (e) Another neurone with a small central receptive field for excitatory sustained responses to short wavelength light which is surrounded by a small field with OFF responses to long-wavelength light. The whole remaining part of the eye causes phasic ON responses to long-wavelength light (Kien and Menzel, 1977b, their Fig. 12). (f) An example of a neurone with complex response patterns and receptive field structure. Strong excitatory responses occur in a small circular field to blue light (M^-) and strong excitatory responses to green light in a bar like vertical field. The remaining large surround gives weak excitatory responses to blue light.*

Binocular receptive fields (g, h): (g) A medulla extrinsic neurone which connects the two medullae by an axon running in the posterior optic commisure (POC, see text) responds to stimulation of both eyes with a slightly different combination of the spectral components (S^- to the one side, S^- to the other). The neurone is sensitive to the whole visual field of both eyes. The intracellular marking reveals extensive branches in both medullae (Hertel et al., *1987, their Fig. 3). (h) The structure of this lobula extrinsic neurone is shown in Fig. 14.10. The responses to stimulation of the two eyes reveals a mirror like composition. The neurone might respond to different regions of the two eyes differently but this was not studied in more detail (Hertel and Maronde, 1987b, their Fig. 6).*

spatial antagonism are found in LMCs and columnar neurones in the medulla. In flies, locusts, and dragonflies, the centre of the LMC receptive field is surrounded by a weak antagonism (Laughlin, 1981). However, nothing is known about a spectral organization in these species or in the honey bee. The small field LMCs and columnar medullary neurones converge on proximal medullary neurones with median size (10°) or large (60°) receptive fields, which always have sharp borders and coextensive excitatory and inhibitory spectral components (Fig. 14.11(a)). Centre-surround antagonism was not found in either the broad band or spectral opponent neurones. A large variety of receptive fields are constructed from these medulla neurones (Fig. 14.11(b)–(h)): very large fields with equally strong spectral opponency over the whole field, left eye–right eye opponencies with or without spectral antagonistic components of the two eyes, dorsal–ventral opponencies with or without spectral properties, and complex arrangements of combined spatial and spectral sensitivities. These latter receptive fields (Fig. 14.11(f)) are more or less selective detectors for certain combined spatial/spectral arrangements (for example, a blue flower on a green petiole as in the case of Fig.14.11(f)), and thus may serve very specific functions. Spatial spectral double opponent, centre/surround neurones, such as those observed in the vertebrate cortex, have not been recorded in the brain of the bee or any other insect species, although cells with a spectrally opponent surround are sometimes mentioned (e.g. sustained neurone in the medulla of the locust, Osorio 1987b). It is tempting to speculate that insects with their relatively small number of visual neurones (approximately 400 000 in honey bees, Witthöft, 1967) avoid the complexity of double opponency (Marr 1982, p 262).

A special case of temporal/spectral coding shall be mentioned here, because it demonstrates the strategy of neural integration in a nervous system in which stimulus properties are combined in the periphery to solve specific features of detection problems, as opposed to the coding of spectral and spatial parameters for a multipurpose analysis. Mote and Rubin (1981) and Mote *et al.* (1981) found neurones between the lamina and medulla of the cockroach, *Periplaneta americana*, which respond to wavelengths shorter than 475 nm with a tonic excitation after long latencies, and to wavelengths longer than 475 nm with phasic ON excitation after much shorter latencies. The receptive fields do not exactly overlap: sensitivity to shorter wavelengths is shifted more dorsally and that to longer wavelengths is shifted more ventrally. These neurones are optimally excited by short-wavelength stimulation at low temporal frequencies in the upper visual field, combined with long-wavelength stimulation at higher temporal frequencies in the lower visual field. A cockroach running under natural conditions in the open field would be exposed to such stimulus combinations. If the body of the animal is aligned in the horizontal direction these neurones would signal strongest excitation. This is just one example of many to be found in the current literature. Nevertheless, complexities may already arise from receptor distribution and the intrinsic properties of the receptors. For example, the time course of the UV receptors in the cockroach is much slower than that of the green receptors (Mote and Goldsmith, 1970), and the UV receptors are more frequent in the dorsal part of the eye, whilst the green receptors more frequent in the ventral part (Walther, 1958; Butler, 1971; Mote and Goldsmith, 1971).

A general principle of neural processing in the visual system of mammals is the segregation of parallel pathways dealing with different aspects of the visual scene. Motion sensitivity, fine grain analysis of orientation and course grain colour coding are the major components of these specialized pathways which project to functionally specialized areas in the prestriate cortex (Livingstone and Hubel, 1984, 1988). Functional separation is also the neural strategy in the visual system of insects, but the segregated pathways do not project to specific areas but rather coexist topographically at more distal levels of visual integration and separate neuroanatomically in more central areas. In the honey bee, the motion sensitive neurones appear as a distinct subsystem and extend from the distal medulla to the more central neuropiles. The most distal neurones are characterized by small receptive fields and non-directional motion sensitivity, while more centrally (proximal, medulla, lobula) they have large receptive fields with often complex combinations of directionality and receptive fields with often complex combinations of directionality and receptive field structures. These neurones never respond to hue contrast and are dominated by the L receptors (Menzel, 1985a; Hertel and Maronde, 1987a,b; Hertel *et al.*, 1987). The non-colour coding broad band, green dominated neurones also exist for stationary stimuli, and once again the receptive fields are small in the distal medulla but show increasing complexity in their central excitatory and inhibitory subfields. Colour coding neurones follow the same strategy with increasing spatial complexity towards the centre, although their receptive fields are already quite large in the medulla where the achromatic neurones may still have small receptive fields. The functional segregation into the three pathways is topographically overlapping and neuroanatomically intermingled at the level of the distal and median medulla and the distal lobula. These pathways separate into a large number of subsystems for specialized tasks, e.g. fast comparison between the two visual systems, control of head and body movement, multisensory integration. However, since so little is known about this central integration, it cannot be excluded that a map-like image of a 'colourful world' is represented in the cup-shaped calyx region of the mushroom bodies.

Colour Contrast Phenomena

Neumeyer (1980, 1981) observed colour induction phenomena for a series of hues along a blue-yellow mixture line. Experiments showed that a blue target on a yellow background looks more blue to the bee than a blue target on a grey background, and a yellow target on a blue background more yellow than if it were on a grey background. This hue shift is also induced by a small coloured ring surrounding the target, even if the coloured ring is separated from the target by a thin black annulus. When bees flew over an extended coloured background and were then presented with the targets on a grey background, an expected hue shift, as a result of chromatic adaptation, was again observed. In this case, yellow appeared more yellow to the bees if they were previously exposed to a blue background, and vice versa. Since the bees were free to move around during the tests it was not possible to distinguish between simultaneous and successive contrast. This point will be further discussed in the section on colour constancy.

A Perceptual Model of Colour Opponency

Colour discrimination experiments with bees can be designed so that a large number of discrimination values are available for multidimensional analysis. In a particular experiment (Backhaus *et al.*, 1987) a full 12×12 matrix (12 different pigment colours, total of 132 discrimination values) was analysed according to the method of complete triads and the law of comparative judgment (Torgerson, 1958). Multidimensional scaling procedures allow for the determination of the minimal number of scales and the composition rules for the reconstruction of the multifold of distance values (Torgerson, 1958; Kruskal, 1964). The best fit between the experimental data and the reconstructed values is determined by special 'goodness of fit' parameters (see Backhaus *et al.*, 1987 for details). The metric of the perceptual colour space appears as a city block metric. This means that the perceptual distance is equal to the sum of the absolute distances on the scales. Furthermore, the minimal number of dimensions of the perceptual colour space is two, and this is represented by two appropriate scales respectively called A and B. These two scales are fixed and cannot be rotated as a consequence of the city block metric. It appears that the intensity or brightness parameters of the colour signals do not contribute to the perceptual dimensions, although the reflectancies of the colour signals used in the experiment differed considerably in total reflectance. Rather the two scales correspond to the Helmholtz parameters hue and saturation, or to a special set of two colour opponent parameters.

Backhaus (in preparation) analysed the particular set of colour opponent processes derived from model calculations which assume a succession of two steps, a non-linear transformation of the signals in the receptors followed by a linear operation between the receptor signals on the level of second and third order neurones. The purpose of the model calculation was to determine the sign and the gain factors of the excitation in each of the three spectral receptor channels, which would describe best the two scales A and B:

$$A' = a_S E_S + a_M E_M + a_L E_L \qquad B' = b_S E_S + b_M E_M + b_L E_L \tag{14.4}$$

where A' and B' are the excitation values of the hypothetical opponent colour coding system, which should correspond to the scales A and B as closely as possible; E is the receptor excitation of the corresponding receptor types (S, M, L), and a and b are the two corresponding unknown gain factors. The two equations do not make any assumption about the kind of spectral antagonism.

When the three receptor types are exposed to the 12 stimuli of the matrix experiment described above, they cause respective excitations (see Backhaus and Menzel, 1987, for more details particularly with respect to the effect of adaptation). Together with the corresponding values for A and B from the multidimensional scaling procedure, the equations can be solved under the assumption that the difference between A, A' and B,B' is minimal (least square solution). The six unknown gain factors are determined by these 12×2 equations and certain best fit assumptions have to be made to minimize the differences between A' and A, and B' and B. The following values have been found for the gain factors:

for A':

$a_S = +14.04$		$a_S = -14.04$
$a_M = -10.03$	or	$a_M = +10.03$
$a_L = -3.21$		$a_L = +3.21$

for B':

$b_S = +6.85$		$b_S = -6.85$
$b_M = -21.65$	or	$b_M = +21.65$
$b_L = +14.69$		$b_L = -14.69$

The distance $D(S_1, S_2)$ between the two loci S_1 and S_2 in the graphical representations of the opponent system is:

$$D(S_1, S_2) = |A(S_1) - A(S_2)| + |B(S_1) - B(S_2)| \tag{14.5}$$

D corresponds linearly to the perceptual difference between the two stimuli.

For the ideal case one would expect that the opponent systems would be totally independent of changes in the intensity of the illuminating light. In that case, the gain factors of each system would add up to zero. Indeed the sum is very close to zero, although the model calculations were not initially restrained to reach zero.

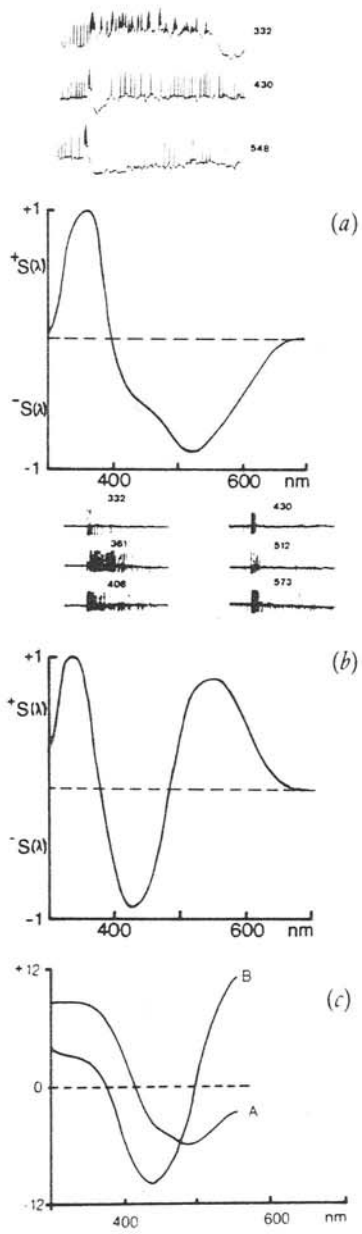

Fig. 14.12 *Spectral antagonism in the visual system of the honey bee. (a) and (b) give generalized spectral sensitivity functions of chromatically antagonistic neurones, which develop antagonism in the sustained response (see insets). The + direction of the ordinate marks excitation, ($^{+}S(\lambda)$), the − direction inhibition ($^{-}S(\lambda)$). Several units of the same kind recorded by Kien and Menzel (1977b) were averaged to generate the two functions. (c) Spectral dependency of the two opponent system A and B as derived from behavioural experiments (see text). The ordinate corresponds to excitation (+, upwards) and inhibition (−, downwards) caused by spectral stimuli of equivalent brightness. Note that (c) is different from (a) and (b) in that it does not plot sensitivity against wavelength but response strength to equally bright spectral stimuli.*

The two scales correspond to the two spectral opponent systems, which we found in the recording experiments ($S^{-}M^{+}L^{+}$ and $S^{-}M^{+}L^{-}$, see above). Each neuronal opponent system also exists in its mirror image form ($S^{+}M^{-}L^{-}$ and $S^{+}M^{-}L^{+}$). Although the gain factors cannot be extracted from recording experiments, the zero crossing should be a sensitive measure for the gain factors of the model. The predictions from the model are 414 nm, 376 nm, and 497 nm, and the neuronal zero crossings are indeed close (400 nm, 385 nm, and 490 nm respectively, see Fig. 14.12). The predictions of the model can be tested in various other ways ($\Delta\lambda/\lambda$-function; correlation between discrimination values and distance in the opponent colour system), and Fig. 14.11 gives a summary. As can be seen, the model is a good description of the experimental data. The most direct test for the gain coefficients would be the measurement of the hue shifts, which should result from an increase in total intensity (Bezold-Brücke shift) or by dilution of a spectral light with white light (Abney shift). These experiments have yet to be performed with the bee.

It should be stressed once again that a quantitative description of colour discrimination by honey bees does not require a perceptual dimension of brightness. This statement holds true for all colour stimuli which differ at least to some extent in hue and/or saturation. If hue differences are zero and saturation differences are also very small, but brightness differences are large, then the bees can be trained by differential procedures to discriminate these stimuli (Backhaus *et al.*, 1988). Discrimination is still very small even for large brightness differences. The Weber-Fechner ratio is $\Delta H/H = 0.39$. This does not mean that bees would not be sensitive to brightness differences, because in other behavioural contexts (e.g. phototaxis) they are indeed very sensitive to this parameter ($\Delta I/I = 0.145$, Labhart, 1974; Menzel and Greggers, 1985), but as a signal for food, brightness differences are ignored or not used when differences in chromaticness exist.

Jacobs (1981) wrote in his book *Comparative Colour Vision* (p 168):

> *I am not aware of any species that fails to show an ability to discriminate small luminance differences under some sets of stimulus conditions. Indeed, the power of luminance differences as cues for discrimination is so great that in many cases an observer will spontaneously use these luminance differences as the relevant dimensions for discrimination, even when others are available. This is particularly manifested in colour discrimination tests... I have often observed that given a luminance difference, as a cue, the animal frequently uses that as a basis for discrimination even if a colour difference known to be discriminable is also available.*

This is certainly not the case in the honey bee.

Colour Constancy

In our own colour experience, even a drastic change in the chromatic composition of illumination does often not noticeably alter the apparent hue of reflecting colours. A particularly impressive demonstration of colour constancy is Land's (1977, 1983a,b, 1986) 'Mondrian' experiment, in which colour plates with smooth and continuous spectral reflection curves are combined to form a multi-colour pattern. Metameric colours, for which the colour constancy phenomenon is much less dramatic, are avoided in Land's arrangement. The 'Mondrian' is still a fair representation of the natural world since natural objects are characterized by smooth and continuous spectral reflections (see Section on Ecology and Evolution of Photopigments and Colour Vision). The colour constancy phenomenon in man requires very fast (1 ms) and spatially long range colour interactions at the level of the visual cortex (Land *et al.*, 1983). In goldfish, colour constancy seems to be performed monocularly and involves subcortical structures such as the diencephalon (Ingle, 1985).

Insects are also exposed to drastic changes of chromatic illumination under natural conditions, e.g. between shaded regions dominated by green light and regions illuminated by direct light from the sun. Since flowers have to be reliably identified according to their colours and under varying conditions of illumination, one would expect that insects also have the ability of colour constancy. Indeed, von Frisch (1914b) postulated colour constancy in the honey bee solely on the basis of these biological arguments, but the first qualitative proof came from Neumeyer (1980, 1981) in a study of colour adaptation phenomena in bees (see above). In a recent study (Werner *et al.*, 1988), bees were tested with an arrangement similar to Land's 'Mondrian'. The experimental bee approached the vertically arranged chequerboard display in flight and was trained to any one of 13 plates. It was necessary to separate each of the colour plates by a dark square, otherwise training of a bee to one plate by rewarding it with sucrose in the middle of the plate would have caused a partial learning of the immediate neighbours. This would have the effect of reducing discrimination, because the arrangement of the colour plates was continuously changed throughout training and testing. The colour stimuli were filters which were illuminated from behind by three broad band light beams (UV, blue, green) whose spectral composition matched the spectral properties of the three receptors types in the bee eye. After training a bee to discriminate one colour plate (e.g. No. 4) from all the others, the three light beams were changed in such a way that one of the other colour plates (e.g. No. 1) transmitted the same amounts of photon fluxes of the three light beams as the trained colour did during training (transition test). Since colour plate 1 is now identical in physical terms with colour plate 4 during training, the bee should choose colour plate 1 if the colour of the stimulus is determined only by the effective photon fluxes in each of the three photoreceptors. Many such transition pairs were tested and it was found that the bee still preferred the trained colour plate (e.g. No. 4) over the matched signal (No. 1), despite the fact that after transition the spectral composition of the transmitted photon fluxes had changed considerably.

Colour constancy requires that the illumination is factored out by some processs which measures the temporal and/or spatial average and compares it with the local fluxes in the spectral pathways defined by the receptor types or any derived spectral pathway (e.g. opponent colour pathway). Selective adaptation at the retinal and interneurone level may account for such a rescaling in the honey bee, since the immediate appearance of the constancy phenomenon within milliseconds, as shown in man by Land (1977), could understandably not be proved experimentally and may not exist in bees. The 'pathway procedure', as described by Land for the calculation of the relationship between the average lightness in each spectral channel and the corresponding lightness of a particular object, may actually be a real pathway for the bee cruising over the stimuli and adjusting its receptors and visual interneurones by adaptation mechanisms. This, however, cannot be the sole solution, because visual areas not faced by that part of the eye directed towards the test target influence the rescaling procedure (Werner, in preparation). These new results indicate a mechanism which Sharpe (1987) called 'the circle approach' to discount the illuminant. Such a mechanism compares the flux emitted from a much larger surrounding area. Single colour opponent neurones, with different but largely overlapping receptive field sizes, may be responsible for this function and have indeed been found in the visual system of the bee. Double opponent neurones, which have been related to the necessary retinex operations (Daw, 1984, Livingstone and Hubel, 1984), appear not to exist in the bee's visual system, and the narrow waveband selective cells recorded in the medulla and lobula (Kien and Menzel, 1977b) do not have the necessary properties to be truthfully called 'colour coded cells' (Zeki, 1985) because they also respond to white light.

Colour Vision and Wavelength-Selective Behaviour

A prerequisite of colour vision is the ability to discriminate equally bright stimuli with respect to differences only in chromaticness. If a behaviour does not include discrimination of chromaticness, it usually depends strongly on the intensity of the stimuli (or on intensity contrast), and

sometimes in a narrow spectral window. It is, therefore, convenient to distinguish between three kinds of visually guided behaviour with respect to wavelength dependence: colour vision, broad band achromatic vision, and wavelength-selective behaviour.

The honey bee provides us with well studied examples. Colour vision is documented for the orientation towards visual targets in the immediate surrounding of potential and actual food sources, and at the entrance of the colony housing (von Frisch, 1914a,b; Review: Menzel, 1985b). Landmarks further away from a feeding place may also be seen in colour, but experimental evidence is weak (Cheng *et al.*, 1987). It appears that colour vision in the two behavioural contexts (feeding place, hive entrance) is very similar in honey bees but may differ in other social Hymenopterans. For example, the tropical stingless bee, *Melipona quadrifasciata*, discriminates bluish-green colours equally well in the two behavioural contexts, but not violet colours which are better discriminated at the feeding place (Menzel, 1985b; Menzel et al., 1989). Furthermore, discrimination of spectral lights as markers of a feeding place is independent of whether they are seen with the ventral or frontal part of the eye region, or whether the bee approaches them in flight or walking (Menzel, 1967; von Helversen, 1972a). Colour vision with the dorsal or lateral region of the eye has yet to be tested. It may exist in the first instance, but not in the latter because all three receptor types are found in the dorsal, ventral and frontal, but not lateral retina, which might be equipped only with L receptors (Milde, 1978).

Several distinct achromatic wavelength-selective behaviours excluding colour vision have been demonstrated in the honey bee: escape phototaxis (most sensitive in UV, Berthoff, 1931; Kaiser *et al.*, 1977), natural open space response (von Hess, 1913; Menzel and Greggers, 1985), optomotor or large field movement response (action spectrum follows that of the L receptors, Kaiser and Liske, 1974; Kaiser *et al.*, 1977), visual scanning behaviour in front of vertical gratings and flight orientation towards vertical and horizontal gratings (dominated or selectively controlled by the L receptors , Lehrer *et al.*, 1985; Srinivasan and Lehrer, 1988), dorsal light response (action spectrum follows that of the S receptor, Menzel, unpublished observations), polarized light orientation (action spectra of the S receptors, von Helversen and Edrich, 1974; Menzel and Synder, 1974), and orientation towards a spotlight as if it were the sun (dominated by the L receptors, Edrich, 1977; Brines and Gould, 1979).

Wavelength-selective behaviours have been described in several other insect species and a few more examples shall be cited here. In flies, the landing response (Tinbergen and Abeln, 1983) and the optomotor response (Kaiser, 1968) are controlled by the receptors R1–6 (broad band sensitive) and are colour blind: moving contrast boarder between two spectral wavelengths can be matched in intensity and in such a way that no response is elicited. The start response initiating flight in flies is also dominated by R1–6 plus a contribution from R7 without any indication of colour effects (Kirschfeld and Vogt, 1985). The polarized light sensitivity of insects in general is monochromatic, either in the UV as in honey bees (and also in the ant *Cataglyphis*, Duelli and Wehner, 1973; in the dorsal margin of the fly eye, Hardie, 1984; in the water bug *Notonecta glauca*; Schwind, 1985) or in the blue as in crickets (Labhart *et al.*, 1984; Brunner and Labhart, 1987; Zufall *et al.* 1989).

Butterflies provide us with an interesting study case of the complications of unravelling the interactions of colour vision and wavelength-selective behaviours. The eye of *Pieris brassicae*, for example, is equipped with four different spectral receptor types ($\lambda_{max} = 360, 450, 540, 620$, see Nos. 56, 114, 215, 231, in Fig. 14.2). Since training experiments have failed to overcome strong innate preferences for intensities and wavelengths (Ilse, 1928, 1937, 1941; Kolb and Scherer, 1982; Scherer and Kolb, 1987) the usual rigid tests for colour vision cannot be performed satisfactorily. However, *Pieris* performs several pronounced behavioural patterns which can be released by spectral lights and which differ considerably with respect to their spectral sensitivities (Fig. 14.13). The open space response is released by all spectral lights (and white light) if the intensity is strong enough, but selectively by UV light at low intensities. The feeding response (Ilse, 1928; Swihart and Swihart, 1970) has two peaks of spectral sensitivity (450 nm, 600 nm) that are separated by a wavelength region (520–580 nm) in which sensitivity is up to 2.5 log units less than at 450 nm. Egg-laying (Ilse, 1937; Kolb and Scherer, 1982) is preferentially released at wavelengths around 540 nm, and the drumming behaviour (rapid repetition of up and down movements of the first pair of legs) at somewhat longer wavelengths (sensitivity peak at 560 nm). White light (with or without UV) may cause an open space response but none of the other three responses. Mixture experiments give a few hints about possible interactions between the spectral inputs. A mixture of 370 nm and 600 nm releases the open space reaction and the feeding response more frequently than equally bright monochromatic lights. If 600 nm is added to 558 nm the drumming response to 558 nm is reduced, and conversely if 558 nm is added to 600 nm the feeding response to 600 nm is reduced. These results suggest that the receptors R 360 and R 620 do not interact at least as far as the open air response and feeding responses are concerned, whereas the three receptors R 450, 540 and 620 may interact in an inhibitory fashion to control feeding, drumming and egg laying. The sharp transition from feeding to egg laying in the wavelength range 500–520 nm gives additional support to this conclusion (Fig. 14.13).

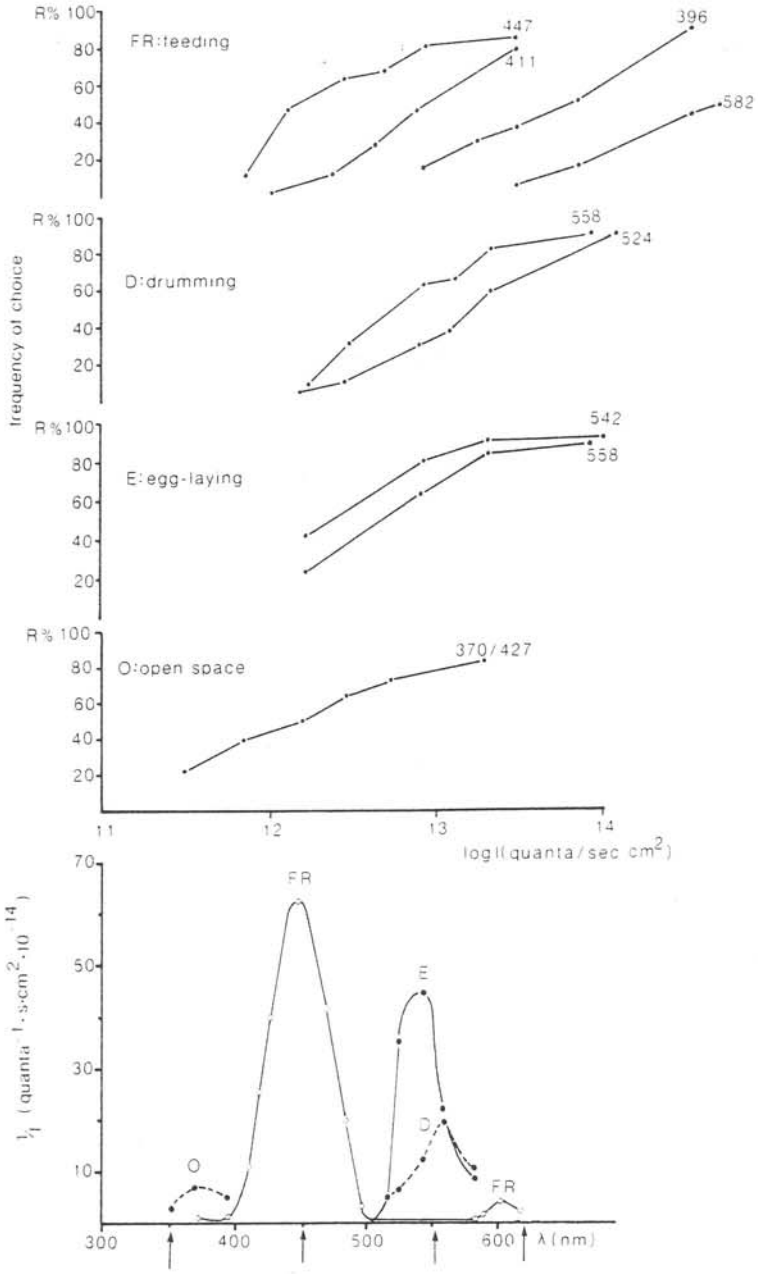

Fig. 14.13 *Wavelength-selective behaviour in the butterfly* Pieris brassicae. *The figure was prepared after Scherer and Kolb (1987). The upper part gives the intensity dependencies of four different behaviours for a few selected wavelengths. The lower figure shows the spectral sensitivities calculated from these and additional intensity response functions for the four behaviours. FR: feeding response, D: drumming, E: egg laying, O: open space response (see text).*

The behavioural observations do not support the conclusion that the spectral receptor types and the spectral opponent neurones in the butterfly brain are used to establish a neuronal representation of colour in the usual sense, rather the chromatic channels may control directly and selectively behavioural subroutines. However, this conclusion is based on the failure to demonstrate the intensity independence of unique behaviours to chromatic stimuli – a prerequisite for any appropriate test of colour vision. In this instance one might argue that proper behavioural methods and particularly training techniques have yet to be developed for butterflies. Such experiments would determine whether butterflies possess colour vision in the traditional sense in addition to a set of wavelength-selective behaviours.

Ecology and Evolution of Photopigments and Colour Vision

Our personal knowledge about the perception of colour, *per se*, is restricted to personal introspection and can be transferred via verbal communication. Non-human animals and more remote animal species are inferred to possess an equivalent sensation of colour if a particular visual behaviour is not eliminated by multiple intensity adjustments between stimuli of different dominant wavelengths. The $\Delta\lambda/\lambda$-function provides a critical experimental paradigm because it quantitatively establishes signal discrimination without intensity discrimination for closely related wavelengths. Such functions are established quite easily if the animal species in question can be trained, but are much harder to obtain if only reflexes or innate behaviours such as optomotor responses, spontaneous preferences, phototaxis, photokinesis or any other unlearned responses (see above) are to be tested. This restriction is usually the case in invertebrates and the example often cited throughout this paper, the honey bee, is an unusual and favourable exception. In fact, no innate behaviour in insects has so far been found to involve colour vision, although many cases are known where different spectral receptor types in the same species control different innate behavioural patterns. There may be one exception to this rule. Fischbach (1979) described colour induction and colour contrast phenomena in the 'innate behaviour of the slow phototactic response' of the fruit fly *Drosophila*. However, if slow phototaxis is a compound of different behaviours that are controlled differentially by the spectral receptor types, then one would expect the same behavioural results as in the case of colour vision. Most importantly, mutually exclusive behaviours may give us the impression that the controlling spectral regions act chromatically in an antagonistic manner on the level of sensory integration. For example, excitation of the UV receptors in the honey bee results in an orientation as if it were to a spot of blue sky and that of the longwave receptor's orientation as if it were to the sun. These two mutually exclusive behaviours in the astromenotactic orientation of bees do not require spectral opponent visual neurones for proper control, if their respective motor commands inhibit each other. Thus, a critical requirement for a cellular basis of colour vision, namely spectral opponent processing in the sensory part of the nervous system (Daw, 1984), may not exist.

These considerations may provide a key for the early steps of evolution of colour vision in invertebrates more than 1 billion years ago in the pre-Cambrian period, at a time when prokaryotes, unicellular eukaryotes and simple multicellular organisms dominated the aquatic life. In water, relatively large chromatic differences at even short distances characterize different habitats. Since water is a chromatic filter which absorbs at mainly longer wavelengths, the dominant wavelength is shifted to shorter wavelength with increasing depth. Furthermore, anorganic particles and phytoplankton absorb predominantly in the short wavelength, and this may lead to dramatic changes in the chromatic composition of the ambient light over small distances. As a consequence, orientation via the control of different motor patterns by separate sensory-photopigments is a common feature of many phylogenetically primitive invertebrates of unicellular organisms and even prokaryotes (bacteria) (for reviews see Diehn, 1979; Naitoh, 1982; Menzel, 1979). For example, the photosynthetic and photosensing *Halobacterium halobium* can swim in two directions and activates or stops its flagellar motor under the control of chromatic illumination. A stop is always combined with a reversal of the flagellar rotation and consequently of the swimming direction. More frequent stops and returns keep the bacteria in a certain area, fewer stops and returns result in a dispersal. Such a 'random walk' procedure allows the bacteria to accumulate in favourable microhabitats of light and chemicals, and to escape from unfavourable ones. UV and blue light increase the frequency of reversals and green light reduces them (Hildebrand and Dencher, 1975; Spudich and Bogomolni, 1984). The antagonism of UV and green originates in a one pigment system, that of the sensory rhodopsin (sR 587) which runs through a slow one-photon cycle when illuminated with green light only, or through a fast two-photon cycle when illuminated with green and UV light. The two-photon cycle causes an increase in stops and reversals by increasing the availability of an intrinsic sensory messenger, while a decrease results from the one-photon cycle which reduces the amount of this postulated sensory messenger (Marwan *et al.*, 1987). An effective but as yet unknown adaptation mechanism constrains these responses to transient changes of illumination. *Halobacterium* contains two other rhodopsin pigments (bacteriorhodopsin and halorhodopsin) both of which are used for energy conversion and photokinesis. The sensory system of this non-neural prokaryote is thus characterized by multiple pigment systems, wavelength selectivity and spectral opponency in the light responses and adaptation to sustained illumination.

Even more complex are the light responses of unicellular eukaryotes such as flagellates (e.g. *Euglena*) and ciliates (e.g. *Paramecium*) (Cecchucci, 1976; Diehn, 1976). In *Paramecium*, at least three different pigments regulate various light responses, namely ciliar reversal to dimming (maxima of action spectrum at 560 nm and 680 nm), ciliar reversal to brightening of illumination ($\lambda_{max} = 520$ nm) and sustained increase of ciliar beat frequency ($\lambda_{max} = 440$ nm).

It is obvious from these selected examples that the phylogenetic ancestors of multicellular organisms, the flagellates and ciliates, had already developed multipigment

systems for light sensing, and that these were connected specifically to motor patterns through intracellular messenger molecules or membrane channels. Multicellular animals separated sensory neural and motor systems in cellular compartments, and consequently photoreceptors equipped with different pigments were selectively connected to motorneurones or their neural commands. For example, the coelenterate *Anthopleura xanthogramma*, bends its tentacles towards the light of longer wavelength ($\lambda_{max} = 500$ nm) and retracts the tentacles to short wavelengths (less than 400 nm) (Clarke and Kimeldorf, 1970). The photoreceptive structures are unknown in the case of this polyp, and the receptive photopigments may reside in particular neurones of the circumoral neural plexus. Since the two behaviours are mutually exclusive, spectral opponency exists in this diffuse nerve net and is probably close to the side of the motor control. Multiple photopigments in small pigment cup eyes are already known from nematodes and the closely related planktonic rotifers, and in the latter case two or three pigments control positive phototactic responses synergistically (Menzel and Roth, 1972; Hertel, 1979). The free-living nematode *Chromadrina viridis* moves away from UV light ($\lambda_{max} = 366$ nm) but towards light for wavelengths longer than 400 nm ($\lambda_{max} = 465$ nm and 570 nm) (Croll, 1966).

It is conceivable that a sensory integration stage had to be developed parallel to the increasing complexity of the motorprogrammes of free moving animals and to the improvements in eye structures. Although nothing is known about the function of the visual neuropiles in the pseudocoelomate and coelomate worms (annelids), the highly organized lens eyes, the well structured pigment cups and compound eyes (Land, 1981) as well as the neuroanatomy of the visual plexus behind the eyes (Bullock and Horridge, 1965) strongly suggest the operation of basic features of neural integration such as lateral inhibition, motion sensitivity and spectral antagonism. The eye of the polychaet *Nereis mediator* is likely to contain more than one photopigment (Yingst *et al.*, 1972), and the different responses of the earthworm to increasing and decreasing illumination appear to have different action spectra (Unteutsch, 1937; Howell, 1939). The behaviours tested in these lower invertebrates can be characterized as wavelength-selective without any indication of colour vision (Menzel, 1979, p 559). Even those species of invertebrates which possess colour vision (e.g. certain insect species and jumping spiders) perform many visual tasks in a wavelength-selective fashion (see previous Section). It appears, therefore, that the majority of invertebrates developed multiple spectral receptor types for wavelength-selective behaviour. The advantages are obvious. Specialized visual tasks are controlled by a subset of receptors, and this drastically simplifies 'neural wiring' in the nervous system. This allows for specialized regions of the eye as adaptations to the environment, and increases the effective photonflux in each of the visual subroutines. The latter point is of particular importance for animals with very small eyes.

It has been argued that the photopigments were selected according to two ecological rules: (a) optimize sensitivity by matching the spectral sensitivity of the receptors ($S(\lambda)$) to that of spectral distribution of local background irradiance $I_b(\lambda)$ (sensitivity hypothesis), and (b) optimize contrast between $I_b(\lambda)$ and $I_R(\lambda)$, to the spectral intensity distribution of light reflected by important objects using two photopigments in concert (contrast hypothesis) (Lythgoe, 1972a, 1979). The evidence presented above suggests a third rule: (c) selective optimal matching between different $S(\lambda)$ values and different $I_b(\lambda)$ values for the selective guidance of different motorpatterns (selection hypothesis). Since the spatial resolution of the small eyes of lower invertebrates and of unicellular organisms is so low, and effective quantum flux is an extremely important limiting factor, object detection is often impossible. Nevertheless, the detection of chromatic contrast in the illuminating light is still highly relevant for selective behavioural control. The improved resolving potential and multiple pigments of the eyes of higher crustaceans, chelicerata and insects ensure better matching of a larger number of specific chromatic irradiances including those reflected from objects. If the neural machinery for colour vision, namely spectral opponent coding in the sensory neuropile, developed in addition to the existing photopigments then the animal is able to detect spectral contrast independent of intensity contrast. The examples discussed in the previous Section demonstrate that at least in insects, but probably also crustaceans and spiders, the capacity of colour vision is limited to certain behaviours and guides visual orientation besides and in addition to wavelength-selective behaviours. In other words, the demonstration of several photopigments is by no means an indication of colour vision.

The ecological conditions for the optimal detection of objects that differ in their spectral reflection from the background are well described by Lythgoe's (1972a, 1979) sensitivity and contrast hypotheses. In most natural habitats, chlorophyll in the foliage will serve as the background. Insect species for which colour vision has been proven (several species of Hymenoptera) match the spectral reflection of chlorophyll ($\lambda_{max} = 530$–540 nm) extremely well with their L receptors (see Fig. 14.2). In other insects, for which colour vision may be of little importance or non-existent (e.g. several species of Diptera, such as *Musca* or *Drosophila*), the maximum $S(\lambda)$ of the L receptors is shifted to shorter wavelengths (490–500 nm). This might indicate an adaptation to low light conditions in the natural habitat, which is characterized by a shift to shorter wavelengths from the sky during dawn. It

is worth noting in this context that similar λ_{max} values (480–510 nm) were also found for several crustaceans (Cronin and Forward, 1988; Forward *et al.* 1988), estuary fish (Lythgoe, 1972b; Munz and McFarland, 1977; Hobson *et al.*, 1981; Crescitelli *et al.*, 1985) and terrestrial vertebrates (Lythgoe, 1972b), although these species are exposed to quite different conditions of chromatic illumination. It appears that their high sensitivity rod-system is adapted to the spectrum of early twilight when photon-flux becomes the limiting factor, rather than the environmental light climate during daylight. The strategy of the above mentioned Hymenopteran species under dim light is to pool neurally the excitation from all receptors, and thereby increase photon capture and shift the effective action spectrum to short wavelengths at the expense of colour vision (Menzel, 1981).

Fireflies provide an interesting example for low light adaptations. As one would expect, the emission spectrum of the flashes is matched to the spectral sensitivity of the L receptors (Lall *et al.*, 1980a,b, 1982). Interestingly, those species starting earlier during twilight have their $S(\lambda)$ functions shifted more to longer wavelengths than those starting later (Lall *et al.*, 1988). At early twilight, spectral irradiance shifts to higher proportions of shorter wavelengths and later shifts back to a spectrum similar to that found during the day (Rozenberg, 1966). This in effect results in an enhanced contrast between the background and flash. So far, there is no evidence for an interaction with a second pigment or for the detection of the colour of the flashes. This is actually quite unlikely because colour vision must reduce absolute sensitivity and is even not necessary for species separation due to the fine tuning of the emission and sensitivity spectrums.

Spectral contrast between an object and the green natural background of chlorophyll will increase with higher reflection at shorter or longer wavelengths, i.e. at wavelengths where chlorophyll absorbs (below 470 nm and above 530 nm). This is in fact the strategy applied by flowers. Since insects often act as vectors for the cross-fertilization of plants, the relationship between flowers and insects (and also other pollinators such as birds, bats, mammals) is especially intimate, and the coloration of flowers and the visual systems of the pollinator have co-evolved since the advent of angiosperms during the early Cretaceous period. For the animal, the profit in such a relationship is the immediate reward of nectar or pollen, while for the plant the reward is an increase in reproductive success (high seed setting, higher genetic variance). Therefore, flowers compete for pollinators, and especially for those which transport pollen effectively between plants of the same species. Floral characteristics are thus selected in order to improve detection at large distances, flower-type identification at closer range, and enable object recognition at a species-specific level. Pollinators also compete between each other, and thus niche separation between flower–pollinator syndromes may be a favourable strategy for all partners.

Colour is a most suitable signal for the detection of small objects by fast flying insects with compound eyes of low spatial resolution. Low spatial resolution is even advantageous because sensitivity is increased, blur caused by fast movement is reduced, and consequently colour vision is improved since a point of view is analysed simultaneously in its chromatic components. The distance at which a flower can be detected will then be the product of chromatic contrast to the background and its size. Darwin (1877) realized that the size of flowers is an important factor for pollination, and Kugler (1943) observed that the distance at which bumble bees turn towards a flower is directly proportional to its diameter. The effective size can be increased by flower clusters (e.g. Compositae, see Plate 24) and the collective signal can be prolonged by keeping the showy parts after fertilization. Thus, it is obvious that particularly small and single flowers should be brilliantly coloured and with as much contrast to the background as possible in order to save the amount of energy invested in the size of their petals.

Field observations support the concept outlined above (Review: Proctor and Yeo, 1973; Kevan, 1978, 1983; Osche, 1986; Menzel, 1987). Most flowers on trees, e.g. apple, cherry, citrus, lime, maple, rhobinia lack colours and appear white or green to our sense of vision. These flowers are mostly seen from below against the bright sky, with their flowers closely packed together. In contrast, single flowers on the ground tend to be more brilliant in colour than clusters or inflorescences. Yellow flowers often also reflect UV at their periphery, and this is important since 'insect-purple' (UV + yellow) contrasts better with a green background than with a yellow alone (see colour plates). If the background strongly reflects UV (e.g. sand, quartz, water, many leaves of climbing plants such as the honey-suckle etc), then the flowers absorb UV (see also Kevan, 1978, p 72), whereas the leaves of plants growing in a UV-rich environment (higher mountains, northern tundras, at the sea, in the desert) are often highly UV reflecting and the flowers black in the UV (see Plate 25 of the alpine composite, *Helichrysum*). In woodland, flowers often tend to be highly UV-reflecting (combined with violet, blue or yellow), although 'white' flowers in woods are often black in the UV. Such flowers contrast particularly well with the predominantly green illumination and brown background.

Kevan (1978) reports that flowers blooming together in time and space tend to be more different in their colours than those not competing for pollinators. It is well documented that red flowers are adapted to visitation by butterflies, violet, blue and insect purple (UV + yellow) flowers to bees, wasps and bee-flies (Diptera: Bombylii-

dae), and single 'white' (without UV) flowers with exposed nectaries and pollen to flies, parasitic Hymenoptera and moths (Knoll, 1921; Kugler, 1943; Procter, 1973; Kevan, 1978; Waser, 1983, 1986). These three groups of insects differ considerably in their ability to handle flowers for nectar extraction and pollination. It is not surprising, therefore, that the colour signals together with the corresponding visual systems group the symbiotic partners to the benefit of all members. Many pollinating species, especially the bees and wasps, are particularly flexible as a result of their effective learning systems and visit many different species of flowers during their lifetime. Other species, especially the short-lived solitary bee, have often developed a close symbiotic relationship to only one or a few plant species. The flowers often adapt their colours accordingly. In most cases this adaptation has occurred on an evolutionary timescale and has resulted in different plant species. However, certain flowers have evolved strategies to cope with the changing conditions of potential pollinators. The scarlet flower gilia (*Ipomopsis aggregata*), for example, changes its colour from deep red to light pink and white every year in accordance with the departure of hummingbirds from the habitat and the appearance of hawkmoths which take over the role as the pollinator (Paige and Whitham, 1985).

The intimate relationship between the colours of flowers and the colour vision system of the pollinators suggests a design strategy of mutual reciprocity with respect to the spectral reflection functions of the flowers and the $S(\lambda)$ functions of the receptors. The ever increasing data on the colour vision system of insects now permits this concept of co-evolution and co-adaptation to be subjected to stringent experimental verification.

Conclusion

Throughout this review, the honey bee has been presented as an example for colour vision in insects. Although bees have attracted investigators from many disciplines for well over a century, much has still to be learned with respect to the ecological constraints and physiological basis of colour vision. As in other animals, trichromaticity at the input level and spectral opponency at the neural level have been shown to be common principles. This does not, of course, imply that the major phenomena of colour vision are necessarily based on similar neural strategies which result in comparable perceptions. Instead, evidence shows that insects, and bees in particular, have specific adaptations to their colour vision systems, and future research should concentrate on these species-specific adaptations.

References

Arikawa, K., Inokuma, K. and Eguchi, E. (1987). Pentachromatic visual system in a butterfly. *Naturwissenschaften*, **74**, 297–298.

Autrum, H.(1958). Electrophysiological analysis of the visual system in insects. *Exp. Cell. Res.*, (Suppl.) **5**, 426–439.

Autrum, H. and Kolb, G. (1968). Spektrale Empfindlichkeit einzelner Sehzellen der Aeschniden *Z. Vergl. Physiol.*, **60**, 450–477.

Autrum, H. and Zwehl, V. von (1963). Ein Grünrezeptor im Drohnenauge (*Apis mellifica*). *Die Naturwissenschaften*, **22**, 698.

Autrum, H. and Zwehl, V. von (1964). Die spektrale Empfindlichkeit einzelner Sehzellen des Bienenauges. *Z. Vergl. Physiol.*, **48**, 357–384.

Backhaus, W. and Menzel, R. (1987). Color distance derived from a receptor model of color vision in the honey bee. *Biol. Cybern.*,,**55**, 321–331.

Backhaus, W., Bricerño, D. and Menzel, R.(1988). Brightness discrimination in bees. In *Sense Organs*. eds. Elsner, N. and Barth, F. G. p. 220. Stuttgart: Thieme Verlag.

Backhaus, W., Menzel, R. and Kreissl, S. (1987). Multidimensional scaling of color similarity in bees. *Biol. Cybern.*, **56**, 293–304.

Backhaus, W., Werner, A. and Menzel, R. (1987). Color vision in honey bees: metric dimensions, constancy and ecological aspects. In: *Neurobiology and behaviour of honey bees*. eds. Menzel, R. and Mercer, A. pp. 172–190. Berlin, Heidelberg, NY: Springer-Verlag.

Barlow, H. B. (1952). The size of ommatidia in apposition eyes. *J. Exp. Biol.*, **29**, 667–674.

Barlow, H. B. (1965). Visual resolution and the diffraction limit. *Science*, **149**, 553–555.

Bennett, R. R. and Ruck, P. (1979). Spectral sensitivities of dark and light adapted *Notonecta glauca* compound eyes. *J. Insect. Physiol.*, **16**, 83–88.

Bennett, R. R., Tunstall, J. and Horridge, G. A. (1967). Spectral sensitivity of single retinula cells of the locust. *Z. Vergl. Physiol.*, **55** (2), 195–206.

Bernard, G. D. (1979). Red-absorbing visual pigments of butterflies. *Science*, **203**, 1125–1127.

Bernard, G. D. (1983). Bleaching of rhabdoms in eyes of intact butterflies. *Science*, **219**, 69–71.

Bernard, G. D. and Stavenga, D. G. (1978). Spectral sensitivities of retinular cells measured in intact living bumble bees by an optical method. *Naturwissenschaften*, **65**, 442–443.

Bernard, G. D. and Stavenga, D. G. (1979). Spectral sensitivities of retinular cells measured in intact, living flies by an optical method. *J. Comp. Physiol.*, **134**, 95–107.

Bertholf, L. M. (1931). Reactions of the honey bee to light. *J. Agr. Res.*, **42**, 379–419.

Bishop, L. G. (1974). An ultraviolet photoreceptor in a dipteran compound eye. *J. Comp. Physiol.*, **91**, 267–275.

Brines, M. L. and Gould, J. L. (1979). Bees have rules. *Science*, **206**, 571–573.

Bruckmoser, P. (1968). Die spektrale Empfindlichkeit einzelner Sehzellen des Rückenschwimmers *Notonecta glauca* L. (Heteroptera). *Z. Vergl. Physiol.*, **59**, 187–204.

Brunner, D. and Labhart, T. (1987). Behavioural evidence for polarization sensitivity in crickets. *Physiol. Entomol.*, **12**, 1–10.

Bullock, T. H. and Horridge, G. A. (1965). *Structure and Function in the Nervous System of Invertebrates*. San Francisco: W. H. Freeman and Co.

Burkhardt, D. (1962). Spectral sensitivity and other response characteristics of single visual cells in the arthropod eye. *Symp. Soc. Exp. Biol.*, 16, 86–108.

Burkhardt, D. (1983). Wavelength perception and colour vision. In *The Biology of Photoreception*. eds. Cosens, D. J. and Vince-Price, D. *Symp. Soc. Exp. Biol.*, **36**, 371–397.

Burkhardt, D. and Autrum, H. (1960). Die Belichtungspotentiale einzelner Sehzellen von *Calliphora erythrocephala*. *Z. Naturforsch.*, **15**(b), 612.

Butler, R. (1971). The identification and mapping of spectral cell types in the retina of *Periplaneta americana*. *Z. Vergl. Physiol.*, **72**(1), 67–80.

Butler, R. and Horridge, G. A. (1973). The electrophysiology of the retina of *Perplaneta americana* L. 1. Changes in receptor acuity upon light and dark adapation. *J. Comp. Physiol.*, **83**, 263–278.

Chappell, R. L. and DeVoe, R. D. (1975). Action spectra and chromatic mechanisms of cells in the median ocelli of dragonflies. *J. Gen. Physiol.*, **65**, 399–419.

Checcucci, A. (1976). Molecular sensory physiology of *Euglena*. *Naturwissenschafttten*, **63**, 412–417.

Cheng, K., Collett, T. S., Pickard, A. and Wehner, R. (1987). The use of visual landmarks by honey bees: bees weight landmarks according to their distance from the goal. *J. Comp. Physiol. A*, **161**, 469–475.

Clark, E. D. and Kimeldorf, D. J. (1970). Tentacle response of the sea anemone *Anthopleura xanthogramma* to UV and visible radiations. *Nature (Lond.)*, **227**, 856–857.

Cornsweet, T. N. (1970). *Visual perception*. New York: Academic Press.

Crescitelli, F., McFall-Ngai, M. and Horwitz, J. (1985). The visual pigment sensitivity hypothesis: further evidence from fishes of varying habitats. *J. Comp. Physiol. A*, **157**, 323–333.

Croll, N. A. (1966). The phototactic response and the spectral sensitivity of *Chromadorina virides* (Nematoda, Chromadorinae) with a note on the nature of the paired pigment spots. *Nematologica (Leiden)*, **12**, 610–614.

Cronin, T. W. and Forward, Jr. R. B. (1988). The visual pigment of crabs I. Spectral characteristics. *J. Comp. Physiol. A*, **162**, 463–478.

Darwin, C. R. (1877). *The Effects of Cross and Self-Fertilization in the Vegetable Kingdom*. New York: Appleton.

Daumer, K. (1956). Reizmetrische Untersuchungen des Farbensehens der Bienen. *Z. Vergl. Physiol.*, **38**, 413–478.

Daw, N. W. (1984). The psychology and physiology of colour vision. *TINS*, **7**(1), 330–335.

Diehn, B. (1976). Photomovement of microorganisms. *Photochem. Photobiol.*, **23**, 455–456.

Diehn, B. (1979). Photic responses and sensory transduction in motile protists. In *Handbook of Sensory Physiology Vol. VII/6A*. ed. Autrum, H. pp. 23–68. Berlin-Heidelberg-New York: Springer Verlag.

Duelli, P. and Wehner, R. (1973). The spectral sensitivity of polarized light orientation in *Cataglyphis bicolor* (Formicidae, Hymenoptera). *J. Comp. Physiol.*, **86**, 37–53.

Edrich, W. (1977). Die Rolle einzelner Farbrezeptortypen bei den verschiedenen Lichtreaktionen der Biene. *Verh. Dtsch. Zool. Ges.*, **70**, 236.

Edwards, D. M. (1982). The cockroach DCMD neuron. II. Dynamics of response habituation and convergence of spectral inputs. *J. Exp. Biol.*, **99**, 61–90.

Eguchi, E. (1971). Fine structure and spectral sensitivities of retinular cells in the dorsal sector of compound eyes in the dragonfly *Aeschna*. *Z. Vergl. Physiol.*, **71**, 201–218.

Fietz, A. (1986). *Charakterisierung der spektralen Empfindlichkeit der Retinulazellen von sechs Hymenopterenarten*. Freie Universität Berlin: Diploma Thesis.

Fischbach, K. F. (1979). Simultaneous and successive colour contrast expressed in 'slow' phototactic behaviour of walking *Drosophila melanogaster*. *J. Comp. Physiol.*, **130**, 161–171.

Forward, Jr., R. B., Cronin, T. W. and Douglass, J. K. (1988). The visual pigments of crabs II. Environmental adaptations. *J. Comp. Physiol. A*, **162**, 479–490.

Frisch, K. von (1914a). Demonstration von Versuchen zum Nachweis des Farbensinnes bei angeblich total farbenblinden *Tieren*. *Verh. Dtsch. Zool. Ges.*, **24**, 50–58.

Frisch, K. von (1914b). Der Farbensinn und Formensinn der Bienen. *Zool. Jb. Allg. Zool. Physiol.*, **35**, 1–182.

Gogola, M. (1967). Die spektrale Empfindlichleit der Doppelaugen von *Ascalaphus macaronius Scop.* (Neuroptera, Ascalaphidae). *Z. Vergl. Physiol.*, **57**, 232–243.

Goldsmith, T. H. and Bernard, G. D. (1974). The visual system of insects. In *The Physiology of Insecta, Vol. II*. Second edition. ed. Rockstein, M. pp. 175–271. New York-London: Academic Press.

Gouras, P. (1985). Colour coding in the primate retinogeniculate system. In *Central and Peripheral Mechanisms of Colour Vision*. eds. Ottoson, D. and Zeki, S. W. pp. 183–198. London: Macmillan.

Gouras, P. and Zrenner, E. (1981). Colour vision: A review from a neurophysiological perspective. In *Progress in Sensory Physiology vol. 1* eds. Autrum, H., Ottoson, D., Pearl, E. R. and Schmidt, R. F. pp. 139–179. Berlin–Heidelberg–New York: Springer Verlag.

Gribakin, F. G. (1988). Photoreceptor optics of the honeybee and its eye colour mutants: the effect of screening pigments on the long wave subsystem of colour vision. *J. Comp. Physiol. A*, **164**, 123–140.

Hardie, R. C. (1984). Properties of photoreceptors R7 and R8 in the dorsal marginal ommatidia in the compound eyes of *Musca* and *Calliphora*. *J. Comp. Physiol. A*, **154**, 157–165.

Hardie, R. C. (1986). The photoreceptor array of the dipteran retina. *TINS*, **9**, 419–423.

Harris, W. A., Stark, W. and Walker, J. A. (1976). Genetic dissection of the photoreceptor system in the compound eye of *Drosophila melanogaster*. *J. Physiol. (Lond.)*, **256**, 415–439.

Hasselmann, E.-M. (1962). Über die relative spektrale Empfindlichkeit von Käfer- und Schmetterlingsaugen bei verschiedenen Helligkeiten. *Zool. J. Physiol.*, **69**, 537–576.

Helversen, O. von (1972a). Zur spektralen Unterschiedsempfindlichkeit der Honigbiene. *J. Comp. Physiol.*, **80**, 439–472.

Helversen, O. von (1972b). The relationship between difference in stimuli and choice frequency in training experiments with the honeybee. In *Information Processing in the Visual System of Arthropods*. ed. Wehner, R. pp. 323–334. Berlin-Heidelberg-New York: Springer Verlag.

Helversen, O. von, and Edrich, W. (1974). Der Polarisationsempfänger im Beinenauge: Ein Ultraviolettrezeptor. *J. Comp. Physiol.*, **94**, 33–47.

Hertel, H. (1979). Phototactic reaction of *Asplachna priodonta* to monochromatic light. *Z. Naturforsch.*, **34**(c), 148–152.

Hertel, H. (1980). Chromatic properties of identified interneurons in the optic lobes of the bee. *J. Comp. Physiol.*, **137**, 215–231.

Hertel, H. and Maronde, U. (1987a). Processing of visual information in the honeybee brain. In *The Neurobiology and Behavior of Honeybees* eds. Menzel, R. and Mercer, A. pp. 141–157. Berlin-Heidelberg-New York-London-Paris-Tokyo: Springer Verlag.

Hertel, H. and Maronde, U. (1987b). The physiology and morphology of centrally projecting interneurons in the honeybee brain. *J. Exp. Biol.*, **133**, 301–315.

Hertel,H., Schäfer, S. and Maronde, U. (1987). The physiology and morphology of visual commisures in the honeybee brain. *J. Exp. Biol.*, **133**, 283–300.

Hertel, H. and Ventura, D. F. (1985). Spectral sensitivity of photoreceptors in the compound eye of stingless tropical bees. *J. Insect Physiol.*, **31**(12), 931–935.

Hess, V. von (1913). Experimentelle Untersuchungen über den angeblichen Farbensinn der Bienen. *Zool. Jahrb. (Physiol.)*, **34**, 81–106.

Hildebrand, E. and Dencher, N. (1975). Two photosystems controlling behavioural responses of *Halobacterium halobium*. *Nature (Lond.)*, **257**, 46–48.

Hobson, E. S., McFarland, W. N. and Chess, J. R. (1981). Crepuscular and nocturnal activities of Californian nearshore fishes, with consideration of their scoptic visual pigments and the photic environment. *Fish Bull.*, **79**, 1–30.

Höglund, G., Hamdorf, K., Langer, H., Paulsen, R. and Schwemer, J. (1973). The photopigments in an insect retina. In *Biochemistry and Physiology of Visual Pigments*. ed. Langer, H. pp. 167–174. Berling-Heidelberg-New York: Springer Verlag.

Höglund, G., Hamdorf, K. and Rosner, G. (1973). Trichromatic visual system in an insect and its sensitivity control by blue light. *J. Comp. Physiol.*, **86**, 265–279.

Horridge, G. A. (1969). Unit studies on the retina of dragonflies. *Z. Vergl. Physiol.*, **62**, 1–37.

Horridge, G. A., Marcelja, J., Jahnke, R. and Matic, T. (1983). Single electrode studies on the retina of the butterfly *Papilio*. *J. Comp. Physiol.*, **150**, 271–294.

Horridge, G. A., Marcelja, L. and Jahnke, R. (1984). Colour vision in butterflies. I. Single colour experiments. *J. Comp. Physiol. A*, **155**, 529–542.

Horridge, G. A., Mimura, K. and Tsukahara, Y. (1975). Fly photoreceptors II. Spectral and polarized light sensitivity in the drone fly *Eristalis*. *Proc. R. Soc. Lond. B*, **190**, 225–237.

Howell, C. D. (1939). The response to light in the earthworm *Pheretima agrestis*, Goto and Hatai, with special reference to the function of the nervous system. *J. Exp. Zool.*, **81**, 231–259.

Ilse, D. (1928). Über den Farbensinn der Tagfalter. *Z. Vergl. Physiol.*, **8**, 658–692.

Ilse, D. (1937). New observations on responses to colour in egg-laying butterflies. *Nature (Lond.)*, **140**, 544–545.

Ilse, D. (1941). On the colour vision of insects. *Proc. R. Philos. Soc. Lond.*, **65**, 68–82.

Ingle, D. J. (1985). The goldfish as a retinex animal. *Science*, **227**, 651–654.

Jacobs, G. H. (1981). *Comparative Colour Vision*. pp. 209. New York-Toronto-Sydney: Academic Press.

Kaiser, W. (1968). Zur Frage des Unterscheidungsvermögens für Spektralfarben: Eine Untersuchung der Optomotorik der königlichen Ganzfliege *Phormia regina M. Z. Vergl. Physiol.*, **61**, 71–102.

Kaiser, W. and Liske, E. (1974). Optomotor reactions of stationary flying bees during stimulation with spectral light. *J. Comp. Physiol.*, **89**, 391–408.

Kaiser, W., Seidl, R. and Vollmar, J. (1977). Spectral sensitivities of behavioural patterns in honey bees. *J. Comp. Physiol.*, **122**, 27–44.

Kevan, P. G. (1978). Floral coloration, its colormetric analysis and significance in anthecology. In *The Pollination of Flowers by Insects*. ed. Richards, A. J. *Linnean Society Symposium Series* No. 6, 51–78

Kevan, P. G. (1983). Insects as flower visitors and pollinators. *Ann. Rev. Entomol.*, **28**, 407–453.

Kien, J. and Menzel, R. (1977a). Chromatic properties of interneurons in the optic lobe of the bee. I. Broad band neurons. *J. Comp. Physiol.*, **113**, 17–34.

Kien, J. and Menzel, R. (1977b). Chromatic properties of interneurones in the optic lobes of the bee. II. Narrow band and colour opponent neurons. *J. Comp. Physiol.*, **113**, 35–53.

Kirschfeld, K. (1967). Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexauge von *Musca*. *Exp. Brain Res.*, **3**, 248–270.

Kirschfeld, K. (1972). The visual system of *Musca*. Studies on optics structure and function. In *Information Processing in the Visual System of Arthropods*. ed. Wehner, R. pp. 61–74. Berlin-Heidelberg-New York: Springer Verlag.

Kirschfeld, K. (1974). The absolute sensitivity of lens and compound eyes. *Z. Naturforsch.*, **29**(c), 592–596.

Kirschfeld, K. (1976). The resolution of lens and compound eyes. In *Neural Principles in Vision*. eds. Zettler, F. and Weiler, R. pp. 354–370. Berlin-Heidelberg-New York: Springer Verlag.

Kirschfeld, K. (1986). Activation of visual pigment: chromphore structure and function. In *The Molecular Mechanism of Photoreception* ed. Stieve, H. pp. 31–49. Berlin-Heidelberg-New York: Springer Verlag.

Kirschfeld, K. and Vogt, K. (1985). The contribution of different colour receptors to a motor output in the fly. *J. Comp. Physiol.*, **157**, 417–421.

Kirschfeld, K. and Vogt, K. (1986). Does retinol serve a sensitizing function in insect photoreceptors? *Vision Res.*, **26**, (11), 1771–1777.

Kirschfeld, K. and Wenk, P. (1976). The dorsal compound eye of Simuliid flies: an eye specialized for the detection of small, rapidly moving objects. *Z. Naturforsch.*, **31**(c), 764–765.

Kirschfeld, K., Transceschini, N. and Minke, B. (1977). Evidence for a sensitising-pigment in fly photoreceptors. *Nature*, **269**, 386–390.

Kirschfeld, K., Hardie, R., Lenz, G. and Vogt, K. (1988). The pigment system of the photoreceptor 7 yellow in the fly, a complex photoreceptor. *J. Comp. Physiol. A*, **162**, 421–433.

Knoll, F. (1921). Insekten und Blumen. II. *Bombylius fuliginosus und die Farbe der Blumen*. *Abh. Zool. Bot. Gesellsch. Wien*, **12**, 17–119.

Kolb, G. (1985). Ultrastructure and adaptation in the retina of *Aglais urticae* (Lepidoptera). *Zoomorphology*, **105**, 90–98.

Kolb, G. and Scherer, Ch. (1982). Experiments on wavelength specific behavior of *Pieris brassicae* L. during drumming and egg-laying. *J. Comp. Physiol.*, **149**, 325–332.

Kong, K-L., Fung, Y. M. and Wassermann, G. S. (1980). Filter-mediated color vision with one visual pigment. *Science*, **207**, 783–786.

Kretz, R. (1979). A behavioural analysis of colour vision in the ant *Cataglyphis bicolor* (Formicidae, Hymenoptera). *J.Comp. Physiol.*, **131**, 217–233.

Kruskal, J. B. (1964). Multidimensional scaling by optmizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, **29**, 1–29.

Kugler, M. (1943). Hummeln als Blütenbesucher. *Ergeb. Biol.*, **9**, 143–323.

Labhart, T. (1974). Behavioural analysis of light intensity discrimination and spectral sensitivity in the honey bee, *Apis mellifera*. *J. Comp. Physiol.*, **95**, 203–216.

Labhart, T., Hodel, B. and Valenzuela, I. (1984). The physiology of the cricket's compound eye with particular reference to the anatomically specialized dorsal rim area. *J. Comp. Physiol. A*, **155**, 289–296.

Lall, A. B., Chapman, R. M., Trouth, C. O. and Holloway, J. A. (1980a). Spectral mechanisms of the compound eye in the firefly *Photinus pyralis* (Coleoptera; Lampyridae). *J. Comp. Physiol.*, **135**, 21–27.

Lall, A. B., Lord, E. T. and Trouth, C. O. (1982). Vision in the firefly *Photirus lucicrescens* (Coleoptera; Lampyridae): Spectral sensitivity and selective adaptation in the compound eye. *J. Comp. Physiol.*, **147**, 195–200.

Lall, A. B., Siegler, H. H., Biggley, W. H. and Lloyd, J. E. (1980b). Ecology of colors of firefly bioluminescence. *Science*, **210**, 560–562.

Lall, A. M., Strother, G. K., Cronin, T. W. and Siegler, H. H. (1988). Modification of spectral sensitivities by screening pigments in the compound eyes of twilight-active fireflies (Coleoptera: Lampyridae). *J. Comp. Physiol. A*, **162**, 23–33.

Land, E. H. (1977). The retinex theory of colour vision. *Sci. Am.*, 108–128.

Land, M. F. (1981). Optics and vision in invertebrates. In *Handbook of Sensory Physiology Vol. VIIB Vision in Invertebrates*. ed. Autrum, H. pp. 471–593. Berlin-Heidelberg-New York: Springer Verlag.

Land, E. H. (1983a). Recent advances in retinex theory. *Vision Res.*, **26**, 7–21.

Land, E. H. (1983b). Recent advances in retinex theory and some

implications for cortical computations: Color vision and the natural image. *Proc. Natl. Acad. Sci. USA*, **80**, 5163–5169.

Land, E. H. (1986). An alternative technique for the computation of the designator in the retinex theory of colour vision. *Proc. Natl. Acad. Sci. USA*, **83**, 3078–3080.

Land, E. H., Hubel, D. H., Livingstone, M. S., Perry, S. H. and Burns, M. M. (1983). Colour-generating interactions across the corpus callosum. *Nature*, **303**, 616–618.

Langer, H., Hamann, B. and Meinecke, C. C. (1979). Tetrachromatic visual system in the moth *Spodoptera exempta* (Insecta, Noctuidea). *J. Comp. Physiol. A.*, **129**, 235–239.

Langer, H., Schmeinck, G. and Anton-Erkleben, F. (1986). Identification and localization of visual pigments in the retina of the moth *Antheraea polyphenius*. *Cell. Tiss. Res.*, **245**, 81–89.

Laughlin, S. B. (1975). Receptor function in the apposition eye: An electrophysiological approach. In *Photoreceptor Optics*. eds Snyder, A. W. and Menzel, R. pp. 479–498. Berlin-Heidelberg-New York: Springer Verlag.

Laughlin, S. B. (1981). Neural principles in the peripheral visual systems of invertebrates. In *Handbook of Sensory Physiology, Vol. VII/B Invertebrate Visual Centers and Behaviour I*. ed. Autrum, H. pp. 133–280. Berlin-Heidelberg-New York: Springer Verlag.

Le Grand, Y. (1948). *Optique physiologique*. Vol. 2. *Luminaire et couleurs*. Paris: Rev. Optique.

Le Grand, Y. (1971). *Light, Colour and Vision*. London: Chapman.

Lehrer, M., Wehner, R. and Srinivasan, M. (1985). Visual scanning behaviour in honeybees. *J. Comp. Physiol.*, **157**, 405–415.

Lieke, E. (1981). Graded and discrete receptor potentials in the compound eye of the Australian Bulldog-ant (*Myrmecia gulosa*). *Biol. Cybern.*, **40**, 151–156.

Lillywhite, P. G. (1978). Coupling between locust photoreceptors revealed by a study of quantum bumps. *J. Comp. Physiol.*, **125**, 13–27.

Livingstone, M. S. and Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *J. Neurosci.*, **4** (1), 309–356.

Livingstone, M. S. and Hubel, D. H. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, **240**, 740–749.

Lythgoe, J. N. (1972a). The adaptation of visual pigments to the photic environment. In *Handbook of Sensory Physiology Vol. VIIH*. ed. Dartnall, H. J. A. pp. 567–603. Berlin-Heidelberg-New York: Springer Verlag.

Lythgoe, J. N. (1972b). List of vertebrate visual pigments. In *Handbook of Sensory Physiology, Vol. VII/1 The Phytochemistry of Vision*, ed. Dartnall, H. J. A. pp. 604–624. Berlin-Heidelberg-New York: Springer Verlag.

Lythgoe, J. N. (1979). *The Ecology of Vision*. Clarendon Press: Oxford.

McIntyre, P. and Kirschfeld, K. (1982). Chromatic aberration of a dipteran corneal lens. *J. Comp. Physiol.*, **146**, 493–500.

Marr, D. (1982). *Vision*. San Francisco: W. H. Freeman and Co.

Marwan, W., Alain, M. and Oesterbelt, D. (1987). Die Geisselbewegung halophiler Bakterien. *Naturwissenschaften*, **74**, 585–590.

Matic, T. (1983). Electrical inhibition in the retina of the butterfly *Papilio*. I. Four spectral types of photoreceptors. *J. Comp. Physiol. A*, **152**, 169–182.

Meffert, P. and Smola, U. (1976). Electrophysiological measurements of spectral sensitivity of central visual cells in the eye of the blowfly. *Nature*, **260**, 342–344.

Meinertzhagen, I. A., Menzel, R. and Kahle, G. (1983). The identification of spectral receptor types in the retina and lamina of the dragonfly *Sympetrum rubicundulum*. J. Comp. Physiol., **151**, 95–310.

Menzel, R. (1967). Untersuchungen zum Erlernen von Spektralfarben durch die Honigbiene, *Apis mellifica*. *Z. Vergl. Physiol.*, **56**, 22–62.

Menzel, R. (1973). Evidence for color receptors in the hymenopteran eye obtained from selective adaptation experiments. *T-T-J Life Science*, **3**, 95–100.

Menzel, R. (1974). Spectral sensitivity of monopolar cells in the bee lamina. *J. Comp. Physiol.*, **93**, 337–346.

Menzel, R. (1979). Spectral sensitivity and colour vision in invertebrates. In *Handbook of Sensory Physiology, Vol. VII/6A Invertebrate Photoreceptors*. ed. Autrum, H. pp. 503–580. Berlin-Heidelberg-New York: Springer Verlag.

Menzel, R. (1981). Achromatic vision in the honeybee at low light intensities. *J. Comp. Physiol.*, **141**, 389–393.

Menzel, R. (1985a). Colour pathways and colour vision in the bee. In *Central and Peripheral Mechanisms of Colour Vision*. ed. Ottoson, D. and Zeki, S. pp. 211–223. London: Macmillan Press.

Menzel, R. (1985b). Learning in honey bees in an ecological and behavioural context. In *Experimental Behavioral Ecology*. eds. Hölldobler, B. and Lindauer, M. pp. 55–74. Stuttgart-New York: Gustav Fischer Verlag.

Menzel, R. (1987). Farbensehen blumen besuchender Insekten. Jahresbericht der Kernforschungsanstalt Jülich.

Menzel, R. and Blakers, M. (1976). Colour receptors in the bee eye – morphology and spectral sensitivity. *J. Comp. Physiol.*, **108**, 11–33.

Menzel, R. and Greggers, U. (1985). Natural phototaxis and its relationship to colour vision in honeybees. *J. Comp. Physiol.*, **141**, 389–393.

Menzel, R. and Roth, F. (1972). Spektrale Phototaxis von Planktonrotatorien. *Experientia*, **28**, 356–357.

Menzel, R. and Snyder, A. W. (1974). Polarized light detection in the bee, *Apis mellifera*. *J. Comp. Physiol.*, **88**, 247–270.

Menzel, R., Backhaus, W., Chittka, L. and Hoffmann, M. (1988a). Honey bee drones are trichromates. In *Sense Organs*. eds. Elsner, N. and Barth, F. p. 217. Stuttgart: Thieme Verlag.

Menzel, R., Steinman, E., de Souza, J. and Backhaus, W. (1988b). Spectral sensitivity of photoreceptors and colour vision in the solitary bee, *Osmia rufa*. *J. Exp. Biol.*, **136**, 35–52.

Menzel, R., Ventura, D. F., Hertel, H., de Souza, J. M. and Greggers, U. (1986). Spectral sensitivity of photoreceptors in insect compound eyes: comparison of species and methods. *J. Comp. Physiol. A*, **158**, 165–177.

Menzel, R., Ventura, D. F., Werner, A., Martins, L. C. and Backhaus, W. (1989). Spectral sensitivity of single photoreceptors and colour vision in the stingless bee, *Melipona quadrifaciata*. *J. Comp. Physiol. A* **166**, 151–164.

Milde, J. (1978). *Bestimmung der spektralen Empfindlichkeit in verschiedenen Augenbereichen der Biene*. Freie Universität Berlin: Diploma Thesis.

Miller, W. H. (1979). Ocular optical filtering. In *Handbook of Sensory Physiology, Vol. VII/6A Invertebrate Photoreceptors*. ed. Autrum, H. pp. 69–143. Berlin-Heidelberg-New York: Springer Verlag.

Miller, W. H. and Bernard, G. D. (1968). Butterfly glow. *J. Ultrastruct. Res.*, **24**, 286–294.

Minke, B. and Kirschfeld, K. (1979). The contribution of a sensitising pigment to the photosensitivity spectra of fly rhodopsin and metarhodopsin. *J. Gen. Physiol.*, **73**, 517–540.

Mote, M. J. and Goldsmith, T. H. (1970). Spectral sensitivity of colour receptors in the compound eye of the cockroach *Periplaneta*. *J. Exp. Zool.*, **173**, 137–145.

Mote, M. J. and Goldsmith, T. H. (1971). Compound eyes: localization of two colour receptors in the same ommatidium. *Science*, **171**, 1254.

Mote, M. J., Kumar, V. S. N. and Black, K. R. (1981). 'On' type interneurons in the optic lobe of *Periplaneta americana*. II. Receptive fields and response latencies. *J. Comp. Physiol.*, **141**, 403–415.

Mote, M. J. and Rubin, L. J. (1981). 'On' type interneurons in the optic lobe of *Periplaneta american*. *J. Comp. Physiol.*, **141**, 395–401.

Mote, M. J. and Wehner, R. (1980). Functional characteristics of

photoreceptors in the compound eye and ocellus of the desert ant, *Cataglyphis bicolor*. *J. Comp. Physiol.*, **137**, 63–71.

Munz, F. W. and McFarland, W. N. (1977). Evolutionary adaptation of fishes to the photic environment. In *Handbook of Sensory Physiology, Vol. VII/5*. ed. Autrum, H. pp. 194–274. Berlin-Heidelberg-New York: Springer Verlag.

Muri, R. B. and Jones, G. J. (1983). Microspectrophotometry of single rhabdoms in the retina of the honeybee drone (*Apis mellifera*). *J. Gen. Physiol.*, **82**, 469–496.

Naitoh, Y. (1982). Protozoa. In *Electrical Conduction and Behaviour in 'Simple' Invertebrates*. ed. Shelton, G. A. B. pp. 1–48. Oxford: Clarendon Press.

Neumeyer, C. (1980). Simultaneous color contrast in the honey bee. *J. Comp. Physiol.*, **139**, 165–176.

Neumeyer, C. (1981). Chromatic adaptation in the honey bee: successive colour contrast and colour constancy. *J. Comp. Physiol.*, **144**, 543–553.

Neumeyer, C. (1988). *Das Farbensehen des Goldfisches. Eine verhaltenphysiologische Analyse*. Stuttgart-New York: Gustav Thieme Verlag.

Osche, G. (1986). Vom 'Erscheinungsbild' der Blütenpflanzen. Zum Evolution optischer Signale. Mannheimer Forum 1986. Boehringer Mannheim, Mannheim.

Osorio, D. (1986). Ultraviolet sensitivity and spectral opponency in the locust. *J. Exp. Biol.*, **122**, 193–208.

Osorio, D. (1987a). The temporal properties of non-linear transient cells in the locust medulla. *J. Comp. Physiol. A*, **161**, 431–440.

Osorio, D. (1987b). The temporal and spectral properties of sustaining cells in the locust medulla. *J. Comp. Physiol. A*, **1612**, 441–448.

Paige, K. N. and Whitham, T. G. (1985). Individual and population shifts in flower color by scarlet gilia: a new mechanism for pollinator tracking. *Science*, **227**, 315–317.

Paul, R., Steiner, A. and Gemperlein, R. (1986). Spectral sensitivities of *Calliphora erythrocephala* and other insect species studied with Fourier interferometric stimulation (FIS). *J. Comp. Physiol. A*, **158**, 669–680.

Peitsch, D. and Menzel, R. (1988). Red receptors in compound eyes of hymenoptera. In *New Frontiers in Brain Research*. eds. Elsner, N. and Creutzfeld, O. pp. 144. Stuttgart-New York: Gustav Thieme Verlag.

Proctor, M. (1973). *The Pollination of Flowers*. London: Collins.

Ribi, W. A. (1979). Coloured screening pigments cause red eye glow in pierid butterflies. *J. Comp. Physiol.*, **132**, 1–9.

Reihle, A. (1981). Color opponent neurons of the honey bee in a hetero-chromatic flicker test. *J. Comp. Physiol.*, **142**, 81–88.

Rodieck, R. W. (1973). *The Vertebrate Retina. Principles of Structure and Function*. San Francisco: W. H. Freeman and Co.

Rossel, S. and Wehner, R. (1982). How bees analyse the polarization patterns in the sky. Experiments and model. *J. Comp. Physiol.*, **154**, 607–615.

Rozenberg, G. V. (1966). *Twilight – a Study in Atmospheric Optics*. New York: Plenum Press.

Rushton, W. A. H. (1972). Pigments and signals in colour vision. *J. Physiol.*, **220**, 1–31.

Schäfer, S. (1984). Characterisierung extrinsischer Grossfeldneuronen aus der Medulla der Honigbiene (*Apis Mellifera*). Freie Universität Berlin: Diploma Thesis.

Scherer, Ch. and Kolb, G. (1987). Behavioural experiments on the visual processing of color stimuli in *Pieris brassicae* L. (Lepidoptera). *J. Comp. Physiol. A*, **160**, 645–656.

Schlecht, P. (1979). Colour discrimination in dim light: an analysis of the photoreceptor arrangement in the moth *Deiliphila*. *J. Comp. Physiol.*, **129**, 257–267.

Schrödinger, E. (1920). Grundlinien einer Theorie der Farbmetrik im Tagessehen. *Ann. Physik*, **63**, 397–520.

Schwind, R. (1985). Sehen unter und über Wasser, Sehen von Wasser. *Naturwissenschaften*, **72**, 343–352.

Shannon, C. E. and Weaver, W. (1949). *The Mathematical Theory of Communication*. Illinois.

Sharpe, L. T. (1987). A Landslide for Colour Science? *Colour Res. Appl.*, **12**,(2), 81–84.

Snyder, A. W. (1979). The physics of vision in compound eyes. In *Handbook of Sensory Physiology Vol. VII/6A Comparative Physiology and Evolution of Vision in Invertebrates*. ed. Autrum, H. pp. 225–314. Berlin-Heidelberg-New York: Springer Verlag.

Snyder, A. W., Menzel, R. and Laughlin, S. B. (1973). Structure and function of the fused rhabdom. *J. Comp. Physiol.*, **87**, 99–135.

Snyder, A. W., Stavenga, D. G. and Laughlin, S. B. (1977). Information capacity of eyes. *Vision Res.*, **17**, 1163–1175.

Spudich, J. L. and Bogomolni, R. A. (1984). Mechanisms of colour discrimination by a bacterial sensory rhodopsin. *Nature*, **312**, 509–513.

Srinivasan, M. V. and Lehrer, M. (1984). Temporal acuity of honeybee vision: behavioural studies using moving stimuli. *J. Comp. Physiol.*, **155**, 297–312.

Srinivasan, M. V. and Lehrer, M. (1988). Spatial acuity of honeybee vision and its spectral properties. *J. Comp. Physiol. A*, **162**, 159–172.

Stavenga, D. G. and Barneveld, H. H. van (1975). On dispersion in visual photoreceptors. *Vision Res.*, **15**, 1091–1095.

Stavenga, D. G. and Schwemer, J. (1984). Visual pigments of invertebrates. In *Photoreception and Vision in Invertebrates*. ed. Ali, M. A. pp. 11–61. New York: Plenum Press.

Steiner, A., Paul, R. and Gemperlein, R. (1987). Retinal receptor types in *Aglais urticae* and *Pieris brassicae* (Lepidoptera), revealed by analysis of the electroretinogram obtained with Fourier interferometric stimulation (FIS). *J. Comp. Physiol. A*, **160**, 247–258.

Struwe, G. (1972). Spectral sensitivity of single photoreceptors in the compound eye of a tropical butterfly. *J. Comp. Physiol.*, **79**, 197–201.

Swihart, S. L. (1968). Single unit activity in the visual pathway of the butterfly *Heliconius erato*. *J. Insect. Physiol.*, **14**, 1589–1601.

Swihart, S. L. (1970). The neural basis of colour vision in the butterfly *Papilio troilus*. *J. Insect. Physiol.*, **16**, 1623–1636.

Swihart, S. L. (1972a). The neural basis of colour vision in the butterfly, *Heliconius erato*. *J. Insect. Physiol.*, **18**, 1015–1025.

Swihart, S. L. (1972b). Modelling the butterfly visual pathway. *J. Insect Physiol.*, **18**, 1915–1928.

Swihart, C. A. and Swihart, S. L. (1970). Colour selection and learned feeding reference in the butterfly *Heliconius charitorius*, *Limn. Anim. Behav.*, **18**, 60–64.

Thomas, J. and Autrum, H. (1965). Die Empfindlichkeit des dunkelund helladaptierten Bienen, *Apis mellifica* für spektrale Farben: Zum Purkinje-Phänomen der Insekten. *Zur Vergl. Physiol.*, **51**, 204–218.

Tinbergen, J. and Abeln, R. G. (1983). Spectral sensitivity of the landing blowfly. *J. Comp. Physiol.*, **150**, 319–328.

Togerson, W. S. (1958). *Theory and Methods of Scaling*. New York: Wiley.

Tsuda, M. (1987). Photoreception and phototransduction in invertebrate photoreceptors. *Photochem. Photobiol.*, **45**(6), 915–931.

Unteutsch, W. (1937). Über den Licht- und Schattenreflex des Regenwurms. *Zool. Jahrb. (allgem. Zool.)*, **58**, 9–12.

Vishnevskaya, T. M., Cherkasov, A. D. and Shura-Bura. T. M. (1986). Spectral sensitivity of photoreceptors of the compound eye in locust. *Neurofiziologya*, **18**, 69–76.

Vogt, K. (1983). Is the fly visual pigment a rhodopsin? *Z. Naturforsch.*, **38**(c), 329–333.

Vogt, K. and Kirschfeld, K. (1983). Sensitizing pigment in the fly. *Biophys. Struct. Mech.*, **9**, 319–328.

Vogt, K., Kirschfeld, K. and Stavenga, D. G. (1982). Spectral effects of the pupil in fly photoreceptors. *J. Comp. Physiol.*, **146**, 145–152.

Wald, G. and Brown, P. K. (1965). Human color vision and color blindness. *Cold Spring Harbor Symp. Quant. Biol.*, **30**, 345–362.

Walther, J. B. (1958). Changes induced in spectral sensitivity and

form of retinal action potential of the cockroach eye by selective adaptation. *J. Insect Physiol.*, 2, 142–151.

Waser, N. M. (1983). The adaptive nature of floral traits: ideas and evidence. In *Pollination Biology*. ed. Real, L. pp. 247–286. Orlando: Academic Press.

Waser, N. M. (1986). Flower constancy: definition, cause, and measurement. *Am. Naturalist*, **127**, 593–603.

Wehner, R. and Toggweiler, F. (1972). Verhaltensphysiologischer Nachweis der Farbensehens bei *Cataglyphis bicolor*. *J. Comp. Physiol.*, 77, 239–255.

Werner, A., Menzel, R. and Wehrhahn, Chr. (1988). Color constancy in the honeybee. *J. Neurosci.*, 8, 156–159.

White, R. H., Brown, P. K., Hurley, A. K. and Bennett, R. R. (1983). Rhodopsins, retinula cell structure, and receptor potentials in the developing pupal eye of the moth *Manduca sexta*. *J. Comp. Physiol. A*, **150**, 153–163.

Witthöft, W. (1967). Absolute Anzahl and Verteilung der Zellen im Hirn der Honigbiene. *Z. Morphol. Tiere*, 61,160–184.

Yingst, D. R., Fernandez, H. R. and Bishop, L. G. (1972). The spectral sensitivity of a littoral annelid, *Nereis mediator*. *J. Comp. Physiol.*, 77, 225–232.

Zeki, S. (1985). Colour pathways and hierarchies in the cerebral cortex. In *Central and Peripheral Mechanisms of Colour Vision*. eds Ottosen, D. and Zeki, S. pp. 19–44. London: Macmillan Press.

Zrenner, E. (1983). Neurophysiological aspects of colour vision in primates. In *Studies of Brain Function* ed. Braitenberg, V. p. 218. Berlin-Heidelberg-New York: Springer Verlag.

Zufall, F., Schmitt, M. and Menzel, R. (1989). Spectral and polarized light sensitivity of photoreceptors in the compound eye of the cricket (*Gryllus bimaculatus*). *J. Comp. Physiol.* (in press).