5 Color Vision in Bees: Mechanisms, Ecology, and Evolution

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The fact that many animals see the world in colors and in ways that are very different from those of human vision has long fascinated scientists. These differences underscore the fact that the world we see is not the "real," or physical world. The world that any organism experiences is a product of the specific sensory filters that the animal has acquired during its evolution.

It was a hymenopteran species that first provided this insight. More than 100 years ago, Lubbock (1889) discovered that ants had ultraviolet sensitivity, demonstrating for the first time a sensory capacity not held by humans. Then, just a few decades later, UV vision in bees was discovered (Kühn, 1924). Subsequently, several generations of bee vision *aficionados* have produced a wealth of information on neural color processing in the tiny brains of these insects. In fact, our knowledge of color vision in bees is more extensive than that of any other animal besides primates. However, there are still many intriguing questions to be asked, some very fundamental. These questions are not limited to the mechanisms of color coding by bees, they also have to do with why bees see colors the way that they do.

Much of early sensory ecology was shaped by a naive panadaptionism, a version of the early twentieth-century naturalists' belief that there is a creator who wields unlimited power and creativity. However, in this case the creator was natural selection. This belief slowed progress in the field substantially. That is, to demonstrate evolutionary adaptation, adaptation itself cannot be the null hypothesis. One needs to consider alternative hypotheses such as an organism's evolutionary history, molecular and phylogenetic constraints, and chance evolutionary events.

In this chapter, we discuss what has been discovered in recent decades about bee color vision and suggest some promising avenues for future research. After our discussion of several key issues in understanding color vision in bees, we will turn to the question of how bees use color signals during foraging. Essentially, we will use bees as a case study of how color vision is used in the economy of nature.

The Spectral Sensitivity and Phylogeny of Bee Photoreceptors

The complex eyes of bees contain between 1000 and 16,000 ommatidia, depending on the species. Honeybees have some 5000 ommatidia (U. Jander and Jander, 2002). Each ommatidium contains nine photoreceptor cells. Eight of these elongated cells are arranged side by side so that they form a quasi-circle. Their rhabdomeres, brush-shaped microvillous extensions that contain the photopigments, protrude into the center of the circle. In bees, these extensions form a fused rhabdom, which means that the rhabdomeres from all eight photoreceptor cells are functionally fused to form a single light-guiding structure (A. W. Snyder, 1979). In honeybees, it was traditionally thought that four of these receptors are green receptors with maximum sensitivity (λ_{max}) at about 540 nm, two are blue receptors ($\lambda_{max} \approx 440$ nm), and two are UV receptors ($\lambda_{max} \approx$ 340 nm). The ninth photoreceptor cell is small and is located near the base of the ommatidium. It is presumably a UV receptor (Menzel and Backhaus, 1991). Recent molecular biological work, however, appears to indicate that there are three types of ommatidia, each with a different set of spectral receptors (Kurasawa et al., 2002).

In bees, each class of spectral receptor contains a distinct visual pigment, which consists of two components. One is the chromophore, retinal (or one of its congeners), which changes its configuration when it absorbs a single quantum of light (Seki and Vogt, 1998). The other component is a protein, the opsin, consisting of about 370 amino acids. Opsins are integrated into the membrane of rhabdomeric microvilli (Deeb and Motulsky, 1996). They consist of seven transmembrane helices in a circular arrangement so that they form a pocket, which contains the chromophore. Specific amino acids in the transmembrane helices oriented toward the center of the pocket (and thus interacting electrostatically with the chromophore) are responsible for spectral tuning (Hope et al., 1997). Spectral sensitivity curves have a roughly Gaussian shape, with a halfbandwidth of approximately 100 nm. The absorption spectra of short-wavelength pigments are generally narrower than those of long-wavelength pigments. This is an intrinsic photopigment characteristic in plots using a linear wavelength scale (figure 5.1).

Long-wavelength pigment absorption spectra have two peaks in the range from 300 to 700 nm, a large α peak and a smaller β peak in the UV. The β peak is caused by the *cis* band of the chromophore. As the visual pigment peak wavelength (λ_{max}) value is shifted toward shorter wavelengths, the β peak gradually is consumed by the larger α peak.

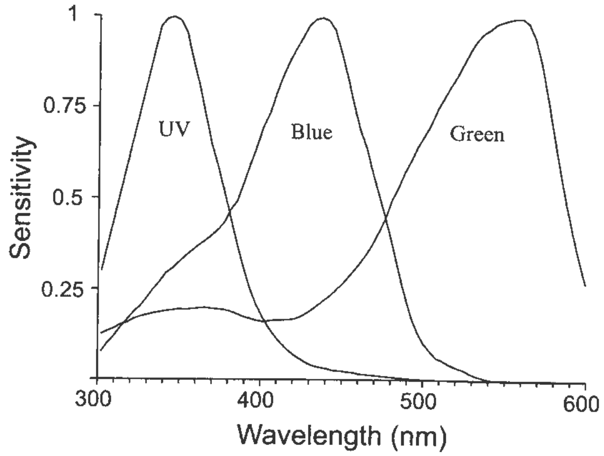


Figure 5.1
Spectral sensitivity of photoreceptor cells in the honeybee *Apis mellifera* (Peitsch et al., 1992). The UV-, blue-, and green-sensitive photoreceptors of the genus *Apis* have spectral sensitivity curves typical of many insects.

In order to understand how visual pigments in bees have changed over evolutionary time, it is important to understand the phylogeny of arthropod opsins. To this end, Briscoe and Chittka (2001) compared the amino acid sequences of the opsins of fifty-four species of arthropods available in the literature, including the different opsins found within each of these species.

Invertebrate opsins fall into distinct functional clades according to their spectral sensitivity (figure 5.2). There is one cluster of UV pigments, a distinct group of blue pigments, and a third group of long-wave pigments, which includes pigments with peak sensitivity from green to red. (For a discussion of the blue-green cluster, see Chittka and Briscoe, 2001) Of particular interest is the fact that chelicerate and crustacean green-sensitive pigments are more similar to insect green pigments than they are to either UV or blue pigments. This suggests that the opsin clades diverged from one another before the major groups of arthropods had diverged, and it is therefore likely that ancient arthropods already possessed (at least) UV and green visual pigments.

The Hymenoptera are especially interesting in terms of visual ecology because the species studied come from a wide variety of habitats, with very different lifestyles and feeding habits (figure 5.3). Nevertheless, there is surprisingly little variation in photoreceptor spectral sensitivity. All species, with the exception of ants, possess UV, blue, and green receptors. The few species for which data on UV and blue receptors are absent (e.g., Symphyta and Ichneumonidae), as well as, for example, *Colletes* and *Lasioglossum*, presumably represent cases where such cells exist but have not as yet been recorded (Peitsch et al., 1992). Some species possess additional red receptors, for example, three species of Symphyta (hence red receptors were probably present in their ancestor species) and one andrenid bee. There are pronounced differences in lifestyle among these species with red receptors; while *Tenthredo* oviposits on leaves, *Xyphidria* is a wood-boring wasp (figure 5.3). *Callonychium* is a solitary bee that appears to visit purple *Petunia* flowers exclusively (Wittmann et al., 1990). Therefore, different selective pressures presumably drove the evolution of red receptors in these species.

The remaining species, those with only UV, blue, and green receptors, also inhabit diverse habitats and have varied life histories. They include not only several generalist nectarivores (such as honeybees, stingless bees, and bumblebees), but also a few species that specialize on a narrow range of flowers (*Andrena*, *Lasioglossum*, *Colletes*). In addition, this group contains generalist (*Vespa*) and specialist (*Philanthus*) predators. Some of these species are ground nesting (e.g., most bumblebees) others nest in trees (*Apis*), and still others utilize termite nests (*Partamona*). All species featured here are primarily diurnal, but some are known to forage at night (Warrant et al., 1996). Some members are obligatorily Alpine species (e.g., *Bombus monticola*), and so forage in a very UV-rich environment, whereas others (e.g., some stingless bees) may do much of their foraging in dense tropical forests, which have relatively little UV light (Endler, 1993).

Peitsch et al. (1992) suggested that the only case of adaptive tuning evident in the Hymenoptera is a long-wavelength shift in the UV receptor of forest-dwelling

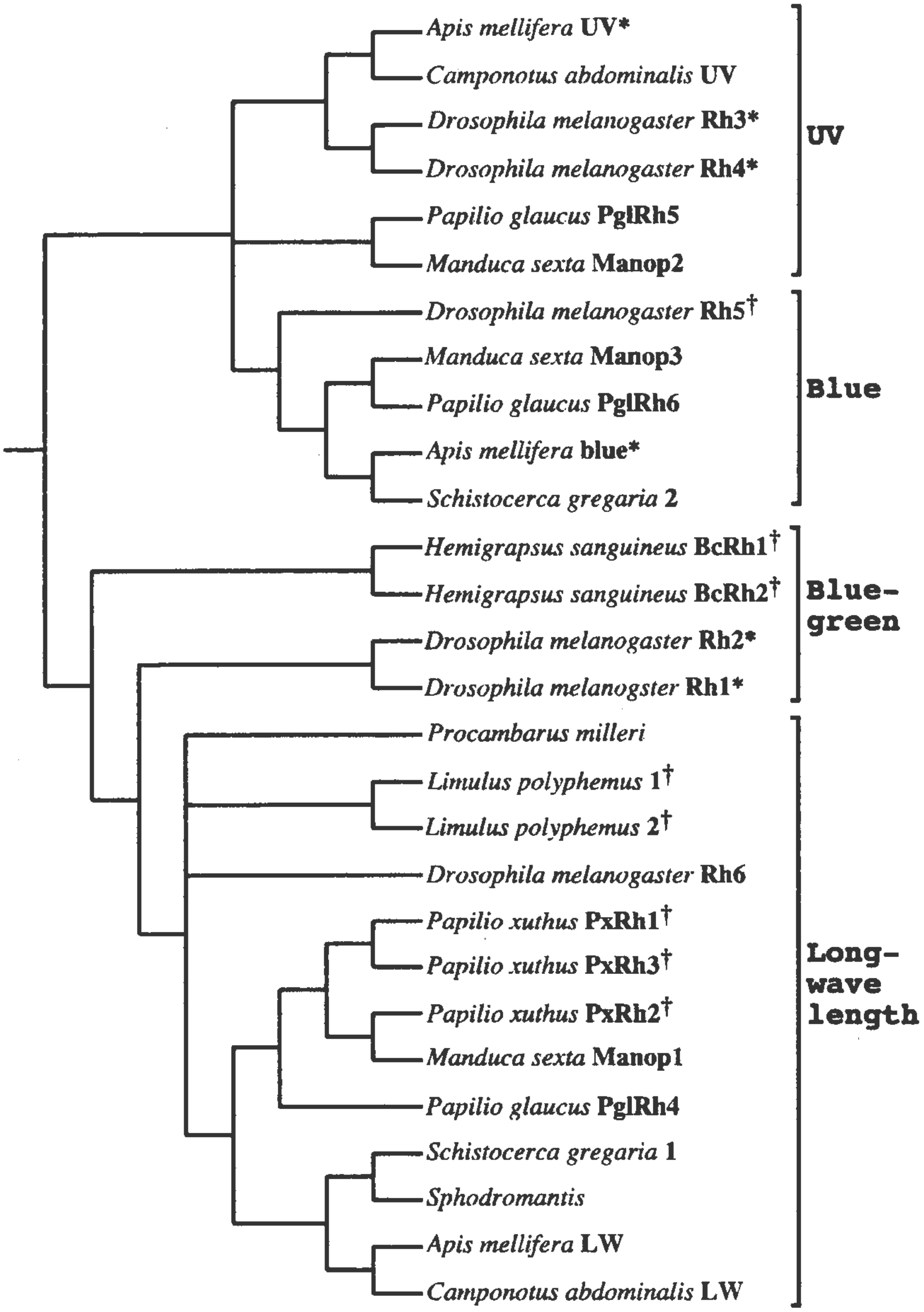


Figure 5.2
Phylogeny of insect, chelicerate, and crustacean opsins, based upon a maximum parsimony analysis of opsin amino acid sequences. The tree shown is simplified from the analysis of a larger data set of fifty-four opsin sequences. Only representative species from available orders or suborders are shown. The brackets indicate measured (asterisk) or inferred (dagger) spectral properties of the visual pigments in each clade. Inferred spectral properties are based upon in situ hybridization or immunohistochemistry in combination with electrophysiological studies. For references for the measured spectra, see Chittka and Briscoe (2001). (From Chittka and Briscoe, 2001, with permission from Springer-Verlag.)

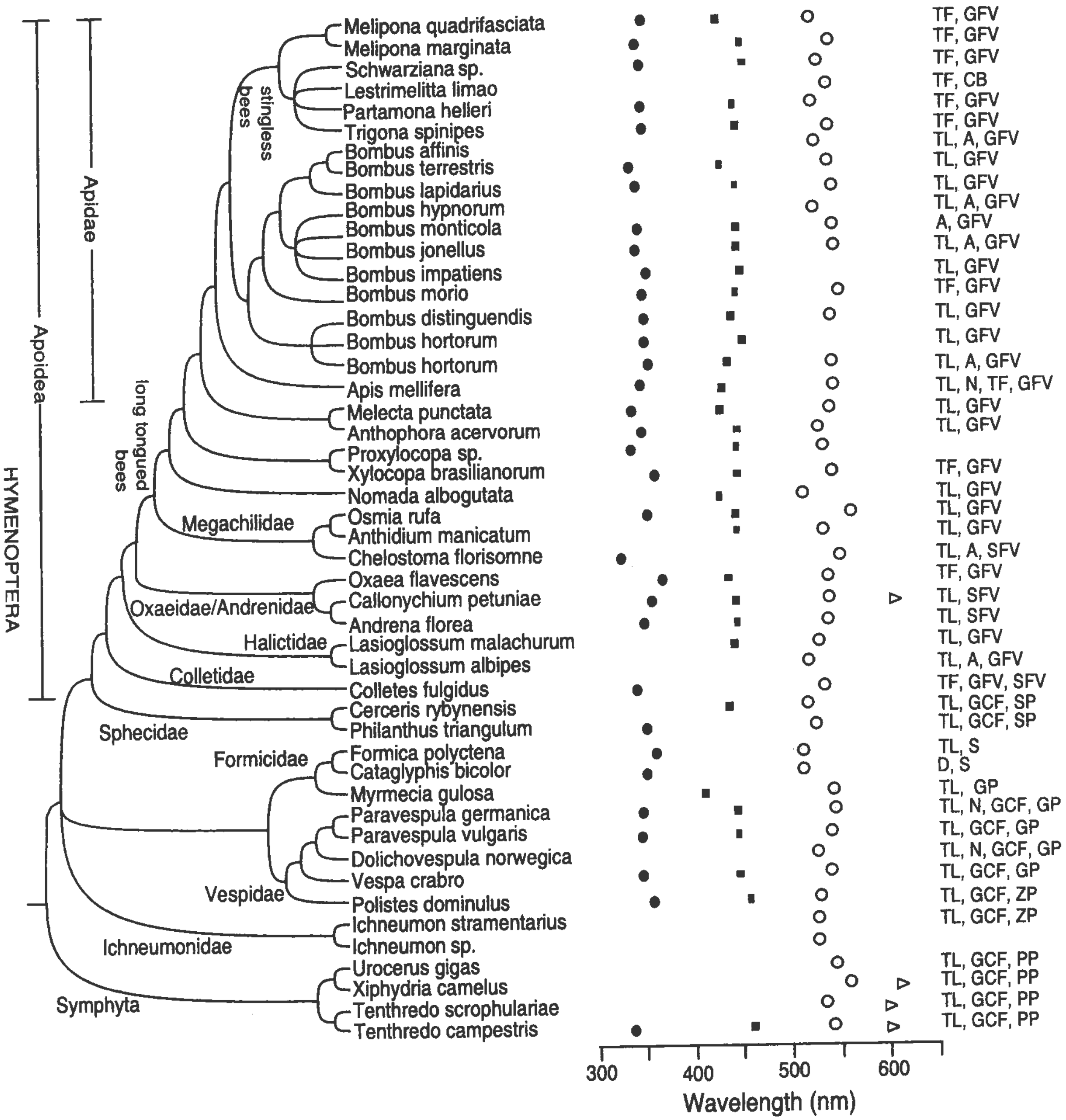


Figure 5.3

Spectral sensitivity of Hymenoptera, superimposed on their phylogeny, and ecological specializations for which vision is important. The values of maximum sensitivity are shown for each known receptor type in each species. For references, see Briscoe and Chittka (2001). Light habitat or type of activity: A, alpine; D, desert; N, nocturnal activity (in addition to diurnal, which is primary in all these species); TF, tropical forest; TL, temperate lowland. Feeding specialization: GFV, generalist flower visitor; SFV, specialist flower visitor; GCF, generalist carbohydrate forager (flowers, fruits, tree sap, and honeydews); GP, generalist predator; SP, specialist predator; CB, cleptobiotic (*Lestrimelitta limao* obtains its food exclusively by robbing the nests of other bees); S, scavenger; PP, phytoparasitism; ZP, zooparasitism (in the latter species, the larvae are parasitic, and the imaginae need to identify appropriate hosts). Circles, squares, and arrows indicate wavelengths of peak sensitivity for UV, blue, green, and red receptors.

stingless bees. An inspection of the λ_{max} values superimposed on the Hymenopteran phylogeny does not reveal strong support for this hypothesis, however. The UV receptors of all stingless bee species fall well within the scatter of other apid bees. In conclusion, despite a wide variety of visual-ecological conditions under which the Hymenoptera live, we find few differences in color receptors among most species, and in the few cases where we do find differences, a convincing adaptive explanation has yet to be found.

Optimal Sets of Photoreceptors for Natural Color Coding

A dozen years ago, one of us (LC), in collaboration with R. Menzel, set out to identify the adaptive significance of bee color vision. The idea was to generate a set of theoretically optimal color receptors for the task of color coding flowers, and to compare this with the system really implemented in bees. We hypothesized that because bees obtain most of their food from flowers, their color vision should be adapted for optimal detection and identification of flower colors. Our evolutionary model calculations consisted of moving three color receptor sensitivity curves along the wavelength scale. For each theoretical combination of receptors so generated, the quality of the color vision system for color coding flowers was determined. The result was striking; the optimal color receptors generated by the evolutionary model invariably occurred near $\lambda_{max} = 330$, 430, and 550 nm, values very close to the most common λ_{max} found in flower-visiting bees (figure 5.4) (Chittka and Menzel, 1992). This result was independent of whether we varied one, two, or all three photoreceptors. It was also independent of the particular set of flowers used (Chittka, 1996). Since the optimal set of color receptors might also depend on the particular kind of opponent coding in the brain, the mode of this processing, too, was varied, and the result remained unchanged (Chittka, 1996).

An engineer could hardly design a better receiver for flower colors than the color receptor set of bees. But does this mean that flower colors drove the evolution of bee color receptors? Our findings led some to think that bee color vision was an adaptation to flower colors, although we explicitly stated that this is not necessarily the case (Chittka and Menzel, 1992).

Indeed, there are several complications. Although models are useful in generating hypotheses of optimality, a correlation between a model and certain biological traits does not resolve the question of how the traits evolved. Using models to reject a hypothesis of evolutionary causality is much more straightforward. Had the optimal color receptors derived from our model calculations been different from the ones found in extant animals, then this would have indicated that evolution has not optimized the photoreceptors according to the model's criteria. At the very least, it would mean that there are other, more important criteria, or that evolutionary constraints might have hindered the animal from evolving along the same lines as the model predicts. In fact, sets of color receptors similar to those of bees occur in animals that occupy entirely different ecological niches.

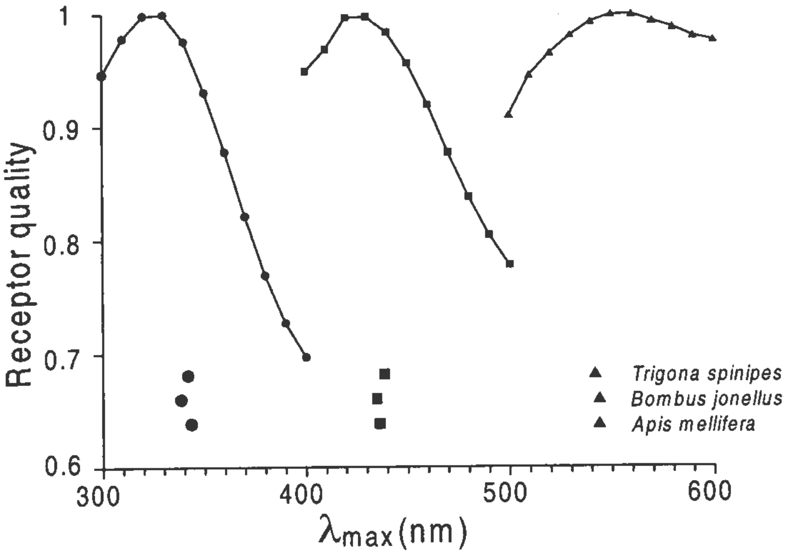


Figure 5.4
Determination of an optimal photoreceptor set for discriminating flower colors. In each of three variations, two receptors were fixed at the wavelength positions where they most frequently occur in Hymenoptera, and the third was shifted in 10-nm steps from 300 to 400 nm, from 400 to 500 nm, or from 500 to 600 nm. The spread of floral color loci in the bee's color space was determined by which set of spectral photoreceptors was used. All of these distances were summed, and the sum serves as a measure for the quality of each receptor set. The single points show the λ_{max} actually found in three species of bees (Peitsch et al., 1992).

Postreceptor Neural Processing

Basic Neuroanatomy of the Optic Lobes

To understand the specifics of color processing in bees, we should first take a general look at arthropods. The basic architecture of the optic lobes in malacostracan crustaceans and insects is extremely similar and was most likely present in a common ancestor (Osorio et al., 1995). The visual information is passed from the receptor level to three successive ganglia, called the lamina, medulla, and lobula (figure 5.5). Of the eight or nine photoreceptors present in each ommatidium, six to seven terminate in the lamina (short visual fibers), while one to three project to the lobula (long visual fibers) (Osorio et al., 1995). Based on comparisons among fruit flies, honeybees, locusts, and crayfish, Osorio et al. (1995) concluded that the ancestral *bauplan* (body plan) of these animals involved long-wavelength sensitivity (blue-green) in the short visual fibers, and at least one long visual fiber with UV sensitivity.

The internal wiring of the lamina, as well as the lamina-medulla connections, are highly conserved across insects from different orders, and even many crustaceans (Osorio et al., 1995). One widespread type of neuron that appears to be central in color vision consists of the large monopolar cells, which relay the information from the

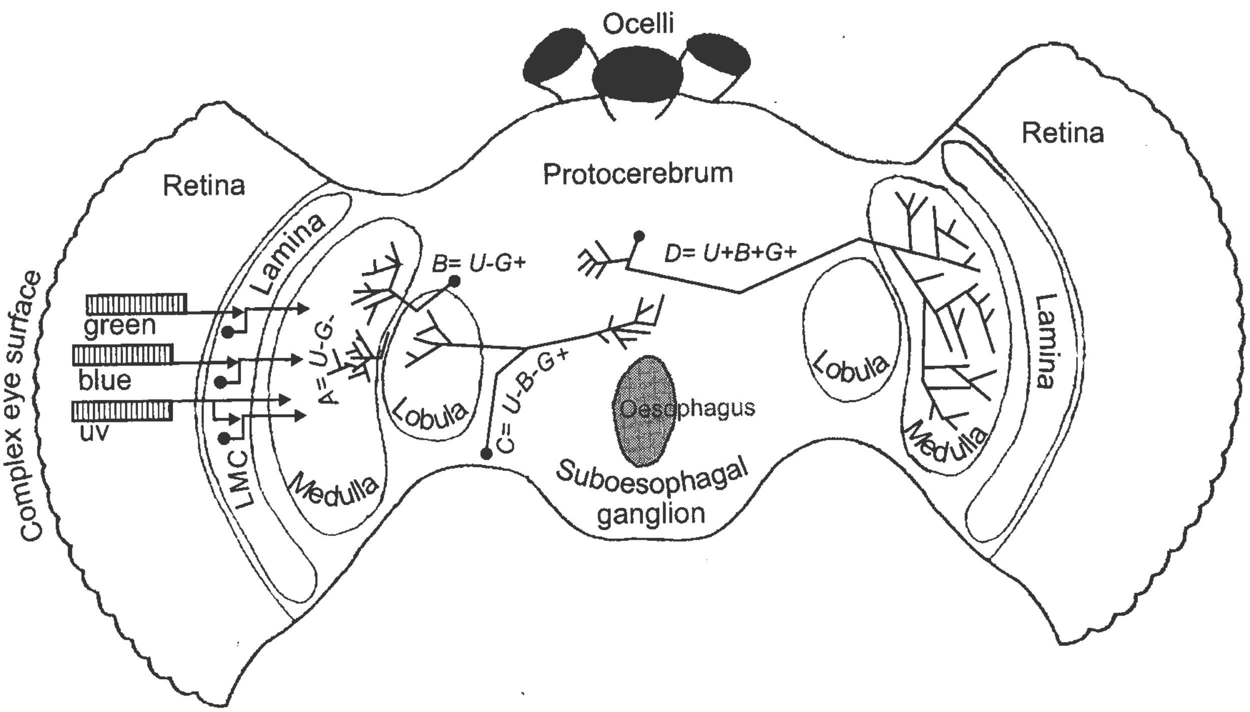


Figure 5.5
Frontal section through the brain of a honeybee showing the neuronal pathways that are most likely involved in color coding. Each ommatidium contains four green and two blue receptors, which project into the lamina (short visual fibers), and three UV receptors, which project into the medulla (long visual fibers). All receptors make contact with lamina monopolar cells (LMCs) in the lamina. These cells convey the receptor signals to the medulla (de Souza et al., 1992). LMCs exist in both depolarizing and hyperpolarizing forms. The distal medulla and lobula contain several types of color-coded neurons, very few of which have been stained. The soma of neuron A (Hertel, 1980, his figure 6) was not dyed. The neuron produced a tonic inhibition (but phasic excitation) to both UV and green light at daylight intensity. Blue light was not tested. Neuron B was inhibited by UV light and excited by green light; blue light produced no response (Menzel and Backhaus, 1991). Neuron C (Hertel and Maronde, 1987, their figure 6) was strictly phasic. This neuron received the opposite input (i.e., long wavelength inhibition and UV phasic excitation from the contralateral eye). Neuron D (Hertel and Maronde, 1987, their figure 2) has arborizations almost throughout the entire medulla and is excited by light of all wavelengths from the ipsilateral eyes, but is inhibited by UV and green light from the contralateral eye. All visual neuronal pathways appear to converge on the protocerebrum, which seems to be an area of higher-level color processing. (Adapted from Menzel and Backhaus, 1991.)

photoreceptor cells to the medulla. Some of these cells appear to amplify the unprocessed signals from particular photoreceptors (de Souza et al., 1992), while others sum inputs from two or three spectral receptor types, possibly to form the initial stage of a brightness coding system used in phototaxis (Menzel and Backhaus, 1991).

The medulla and lobula of the honeybee, *Apis mellifera*, contain a bewildering variety of neurons that might be related to color coding. Such neurons can have phasic properties, which means that they respond only to the onset (and/or offset) of a light stimulus (of a particular wavelength) with a burst of action potentials. Other neurons have tonic responses; i.e., they produce a sustained series of action potentials, or are continuously inhibited, in response to light of a particular spectral domain. For color identification, it is presumably necessary that a tonic component be present. Otherwise the signal would vanish as the bee approaches the target (a flower, for example). While there are some neurons in the optic lobes of the bee that are purely phasic, all tonic neurons so far found in the bee optic lobes also have a phasic component, so that signals are amplified when a target occupies only a small portion of the receptive field.

Wavelength-Selective Behavior

The processing of spectral stimuli has been divided into two types, wavelength-selective behavior and color vision (Menzel, 1979). Wavelength-selective behavior occurs when specific behavioral responses are triggered by specific configurations of signals from the photoreceptors (Goldsmith, 1990). For example, sea anemones retract their tentacles when they are exposed to UV light, but bend them toward visible light (Menzel, 1979). This behavior has no plasticity; it cannot be altered by learning. In such cases, it is reasonable to assume that the motor circuits are connected to rather unprocessed output from the visual periphery in a hard-wired fashion.

Phototaxis in bees is an example of wavelength-selective behavior. When honeybees leave the hive or a flower, or when they are trying to escape from a precarious situation, they seek out bright daylight. This response is color-blind: when given the choice between two routes, bees will invariably pick the brighter one, irrespective of spectral content. Brightness, in this context, is the weighted sum of all three spectral receptors' responses, where the strongest input appears to come from the UV receptors (Kaiser and Seidl, 1977; Menzel and Greggers, 1985). Neurons whose activity might underlie this behavior have been found in all optic ganglia of the honeybee. These cells, phasic or tonic, sum up the signals from the UV, blue, and green receptors (Kien and Menzel, 1977a; Hertel and Maronde, 1987b; de Souza et al., 1992).

Another example of wavelength-selective behavior is related to navigation using a sun compass. If the sun itself is obscured by clouds, bees will use the polarization pattern of sky light to reconstruct the position of the sun (K. von Frisch, 1967). This is accomplished using specialized, polarization-sensitive UV receptors in the dorsal margin of the compound eyes (Wehner, 1989a). In the laboratory, bees will interpret small, nonpolarized, and long wavelength-dominated light sources as the sun, whereas extended light sources with a strong UV component (polarized or unpolarized) will be interpreted as open sky (Edrich et al., 1979; Rossel and Wehner, 1984). Neurons that are UV–bluegreen antagonistic, which might be used in this behavior, have been recorded frequently in the medulla of bees (Kien and Menzel, 1977b).

Several types of motion-related behaviors are also color blind. All appear to be driven entirely by a single class of receptor, the bees' long-wave, or green receptor.

One classic experimental paradigm used to study, for example, the temporal resolution of vision in different animals, is the optomotor response. Animals placed in a rotating drum with vertical stripes will typically turn in the direction of the drum's rotation, which stabilizes their position within the visual environment. Under natural conditions, this is equivalent to compensating for involuntary displacements from the intended position or direction of movement. However, honeybees will only follow the direction of movement if the stripes present contrast in the green domain of the spectrum (Kaiser, 1974). Other types of behavior controlled by the input from the green receptor are movement avoidance, motion parallax, and edge detection (Lehrer, 1998).

The green receptors are also important in floral detection by bees. Before honeybees are able to analyze the color of a flower, they detect the flowers by means of green contrast. This means that the bees compare the signals from the green receptors stimulated by the flower with the signals from the green receptors stimulated by the background (Giurfa and Lehrer, 2001). One might expect a phasic neuronal channel to drive these motion-related behaviors (Horridge, 2000), and indeed, phasic green-sensitive neurons have been found in each of the bee's optic ganglia (de Souza et al., 1992; Kien and Menzel, 1977b).

It is intriguing that Kien and Menzel (1977a) found a cell that responds to green light with a phasic response, but responds tonically to a mixture of UV and green light. This cell might be used both for green receptor-driven detection and for subsequent color identification of a target.

In bumblebees, the green channel appears to be used only for detection of very small flowers. For larger flowers, in a tradeoff between detection and correct identification, bumblebees seem to use the more reliable color channel for detecting flowers (Spaethe et al., 2001). In fact, bees of several genera use color vision for identification of flowers (Chittka et al., 2001) and their nest entrance (Chittka et al., 1992). They also respond to colored landmarks seen en route between the nest and a food source (Cheng et al., 1987; Chittka et al., 1995; Zhang et al., 1996), but it remains to be shown whether color (rather than, for example, the signal generated by the green receptors) is a cue used in identifying these landmarks.

Color Vision

An essential prerequisite for color vision is the presence of color opponent coding by neurons that compare inputs from different color receptor types. Menzel and Backhaus (1989) and Backhaus (1991) postulated that in honeybees the photoreceptor signals are evaluated by means of two types of color opponent processes, one of which is UV–bluegreen antagonistic, and another that is blue–UV-green antagonistic (figures 5.6 and 5.7). This model has been widely referenced and appears to be useful in predicting how honeybees discriminate colors.

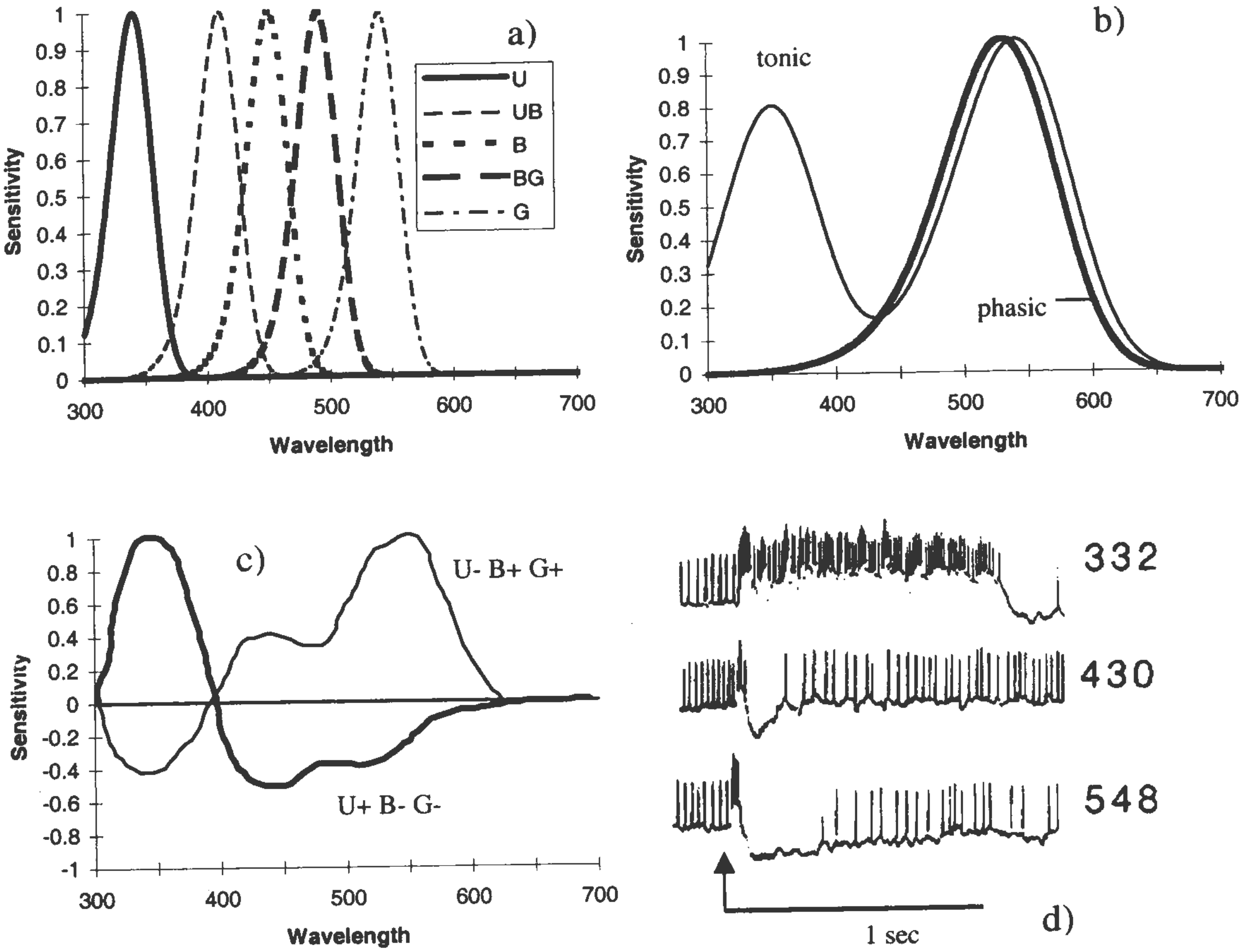


Figure 5.6

Spectral sensitivity of neurons related to color coding in the bee optic lobes (Kien and Menzel, 1977b; Hertel, 1980; Hertel and Maronde, 1987b). Sensitivity functions are smoothed and stylized to emphasize the important features. (*Upper left*) Narrow-band neurons from the lamina and medulla, most sensitive in the UV, violet, blue, blue-green, and green. These cells can be phasic-tonic or strictly phasic. (*Upper right*) A cell with different responses in different temporal phases of the stimulus; the phasic response is predominantly to green light, while in the sustained phase, UV and green wavebands excite the cell. (*Lower left*) Color opponent neurons of two types. (*Lower right*) Spike trains of a UV+ B- G- cell in response to UV (332 nm), blue (430 nm), and green light (548 nm). (From Menzel and Backhaus, 1989, with permission from Springer-Verlag.)

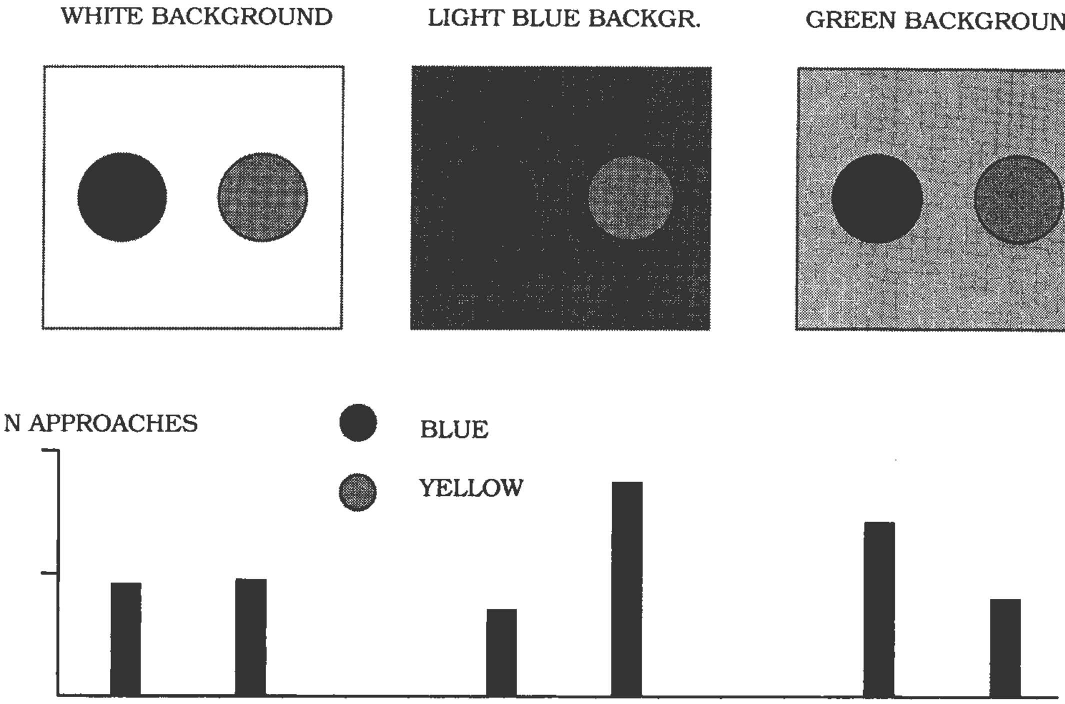


Figure 5.7
The attractiveness of yellow (bee green) and blue (bee blue) dummy flowers for bumblebees (*Bombus terrestris*) depends on the background color. On a white background, both flower types are approached equally frequently. On a light-blue background, yellow flowers are more attractive. On a green background, blue flowers are more attractive. (From Lunau et al. 1996, with permission from Springer-Verlag.)

The neurophysiological evidence underlying Backhaus' proposed opponencies is not strong, however. Kien and Menzel (1977b) frequently found only one type of tonic color opponent neuron. These cells were excited by UV light and inhibited by blue and green light (UV+B-G-). However, the cells differed widely in the strengths of inputs from the blue and green receptors, and so the assumption of a single set of weighting factors is a simplification. A single UV-B+G+ cell was also found. However, the existence of the other type of neuron postulated by the model, a tonic neuron with excitatory input from blue receptors and inhibitory input from UV and green receptors (UV-B+G-), or its mirror image, UV+B-G+, is uncertain.

To make matters even more complicated, a number of color-coded neurons not included in the model have also been described. A strictly phasic neuron that reacted antagonistically to blue and UV-green was found by Hertel (1980). It produced a brief burst of action potentials at the onset of blue light and also a brief burst when the UV or green light was switched off. There was no inhibitory response to UV and green while the stimulus was ongoing. Hertel and Maronde (1987b) also found a phasic neuron that was green versus UV-blue antagonistic. The functions of these cells are unclear, but they might be used in coding successive color contrast (Neumeyer, 1981) or turning the bee's attention to a target seen in flight.

Single-waveband neurons, tuned to only a narrow section of the wavelength scale, were found in both the medulla and the lobula of bees (figure 5.6). Neurons with maximum signal response to UV (antagonistically $\lambda_{max} = 340\,nm$), violet ($\lambda_{max} = 410\,nm$), blue ($\lambda_{max} = 440\,nm$), blue-green ($\lambda_{max} = 490\,nm$), and green ($\lambda_{max} = 540\,nm$) were found (Kien and Menzel, 1977b). All of them had very narrow spectral sensitivity functions compared with those of photoreceptor cells. For example, the green-sensitive neurons had no beta peak in the UV. This suggests that not even those cells with a λ_{max} similar to that of the photoreceptors simply relay unprocessed receptor signals to the protocerebrum. Rather, there must have been inhibition from other wavebands. A cell that responded with a tonic excitation from both UV and green light was also found (Kien and Menzel, 1977a).

The function of these neurons might be in unique hue coding or in the formation of color categories. The neurons themselves, of course, cannot code for hue any more than single receptors can (because wavelength is always confounded with intensity); but hue coding through such wavelength-tuned cells might be possible in conjunction with a color opponent system. We certainly need more neurophysiological data before we can be sure how color coding functions in the honeybee brain. And we also have to lament the complete absence of neurophysiological data for any hymenopterous species other than *Apis mellifera*.

Higher-Order Color Processing

How do bees really perceive colors? Do they actually see a colored image, or are different components of the visual scene processed in parallel, never to be reassembled into a picture, as some researchers suggest (Horridge, 2000)? Can bees process hue, brightness, and saturation independently, as do humans? Do they categorize colors, so that the hundreds of colors they might be able to distinguish (Chittka et al., 1993) are grouped into sets of similar ones? How does the bee achieve color constancy, the ability to identify colors despite changes in the spectral content of the illumination?

Spectral Purity and Saturation

Spectral purity, or the corresponding perceptual term, *saturation*, is the degree to which colors differ from being uncolored. For humans, black, white, and gray have zero saturation; pastel colors have low saturation; and monochromatic lights (which contain only a single wavelength) have the highest possible saturation (at least at optimum intensity). In color space, spectral purity can be measured as the distance from the uncolored point. Lunau (1990) assumed that bumblebees (*Bombus terrestris*) analyze stimulus saturation because he found that they preferred more spectrally pure colors over those that had a strong uncolored component. However, the most spectrally pure colors were also those that produced the strongest color contrast to the background, which makes pure colors also easily detectable (Spaethe et al., 2001). Therefore these early experiments could not unambiguously demonstrate an independent mechanism that codes for saturation.

Lunau et al. (1996) performed experiments with backgrounds of different colors and confirmed that color contrast to the background was important in determining floral attractiveness for naive bees (figure 5.7). However, in a series of tests with bicolored flower dummies (corollas with nectar guides), the authors clearly showed that color contrast alone was not sufficient to explain the data. Two types of reactions of naive bees to flower dummies were analyzed: the frequency of approach flights and the percentage of approach flights that ended in antennal contact with the nectar guide. The latter could not be explained by color contrast. Whether the approach flights were interrupted or whether they ended in an antennal contact with the nectar guide was strongly dependent on the direction (sign) of color contrast, not only its magnitude. Bees strongly preferred saturated nectar guides on unsaturated corollas, but not the reverse condition in which color contrast between nectar guide and corolla was equal. It seems, therefore, that bumblebees possess the perceptual dimension of saturation.

Dominant Wavelength and Hue

In color space, the dominant wavelength of a color locus can be measured by drawing a straight line from the center of color space through that locus and extrapolating to the spectrum locus (the line that connects the loci of monochromatic lights). The point of intersection at the spectrum locus marks the dominant wavelength. Hue is the corresponding perceptual term; it is the attribute of color perception denoted by yellow, red, purple, etc. (Wyszecki and Stiles, 1982). Clearly, bees can distinguish stimuli that differ in dominant wavelength (von Helversen, 1972), but this does not necessarily mean that hue is a meaningful concept in color perception by bees. We need to compare pairs of stimuli that have equal color contrast with one pair that has the same dominant wavelength and the another that does not. If it can be demonstrated that bees somehow group stimuli of the same dominant wavelength, we can conclude that they have the perceptual dimension of hue.

An interesting observation is that floral colors are strongly clumped in the color space of bees, so that there are some dominant wavelengths where many flower colors occur and others where there are hardly any. The reason is not that bees have a mechanism that facilitates such clustering (e.g., color categorization); rather, there is a limited number of distinct types of spectral reflectance functions (Chittka et al., 1994). It is intriguing that the dominant wavelengths at which floral colors are most common are also those at which interneurons in the bee optic lobes are most sensitive (figure 5.8). However, it is not known whether these neurons are in fact involved in coding specific, biologically relevant hues.

Backhaus (1992b) and Chittka (1992) predicted that the Bezold-Brücke phenomenon, known in human color vision, should exist in bees also. The Bezold-Brücke effect occurs mainly at high intensities: subjectively, hue changes even though the spectral distribution of the stimulus remains the same. So far, behavioral tests have only shown that the discriminability of monochromatic lights from uncolored stimuli changes with stimulus intensity, an effect that is based on the nonlinear transduction

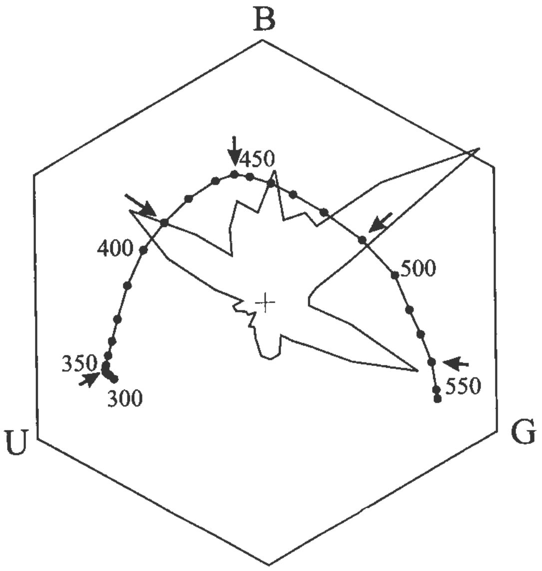


Figure 5.8
Clustering of floral hues in the bee's color space and maximum sensitivity of interneurons in the honeybee optic lobes. The relative number of flowers occurring in each 10-deg hue category is plotted as a circular histogram. A total of 1965 flower colors were evaluated. Clusters appear roughly every 60 deg. The spectrum locus is given from 300 to 560 nm, with solid circles in 10-nm steps. The cross specifies the neutral locus. Arrows mark the wavelength values at which bee interneurons are most sensitive. Note the correspondence of the angular position and peaks in the floral hue distribution.

process in the photoreceptors (Backhaus, 1992b; Chittka, 1992). The same phenomenon would also be expected for broadband reflection functions such as those of flowers (figure 5.9). Whether the predicted hue shifts are actually measurable in bee behavior remains to be determined.

Intensity and Brightness

In human color perception, stimulus brightness (the sensations by which a stimulus appears more or less intense; Wyszecki and Stiles, 1982) is an important dimension of color perception. In bees, this seems not to be the case. Numerous studies have found that it is much more difficult to train bees to attend to differences in stimulus intensity than to differences in spectral quality (von Helversen, 1972; Backhaus and Menzel, 1987; Chittka, 1999). All models of color vision in bees agree in terms of one aspect: all are two-dimensional and do not include a brightness dimension (Vorobyev and Brandt, 1997). It is important here to distinguish between a brightness dimension in color vision in the context of feeding, and intensity-dependent responses generated outside the realm of color vision. For example, honeybees will respond to stimulus intensity in their phototactic escape response (Menzel and Greggers, 1985), but this has no relationship to color vision. If they are extensively trained, however, bees can

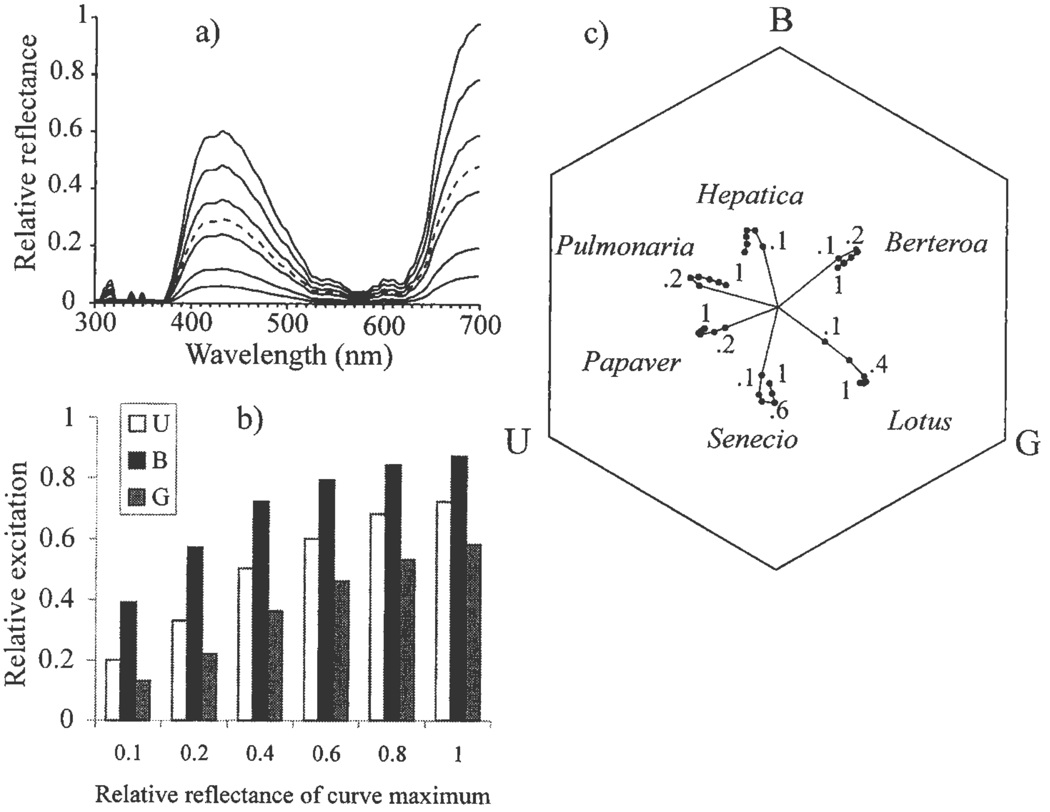


Figure 5.9
Intensity-dependent changes in flower color. (*a*) The intensity of *Hepatica nobilis* is adjusted to six values of maximum reflectance. The maximum of the original measurement is 0.53 (dashed line). (*b*) A set of three color receptor voltage signals is calculated for each curve intensity (ultraviolet, Blue, and green). (*c*) Intensity-dependent color shifts are shown for six typical flower colors. For full species names and reflectance functions, see Chittka et al. (1994). For each color, the curve starts at intensity zero in the uncolored point; it ends at intensity one. The intermediate points correspond to the intensity values 0.1, 0.2, 0.4, 0.6, and 0.8. At very high and very low intensities, the receptor signals are closer to equal than at intermediate intensities; the color locus lies closer to the uncolored point in the hexagon. At some intermediate intensity value, the receptor signals become maximally different from each other; a color with maximal spectral purity will be generated. The type of shift is different for different colors. For all colors, there is a certain intensity between zero and one that generates a maximal spectral purity. Flowers may evolutionarily optimize their detectability by adjusting their intensity. The optimal intensity is low for the UV-blue *Pulmonaria* (optimal intensity, 0.2) and the blue *Hepatica* (optimum at 0.4), whereas it is higher for all other colors.

discriminate stimuli that differ only in intensity (Menzel and Backhaus, 1991), so that bees can apparently learn to attend to cues that they do not naturally use. It is also important to bear in mind that another type of intensity-dependent signal, that produced by the green receptor, is very important in driving several kinds of motion-related behavior (Giurfa and Lehrer, 2001).

Color Categories

Humans form color categories, and cross-cultural studies find consistencies in terms of the boundaries between categorical color names (Ratliff, 1976; Kay and McDaniel, 1978; Zollinger, 1988), which suggests a physiological basis (but see Saunders and van Brakel, 1997). Clearly, the question of whether a similar categorization occurs in animals is interesting but we do not have the answer for a single nonhuman animal. One reason is that in humans, the scientist's access to perception is through language. Another reason is that standard tests to understand color perception in animals do not work for color categories. Color discrimination, for example, is independent of whether two stimuli lie within a category or on the two sides of a boundary between two categories (Heider and Olivier, 1972). Some workers have mistaken sharp discontinuities in color discrimination along the wavelength scale as boundaries of color categories (Goldman et al., 1991). But such discontinuities occur naturally because animals are particularly good at distinguishing wavelengths in spectral ranges where the slopes of two spectral sensitivity functions overlap in opposite directions (Chittka and Waser, 1997), and so they may have no relationship to color categorization. Thus, wavelength discrimination probably is an inappropriate paradigm for studying color categories. Generalization or transfer tests (in which bees are trained to one color, then confronted with two alternative colors) may reveal boundaries of categories (Neumeyer and Kitschmann, 1998), or one might use nonverbal tests that have been developed for infants (Teller and Bornstein, 1987).

Color Constancy

Color constancy is the ability of a visual system to identify a stimulus by its spectral properties, independent of the spectral distribution of the illuminant. This is an important capacity because the spectral radiant power of light varies substantially between sunlight and forest shade, and between noon and sunset (Dyer, 1998; Endler, 1993). Thus the physical quality of light reflected from an object changes, and so without a mechanism to compensate for this change, identification of an object may be compromised. Behavioral experiments, however, show that bees can compensate for the change, and so experience color constancy (Mazokhin-Porshnyakov, 1966; Neumeyer, 1981; Werner et al., 1988). Early workers generally assumed that color constancy is, and has to be, essentially perfect. This is not the case, however. Tests in humans (Maloney, 1986) as well as bees (Neumeyer, 1981) have shown that there are conditions in which color constancy is not flawless. Dyer (1998) has recently started to explore the mechanisms that might underpin color constancy in bees. While some authors have assumed that complex central nervous system operations are necessary for color constancy in bees (Werner et al., 1988), Dyer points out that a more parsimonious approach is in order.

Using an approach developed earlier for human vision (von Kries, 1905), Dyer asked whether color constancy might not simply be explained by von Kries's receptor adaptation. This simply assumes that receptors increase their overall sensitivity when the average illumination that reaches them is low in intensity and decrease their sensitivity when they are strongly stimulated. Clearly, this assumption is fulfilled in insect photoreceptors (Laughlin, 1981). Dyer (1999) showed that such a simple mechanism would yield a rather efficient color constancy mechanism. On the other hand, he predicted specific deviations from perfect color constancy under some conditions, especially in the UV region of color space. Dyer proposed that these deviations occur because of the asymmetric overlap of the spectral sensitivity curves of the spectral receptor types. There is little overlap at longer wavelengths, but the bees' long wavelength receptors, because of their β peak (figure 5.10) overlap strongly with that of their UV receptors (Dyer, 1999). Empirical evidence for these predictions has recently been found (Dyer and Chittka, 2004).

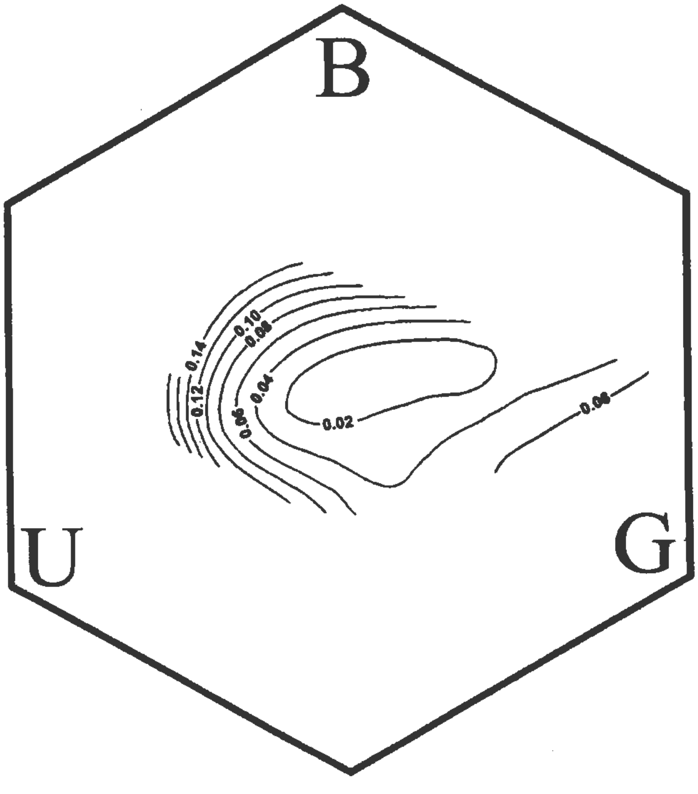


Figure 5.10
Predicted color shift in different parts of bees' color space, assuming von Kries's color constancy. The numbers on the contours indicate the distance that a color in that region of color space would shift for a change in correlated color temperature from 4800 to 10,000 K. For comparison, the distance from the center of the hexagon to any of the corners is unity. The color shift is greatest in the UV and UV-blue areas of color space. (Figure redrawn from P. G. Kevan et al., 2001.)

It should be emphasized that such failures of color constancy are as important for understanding mechanism and ecology as are the instances when color constancy works. Do flower colors "avoid" areas of color space where failures of color constancy would make them hard to identify (Dyer, 1999)? What strategies do bees use to cope with imperfections of color constancy? Do they place stronger emphasis on other floral cues, such as odor, shape, or position in space, when color constancy fails? These will be rewarding topics to explore experimentally in the future.

The Use of Color in Natural Foraging

Much of the diet that most animals consume is cryptic. Bees are fortunate because their food "wants" to be seen. Most species of bees obtain pollen and nectar from plants, which advertise these rewards with conspicuous and colorful signals, the flowers. Flower colors can contain information about the kind of reward that they offer (e.g., pollen or nectar), its quantity, its quality (e.g., nectar volume and sugar concentration), and its variability, as well as information about the handling procedures needed to exploit the flowers (H. Wells and Wells, 1986; Chittka et al., 1999).

In turn, the behavioral response to the flower's color information tells us something about the bee's information processing and, perhaps, the cognitive capacities. Foraging behavior, the repetitive decision-making process of choosing which flowers to visit, has provided a wealth of knowledge about how bees process and perceive color information.

Innate Flower Color Preferences

Many newly emerged insects that have never seen flowers prefer certain colors over others. Such innate color preferences help naive insects find food, and, possibly, select profitable flowers among those that are available.

Floral preferences can be overwritten by learning to some degree, but there is evidence that in some situations (for example, when rewards are similar across flower species), bees will revert to their initial preferences (Heinrich et al., 1977; Banschbach, 1994; Gumbert, 2000). We believe that these innate preferences reflect the traits of those local flowers which are most profitable for the bees. We also think that evolutionary changes in such preferences require changes only in the synaptic efficiency between neurons coding information from color receptors. Therefore, color preferences might adapt more readily to environmental pressures than the wavelength sensitivities of color receptors. Bee color preferences are a promising model system for appreciating, not only the use of color by animals in their natural setting, but also for understanding patterns of heredity of a basic color-related behavior.

For instance Giurfa et al. (1995) found a correlation between the color preferences of naive honeybees and the nectar offerings of different flowers in a nature reserve near Berlin. Honeybees preferred the colors violet (bee UV-blue) and blue (bee blue), which were also the colors most associated with high nectar rewards. Of course, correlation does not indicate causality. To show that color preferences evolved to match floral offerings, we need to compare a set of closely related bee species (or populations of the same species) that live in habitats in which the relationship between floral colors and rewards varies.

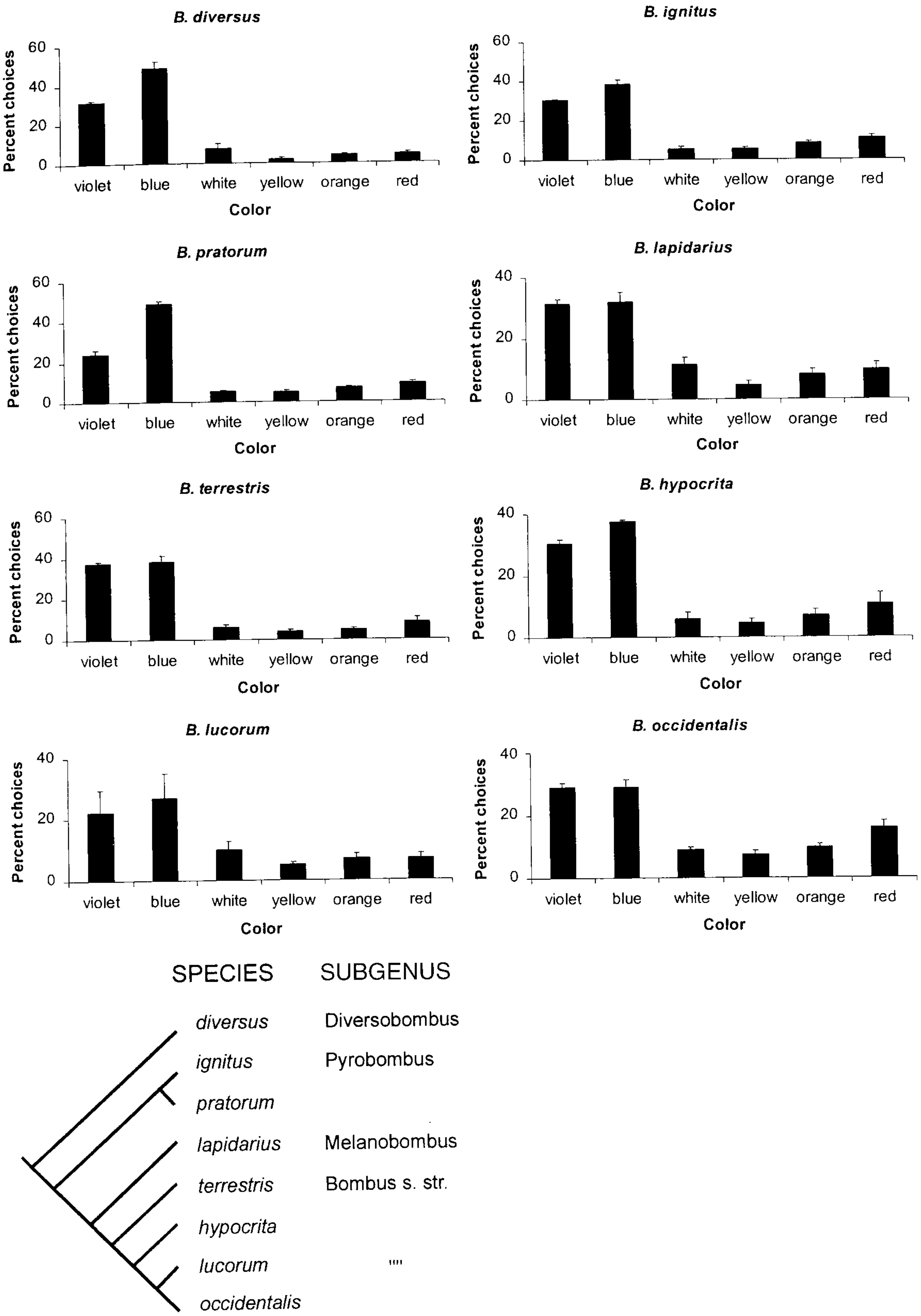
We did this by testing eight species of bumblebees from three subgenera: four from central Europe (*B. terrestris terrestris*, *B. lucorum*, *B. pratorum*, and *B. lapidarius*); three from temperate East Asia (*B. diversus*, *B. ignitus*, and *B. hypocrita*); and one from North America (*B. occidentalis*). We found that all species preferred the violet-blue range, presumably a phylogenetically ancient preference (figure 5.11). In addition, however, *B. occidentalis* had the strongest preference for red of all the mainland bumblebee populations examined. This is intriguing because this species frequently robs nectar and forages heavily from red flowers whose morphology seems well adapted for pollination by birds (Chittka and Waser, 1997; Irwin and Brody, 1999). Obviously, this red preference is derived and therefore might be an adaptation unique to *B. occidentalis*.

We also tested *Bombus terrestris terrestris* from Holland, *B. terrestris terrestris* from Germany, *B. terrestris dalmatinus* from Israel, *B. terrestris dalmatinus* from Rhodes, *B. terrestris sassaricus* from Sardinia, *B. terrestris xanthopus* from Corsica, and *B. terrestris canariensis* from the Canary Islands. The rationale for testing island populations was that islands are hot spots of evolutionary change. The effects of chance will be more manifest on islands than in large mainland populations. In addition, small populations might adapt more readily to local conditions, whereas in large populations, gene flow across long distances may prevent local adaptation. The island populations of *B. terrestris* are particularly interesting because they are genetically differentiated from each other and from the mainland population, whereas the entire mainland population, which stretches through central, southern, and eastern Europe, appears to be genetically more homogeneous (Widmer et al., 1998).

No strong differences in color preferences were found among the mainland *B. terrestris* populations; all showed the same strong preference for violet-blue shades as the other species. But some island populations showed an additional red preference (Chittka et al., 2001). In *B. t. sassaricus*, this preference is stronger than that for blue colors in some colonies and is highly significant in all colonies. In *B. t. canariensis*, four of five colonies showed a significant preference for red over yellow and orange.

Figure 5.11 ▶

The color preferences of eight species of bumblebees, with their phylogeny (P. H. Williams, 1994). Each bee was experimentally naïve at the start of the experiment, and only the first foraging bout was evaluated. Three colonies were tested per species, except for *B. terrestris*, where we tested twenty-one, and *B. occidentalis*, where four colonies were tested. The bees were individually tested in a flight arena. They were offered the colors violet (bee UV-blue), blue (bee blue), white (bee blue-green), yellow, orange; and red (the latter three are all bee green). The height that bars indicates the average of choice percentages. The whiskers indicate standard errors.


B. diversus
B. ignitus
B. pratorum
B. lapidarius
B. terrestris
B. hypocrita
B. lucorum
B. occidentalis
Percent choices
0
20
40
60
violet
blue
white
yellow
orange
red
Color
SPECIES
SUBGENUS
diversus
Diversobombus
ignitus
Pyrobombus
pratorum
lapidarius
Melanobombus
terrestris
Bombus s. str.
hypocrita
lucorum
""
occidentalis

The adaptive significance of such red preference is not easy to understand. Some red, UV-absorbing, and pollen-rich flowers exist in the Mediterranean basin, particularly the eastern part, with the highest concentration in Israel (Dafni et al., 1990). In Israel, however, bumblebees do not show red preference, and the red flowers there appear to be predominantly visited by beetles (Dafni et al., 1990).

In Sardinia, red, UV-absorbing flowers are neither more common nor more rewarding than flowers with other colors (Schikora et al., 2002). The Canary Islands harbor several orange-red flower species. These are probably relics of a Tertiary flora, and some seem strongly adapted to bird pollination (Vogel et al., 1984). Bird visitation has been observed in at least some of these species, but it is not known whether bees utilize them (Vogel et al., 1984). Thus we are left with an interesting observation: Flower color preferences are clearly variable within *B. terrestris*, but we cannot easily correlate the color preferences in different habitats with differences in local flower colors. The possibility that genetic drift has produced the color preferences in some island populations certainly deserves consideration.

To test experimentally whether a trait is adaptive, we should exploit heritable variation to see if animals that have the trait in question are in fact more efficient foragers, and, ultimately, more efficient than those that do not. To this end, we need to show that the variance we find among colonies is heritable. To examine this question, we inbred queens from colonies of different populations with their brothers. The resulting F_1 colonies were practically mirror images of their parental colonies (figure 5.12). For instance, if we cross *Bombus terrestris terrestris* from Germany with *Bombus terrestris sassaricus* from Sardinia, we obtain an F_1 with intermediate red preference. This means there is a strong possibility of doing selection experiments in which we can test the influences of directional selection (Endler et al., 2001) and then perform fitness tests.

Finally, could the peculiar long-wavelength preferences of some island bees be underlain by specialized red receptors? Schikora et al. (2002) made extracellular recordings from bumblebees from Sardinia, and found that indeed their sensitivity to long-wavelength light is significantly higher than in mainland bumblebees. This could mean that some island bees could see colors differently than their mainland relatives, as a consequence of evolutionary chance processes.

Color Learning and Foraging Decisions

In simple laboratory setups where one flower type contains a large reward and alternative flower types typically contain none, bees very rapidly learn to associate floral colors with rewards. A single rewarded visit to a color target is sufficient to induce a measurable change in behavior in honeybees and bumblebees (Schulze Schencking, 1969), and three such visits are sufficient to establish a life-long memory (Menzel, 1985). Colors are first stored in a transient short-term memory, where they are sensitive to interference, and, on repeated exposure, are stored in more stable long-term memory (Menzel, 2001). Mirroring their innate preferences (Giurfa et al., 1995), honeybees learn violet and blue colors even more rapidly than others (Menzel, 1985).

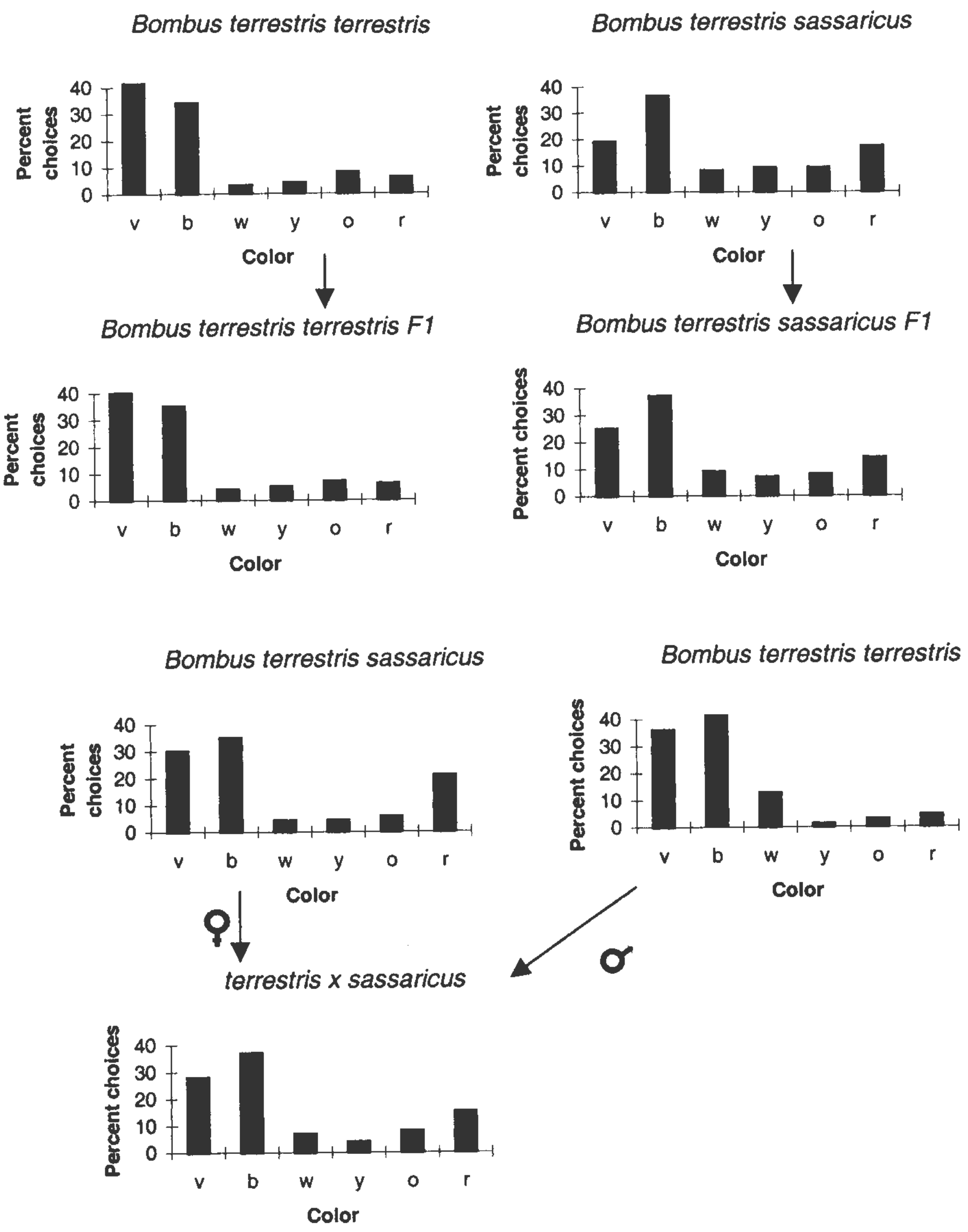


Figure 5.12
Heritability of innate color preference in *Bombus terrestris*. Individual worker bees were tested as explained in figure 5.7. (*Upper four graphs*) Queens from *B.t. terrestris* (Germany) and *B.t. sassaricus* (Sardinia) were inbred (mated with their brothers). Preferences are shown for the parental colonies and the colonies founded by the mated queens. (*Lower three graphs*) Intermediate red preference for a colony founded by a Sardinian queen mated with a German male. The preferences of the workers from the parental colonies are also shown.

Learned preferences can be rapidly reversed if the reward situation changes (Chittka, 1998).

However, when exposed to realistic situations where flowers of two or more types of different colors are intermingled and differ only gradually in rewards, bees will often choose the more rewarding flowers (Heinrich, 1979; Menzel, 2001), but there are cases in which innate preferences (Banschbach, 1994) or cognitive limitations (Chittka et al., 1999; P. S. M. Hill et al., 2001) will make bees deviate substantially from the optimal choice.

The time needed to detect flowers is strongly influenced by floral color (Spaethe et al., 2001). Thus the optimal choice of flowers is not only dependent on the reward and the handling time, but also on the search costs, which are affected by flower color. It is not known if bees take these costs into account when choosing flowers.

Bees also learn to use color to predict the variance of rewards. Tests to deduce such "risk-sensitive" foraging must involve equal average rewards, but differences in reward consistency among flower types of two colors, for example, yellow and blue. In some cases, bees have avoided the flowers with a higher variance in reward; i.e., they were "risk averse" (e.g., Cakmak et al., 1999; Waddington, 2001). The reasons for this behavior are controversial. Both mechanistic (Waddington, 2001; Chittka, 2002) and ultimate explanations (H. Wells and Wells, 1986) have been proposed. In some conditions, bees did not respond at all to reward variance (Fülöp and Menzel, 2000; Waddington, 2001). These differences in reported behavior may be due to alternative experimental designs. However, the possibility of genuine differences among populations has been left largely unconsidered. For example, when different taxa were compared under controlled conditions, differences were found not only among various *Apis* species (N. Muzaffar and H. Wells, unpublished results), but also among *A. mellifera* subspecies (Cakmak et al., 1998, 1999). Possibly the endemic taxa's environment might determine where variance-sensitive foraging occurs.

Flower Constancy

Flower constancy occurs when bees temporarily specialize on one species or morph of flower and bypass other rewarding flowers (H. Wells and Wells, 1986; Waser, 1986). Flower constancy favors an efficient and directed pollen transfer between conspecific plants (Chittka et al., 1999). Color is one important clue by which bees recognize flowers (P. S. M. Hill et al., 1997). To understand the kind of color diversity in flowers that can be expected to evolve as a strategy to promote constancy, it is critical to know the range over which a pollinator-subjective color difference is correlated with flower constancy. For example, if a barely distinguishable contrast between two flower colors can produce 100% constancy, then flower constancy may drive only small-scale color differences, such as that between two similar, but just distinguishable, shades of blue. However, character displacement across color categories, such as blue to yellow, would be harder to explain by pollinator constancy if this were the case.

Previous work allows us to predict how color discrimination improves with color distance (Chittka et al., 1992), but flower constancy and discrimination are unlikely to increase with color difference in the same way. In measuring flower constancy as a function of floral color difference, we do not ask: "How well can bees distinguish colors?" Instead, the appropriate question is: "How readily do bees retrieve memories for different flower types, depending on how similar they are to the one currently visited?" The ability to discriminate flowers sets the upper limit for constancy, but there is no a priori reason to assume that constancy is directly determined by this factor.

In order to measure flower constancy as a function of color distance between flower types, we tested six species of apid bees on fifteen pairs of plant species or color morphs of the same species, using a paired-flower, bee-interview protocol (Thomson, 1981). Even though our analysis ignores differences other than color, there is a clear relationship between bee-subjective color difference and flower constancy (figure 5.13). Constancy does not deviate from chance at color hexagon distances up to 0.1 (where bees already discriminate well between colors; A. Dyer and L. Chittka, 2004). At distances of about 0.2, constancy levels rise sharply in all pollinator species and above 0.4, constancy is generally above 80%. Thus, flower constancy is negligible at small color differences, even for some differences easily discriminated by bees; it is at its maximum only in cases of pronounced differences. In the case of such pronounced differences, such as those between yellow and blue flowers, individual honeybees will sometimes stay constant to the less rewarding flower morph without even sampling the alternative (H. Wells and Wells, 1986; P. S. M. Hill et al., 1997, 2001). But even

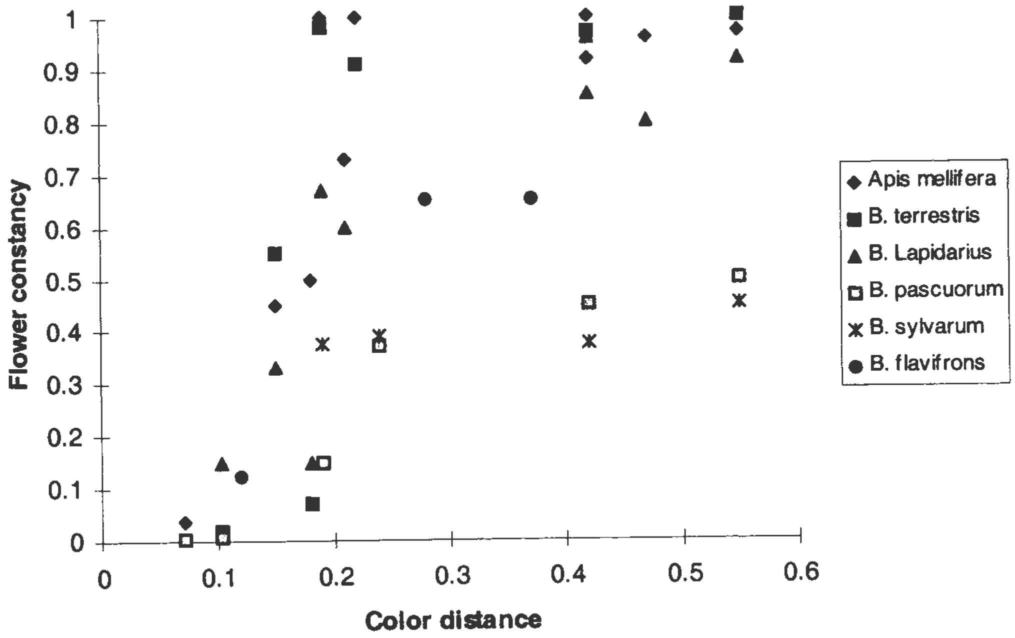


Figure 5.13
Flower constancy in several species of bees as a function of color distance between pairs of flower types. For each pair of flower types, we recorded at least eighty choices. Flower constancy data are calculated as explained in Chittka et al. (2001). (Figure reproduced from Chittka et al., 2001, with permission from Cambridge University Press.)

when rare sampling does occur, or is forced to occur, constancy results in a manner that ignores harvest rate (Hill et al., 1997).

The Relation of Flower Color with Other Cues

Floral color not only serves as a predictor of rewards but also of the particular motor pattern required to exploit flowers of complex morphology (Chittka and Thomson, 1997). In addition to this, the interactions between color and other floral cues, such as scent or pattern, are complex and often poorly understood.

In honeybees, minor changes in flower morphology or arrangement may have major effects on flower constancy, without changes in the colors of the flowers (H. Wells and Wells, 1986). Deviations in flower structure (e.g., adding pedicels; Waddington and Holden, 1979; H. Wells et al., 1986), adding a color pattern without a difference in flower structure (cf. Banschbach, 1994; P. S. M. Hill et al., 1997), and spatial arrangement (e.g., P. S. M. Hill et al., 2001) each affect behavior substantially.

Scent is clearly important in identifying flowers (Raguso, 2001), but the relative importance of scent and color depends on the particular scents and colors involved and on the individual bee (P. H. Wells and Wells, 1985). For example, in a patch of color-dimorphic flowers, some honeybees were constant to yellow and some to blue flowers when all flowers provided a clove-scented reward. The flower constancy of individual bees was not altered when the scent of all the rewards was changed to peppermint. However, when the scent of only one color morph was changed, some bees remained constant to color, whereas others switched color attachment and remained constant to odor (H. Wells and Wells, 1985). The presence of scent can also improve discrimination between rewarding and unrewarding flowers of two colors, even when both types have the same scent (J. Kunze and Gumbert, 2001).

The interaction of floral color with pattern is especially controversial (Giurfa and Lehrer, 2001). Menzel and Lieke (1983) trained bees to bicolored patterns of different orientation and found results that defied any simple explanation. Recently, Hempel de Ibarra et al. (2001) presented a center-surround model to explain how green receptor input from the retina is used in the detection of bicolored patterns. In an interesting analogy to human visual search (Desimone, 1998; Chittka et al., 1999), bees are less efficient at foraging when multiple flower types differ only along a single stimulus dimension (e.g., color), rather than along several dimensions (e.g., color, size, and pattern; Gegear and Laverty, 2001).

Conclusion

Bees, especially honeybees, have long been model organisms for highlighting how complex visual perception is achieved with miniature nervous systems. Their visual spectrum differs fundamentally from our own, as do other aspects of their vision, for example, the apparent lack of a brightness coding dimension in the bee's color space. On the other hand, bee color vision shares surprisingly many general principles with that of humans. Most bee species, just as humans, are trichromatic on the receptor level. Both humans and bees appear to use two spectrally antagonistic mechanisms for color coding. Color and motion are largely processed in parallel in humans as in well as in bees.

Because of such similarities, it was once thought that some invertebrate models might eventually help us understand neural information processing in higher vertebrates, including humans (e.g., Huber, 1983). This hope has remained largely unfulfilled, especially because research on primate color processing has progressed at such a rate that neurobiological work on insect color vision seemed comparatively frustrating. The result is that development of the field has slowed in the past decade.

We think this is unfortunate because the study of color vision in bees has tremendous potential in its own right. In no other organisms do we have as profound an understanding of color used in natural foraging as we do in bees. If we wish to understand how color vision evolves, both as a result of adaptation and chance, bees are a magnificent model system, as we hope to have shown in this review. Primates, conversely, are simply not as amenable to selection experiments and fitness tests as are bees. Other organisms, such as *Drosophila*, offer a wider variety of mutants of the visual system, but testing their fitness under biologically relevant conditions (i.e., natural densities of food, predators, and mates) is virtually impossible, whereas it is straightforward in bees. It is for these reasons that we must continue to study the mechanisms of postreceptor color processing in bees as well. For if we have no information on differences in such processing among species, populations, and individuals, we have nothing to study if we are asking questions about adaptation to the environment. We think that recognizing these shortfalls in our knowledge, rather then resting on what has already been achieved, will bring us much closer to a comprehensive understanding about color vision in the animal kingdom.

Acknowledgments

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