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Recognition of flowers by pollinators

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The flowers of angiosperm plants present us with a staggering diversity of signal designs, but how did this diversity evolve? Answering this question requires us to understand how pollinators analyze these signals with their visual and olfactory sense organs, and how the sensory systems work together with post-receptor neural wiring to produce a coherent percept of the world around them. Recent research on the dynamics with which bees store, manage and retrieve memories all have fundamental implications for how pollinators choose between flowers, and in turn for floral evolution. New findings regarding how attention, peak-shift phenomena, and speed–accuracy tradeoffs affect pollinator choice between flower species show that analyzing the evolutionary ecology of signal–receiver relationships can substantially benefit from knowledge about the neural mechanisms of visual and olfactory information processing.

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Introduction

Our rationale for this article is that many plant biologists are hard-pressed to keep up with developments in the rapidly expanding fields of pollinator neuroethology and psychophysics. Here, we review recent developments from sensory biology, neuroscience, and psychophysics, as they pertain to the processing of floral signals by pollinators. We focus on bees, as they are the most studied pollinators in this respect, especially the relevance of color vision and olfaction for floral recognition and, in turn, their implications for floral evolution. We do not cover pattern vision [1,2], tactile cues [3], or the question of how reward properties of flowers might co-evolve with pollinator cognition [4]; these topics have been addressed in detail elsewhere [1–4].

One way to explain the diversity of flower signals is to use the concept of pollination syndromes, which holds that

particular classes of pollinators are specifically associated with particular floral traits, including floral color [5]. There has been empirical support for this hypothesis in some cases, for example the association of red flowers with hummingbirds [6]; also many species of solitary bees appear to have particular affinities with certain plant species [5]. Here, we are concerned with generalist flower visitors, such as honeybees and bumblebees. These bees have to choose adaptively between multiple plant species all differing in color, pattern and scent; as they fly over a meadow, they might sequentially or simultaneously encounter flowers from several different species each second, and have to juggle multiple memories (from different sensory modalities), some from the immediately preceding experience and some from the more distant past. These social bees are often abundant and important pollinators, and their strategies in choosing flowers will therefore generate strong selection pressures on flowers to optimize their signals. Relatively subtle changes in floral characters, even those produced by a single mutation, can substantially affect pollinator behaviour [7,8] — but what are the mechanisms by which pollinators perceive these changes, and what are the resulting selective pressures for plants?

Should flower species that bloom simultaneously in the same habitat diverge or converge in color, depending on their local abundance [9]? Should rewardless orchids converge, in color and scent, on a common rewarding model species [10••]? Answering these questions requires an understanding not only of how bees perceive floral color and scent but also of how they integrate input from distinct sensory modalities, match incoming stimuli with previously memorized information, and can use selective attention in the face of multiple conflicting stimuli.

The spatial resolution of the bee eye

Bee eyes are composed of several thousand functional units, the ommatidia, each containing its own lens and set of photoreceptors [11,12]. The resolution of compound eyes is about 100 times worse than ours: for example, in honeybees, the resolving power of the ommatidial array is approximately 1° [12]. But the spatial resolution of bee vision is limited not only by the interommatidial angle but also by subsequent processing. The receptive fields of color-coding neurons, as inferred from behavioral studies, are comparatively large, so that an area of 15° (equivalent to 59 ommatidia of the compound eye [1]) must be subtended for a honeybee to identify a flower by its color. Thus, from a distance of 1 m, a flower must be enormous (26 cm in diameter) to enable a bee to either recognize its color or detect it using color contrast! But bees are able to use a different neuronal channel with a smaller receptive

field when they are further away from a flower. When a flower is seen in an area subtending at least 5° (and no more than 15°), bees employ green contrast for detection: that is, the difference in signal provided by the green receptor between background and target [1,13]. This still means, however, that a honeybee must be no more than 11.5 cm from a 1 cm diameter flower to detect it! This severely constrains the rate at which flowers can be found. Accordingly, search time decreases strongly with increasing flower size over a biologically realistic range [13]. This poor visuo-spatial resolution also means that some fine-grained visual aspects of floral patterning that are obvious to humans may simply be invisible to pollinating bees [14].

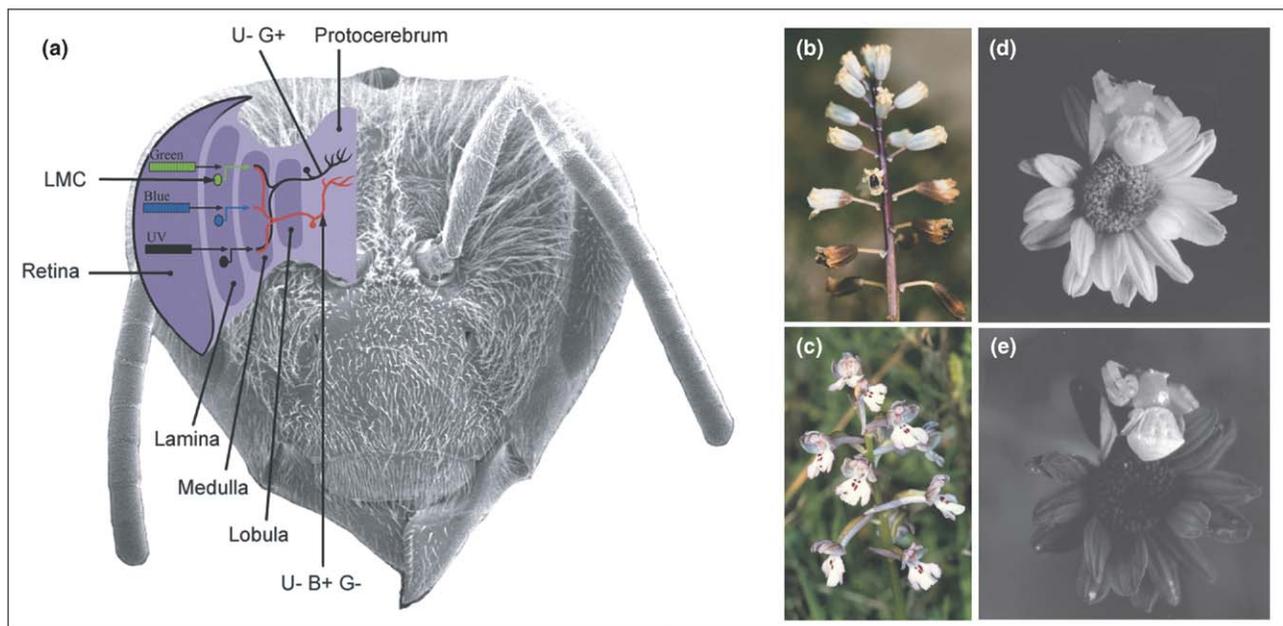
Bee color vision and perceptual color space

In the early 1990s, the question of how the bee visual system codes color appeared largely resolved. It was thought that all ommatidia (except those in the dorsal margin area) contained an identical set of spectral receptor types: three UV, two blue and four green receptor cells [15]. In this view, every ommatidium contained the equipment necessary to analyze a 'pixel' in the bee's

visual field for its spectral input. It now appears that color coding in the bee visual system is substantially more complicated. Each ommatidium contains six green receptor cells [16], that is, the types of receptors that are responsible for motion vision and small target detection [1,11]. However, the sets of other color receptor types vary, so that there are three types of ommatidia, which contain either two UV, or two blue, or one UV and one blue receptor [16,17]. This means that two neighboring ommatidia, looking sequentially at the same spot in space, might see it in different colors.

To code color independently of intensity, the nervous system has to compare the signals from receptors that differ in spectral sensitivity by means of so-called color opponent cells (Figure 1). Two types of such color opponent neurons were identified in the honeybee brain in the early 1990s [15]. However, this relatively simple and attractive view of color coding needs to be revised because it is now known that at least seven different types of color opponent neurons exist in the bee optic lobes [18]. How the brain identifies color targets, such as flowers, with such a seemingly chaotic retina and neural

Figure 1



Understanding neuronal color processing in the bee brain allows us to quantify the bee-subjective similarity between biologically relevant objects. (a) Frontal view of a bee's head (scanning electron micrograph) showing essential features of color coding in the brain. Information from the UV, blue, and green receptors is relayed from the first optic ganglion (the lamina) to the second optic ganglion (the medulla) by so-called monopolar cells (LMCs); cell bodies are symbolized by filled circles. These cells feed into color opponent cells (drawn in red and black) that are found both in the medulla and lobula, either directly or via interneurons. Chromatic opponent cells receive antagonistic input from the different color channels, and project to the protocerebrum [15]. Modified from Chittka and Brockmann [19]. Modeling bee color vision on the basis of the neuronal circuitry of color coding makes it possible to assess how pollinators actually perceive the similarity between a rewarding flower species, in this case (b) *Bellevalia flexuosa*, and (c) its putative mimic, the orchid *Orchis israelitica* [10**]. (From [10**] with permission from the authors and publisher.) (d) The white crab spider *Thomisus spectabilis* lying in wait for pollinators on *Chrysanthemum frutescens* flowers is cryptic when viewed in the human visible spectrum, but knowing how bees integrate information from UV receptors with that from other receptors allows precise predictions of spider color similarity with the substrate. (e) The same spider is highly conspicuous when viewed under UV light and is thus not cryptic for bees [46]. (From [46] with permission from the authors and publisher.)

coding remains to be determined. However, any combination of two color opponent neurons can be used to code input from three types of color receptor [19[•]]. It is thus possible that the precise mechanisms of color opponent coding are not genetically determined but are 'learned' by de-correlating the inputs from different receptor types through experience [20]. Color discrimination can be modeled, at a behavioral level, by assuming that color is coded using only two color opponent mechanisms [19[•]]. This has led to the development of a two-dimensional color opponent space, that is, a perceptual space that can be drawn out in the form of a map allowing us to visualize a bee's subjective colored view of the world. Such a map allows us to predict the similarity of two stimuli (e.g. two colors) by inspecting the distance between the loci they produce in a perceptual space, and helps us predict precisely how well a bee will be able to distinguish two flower colors [19[•]].

Flower odor similarity and the bee's perceptual odor space

Can the concept of perceptual spaces be applied to odor perception? This would seem a daunting task, given that the number of different types of odor receptors in bee antennae is not three, as in color vision, but at least 130 (H Robertson, pers. comm.). Nevertheless, recent research indicates that a low-dimensionality odor space can be used to predict perceptual odor similarity, and thus can be used to predict the accuracy with which bees choose between floral scents [21^{••}]. To construct such an odor space, we first need to understand how the brain makes sense of the diversity of scents encountered in nature (Figure 2).

Axons from like receptor cells (i.e. those that express the same receptor protein and therefore bind the same odorants) project to one or a few glomeruli. Glomeruli are globular, anatomically distinct subunits of the antennal lobes and form the first neuronal centre of olfactory information processing. The honeybee's antennal lobe contains 160 glomeruli [22]. Individual chemicals reliably activate sets of identified glomeruli, and glomeruli coding for similar substances are located close together in the antennal lobes, whereas those that code for distinct scents are spatially segregated [22].

But does the neuronal activity map of the antennal lobe correspond to the olfactory perceptual space? On a behavioral level, how many axes must the olfactory perceptual space have so that distances between odors can be used to predict how similar those odors will appear to bees? It appears that the multidimensional receptor space might be collapsed onto very few perceptual axes because many of the odor similarity judgments can be explained by a three-dimensional space [21^{••}]. The most important axes spread out scents according to carbon chain length and functional group, that is, they separate primary and

secondary alcohols, aldehydes, and ketones. Distances between odor loci in this three-dimensional space correlate well with odor discriminability [21^{••}]. This means that we now have quantitative tools to predict how similar two floral scents, for example those of a rewardless orchid mimic and its putative model, will be perceived [10^{••}].

Speed-accuracy tradeoffs in flower choice

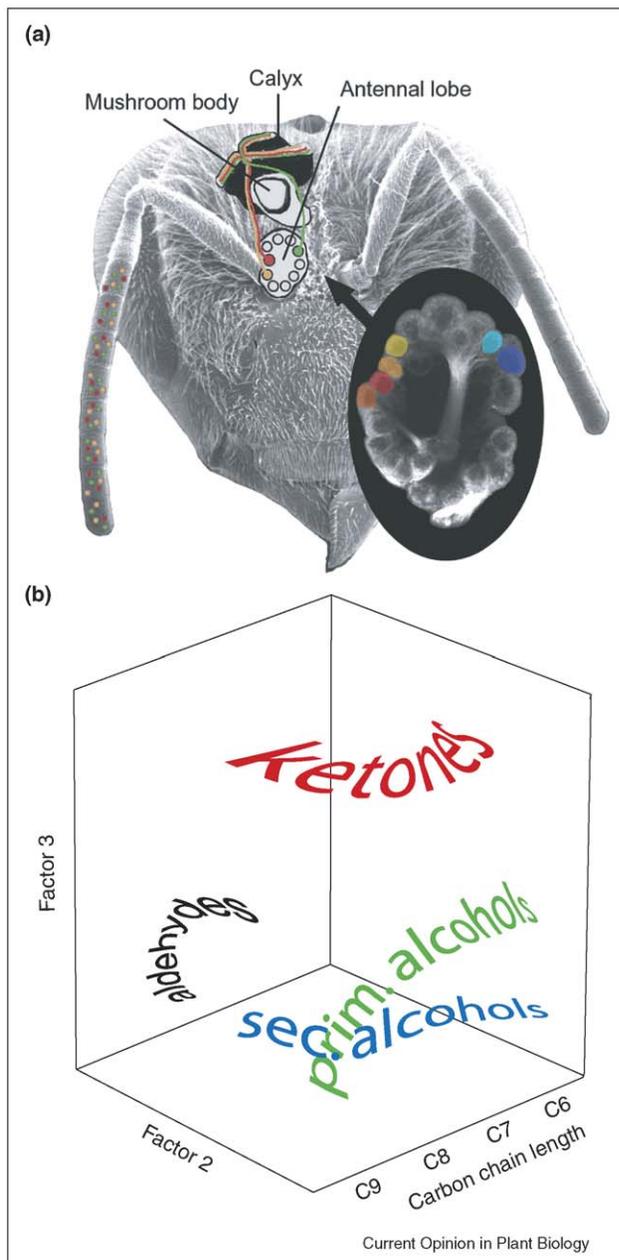
Foraging bees continually face decisions about which flower species, of the many on offer, they should visit; but is it always better to choose correctly? Behavioral scientists often assume that animals faced with a discrimination task always do their best, and that one can therefore extrapolate from their performance levels to the underlying neuronal mechanisms ultimately constraining performance. Recent work suggests, however, that bees can modulate their response time to solve problems depending on the perceived difficulty and context of a task, so trading off the accuracy and speed of their choices [23,24]. Potentially then, focusing solely on choice accuracy might lead us to misconstrue the optimal behavioral strategy in a given discrimination task. Chittka *et al.* [23] trained bumblebees to two very similar colors of computer-generated 'virtual flowers'. Measuring both choice accuracy and decision speed, they found pronounced differences between bees: the more time an individual invested in deciding between the rewarded and distractor flower colors, the more accurate her choices. The fast, error prone bees remained fast and error prone even under conditions when the cost of errors was increased by pairing an aversive stimulus (quinine) with the distractor color. Interestingly, the decision accuracy of all bees went up significantly with the introduction of these penalties. So, if bees can make more accurate choices than they do in the absence of penalties, does the low accuracy shown by bees making quick decisions represent an adaptive foraging strategy?

Using the same data set, Burns [25^{••}] found that when the cost of investigating flowers is low, bees making fast-inaccurate decisions would collect nectar at a higher rate than bees taking longer to make more accurate choices. This work highlights the fact that accuracy alone is not necessarily the best correlate of efficiency (or a good means by which to assess underlying decision mechanisms), and it suggests that previous studies in which accuracy was the only performance measure recorded could require re-interpretation.

Peak shift and signal evolution

When learning to associate a particular color with reward, bees generalize to some extent by choosing similar colored flowers. The generalization pattern is typically normally distributed with maximum response corresponding to the trained color (Figure 3). However, following some training conditions, animals might display a preference for a novel color that they have not been

Figure 2



Neural odor coding and odor space in bees. **(a)** Schematic view of odor processing in the honeybee brain. Some 60 000 odorant receptor cells are distributed along the antenna. These belong to several different types (illustrated with different colors), each responsive to a different set of chemicals. Axons from like receptors project to one or a few glomeruli in the antennal lobe [22]. The glomerular map is organized so that similar odors are mapped to nearby spatial locations (shown here in pink and red), whereas dissimilar odors stimulate glomeruli that are located further apart (green). The inset shows a confocal microscope image of the antennal lobe (courtesy of A Brockmann), with glomerular structures clearly visible (similar colors indicate response to similar scents). Axonal projections extend from the antennal lobe to higher processing centers, such as the calyx of the mushroom body. **(b)** Putative three-dimensional odor space for bees. Guerrieri *et al.* [21**] trained bees to associate one of 16 odors with a sucrose reward and then faced bees with the other 15 odors to see how similarly bees judged these to the training odor.

exposed to during training, and this 'peak shift' phenomenon has recently been found in bumblebees [26**]. When bees are exposed to two similar flower colors, one of which is associated with reward (S+) while the other is penalized with NaCl solution (an aversive stimulus: S-), they preferentially select a novel flower color, with their peak response shifting from the color rewarded during training in the direction away from the penalized color (Figure 3). Peak shift was augmented by either increasing the risk of choosing the unrewarded flower color (either by decreasing the relative abundance of S+ flowers or by making S+ flowers more variable in color), or by decreasing the quality of reward offered by flowers during training [26**]. Thus, Lynn *et al.* [26**] suggest that peak shift could potentially drive the evolution of floral character when the risks and costs to pollinators of misidentifying flower species are high. In such scenarios, for example in Batesian mimicry systems, pollinators should show peak shift towards the color variants of the rewarding species that are least similar to unrewarding plants. Under uncertain conditions, novel flowers types that are easy to identify accurately are predicted to be at a pollination advantage. Thus, Batesian mimics could affect model evolution through the effects of signal-borne risk on flower visitation decisions. Peak shifts that result from unrewarding flowers under natural conditions are, however, likely to be smaller than those produced by penalties. The presence of penalties affected the way bees responded to positive stimuli in both the speed-accuracy and peak-shift studies. Perhaps predation risk from crab spiders represents an ecologically feasible penalty in such cases [27].

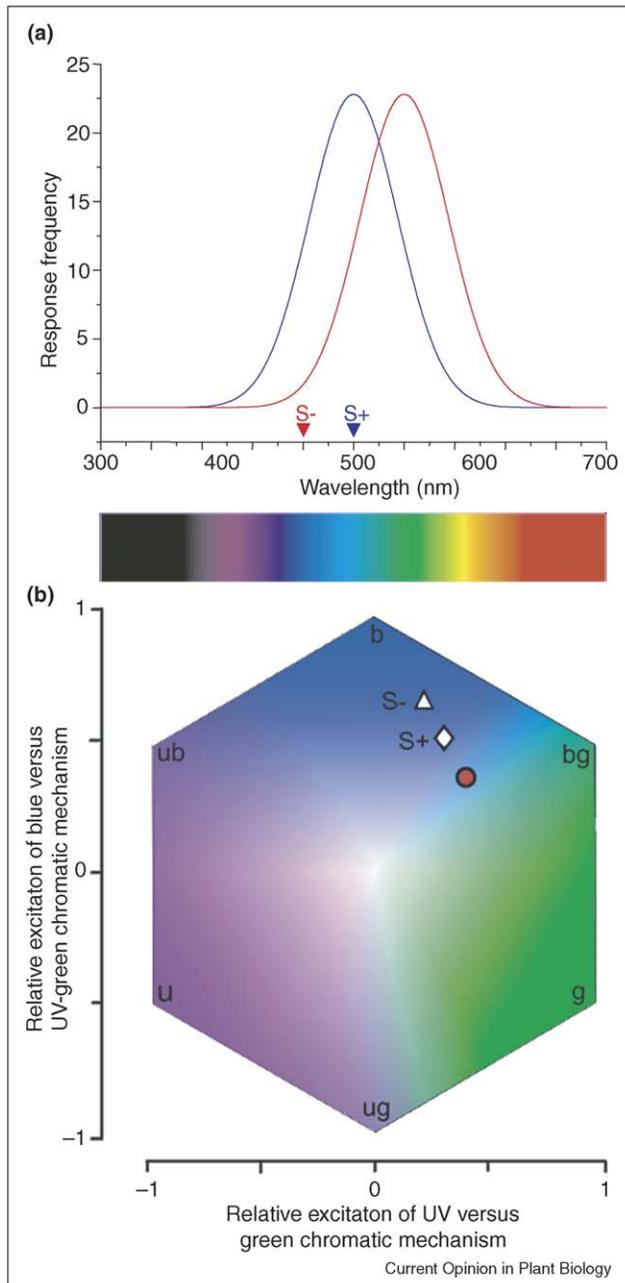
This work also highlights the fact that receiver cognitive processes, as well as sensory systems, must be considered when analyzing the evolution of signaling systems (e.g. floral displays). Although response biases, such as peak shift, might represent constraints resulting from the neural system organization or development, it seems increasingly likely that they represent strategies for discriminating stimuli that are susceptible to natural variation [28].

Attention

In most animals, the amount of information perceived by peripheral sensory systems exceeds the brain's information processing capacity by several orders of magnitude [29]. Attention is a kind of 'inner eye' that allows animals to focus selectively on different aspects of information

Distances between these substances in a three-dimensional space predict the bee-subjective similarity of the odors. The most important axis corresponds to the carbon chain length of the substances tested; the other two dimensions separate substances according to functional group. Each word illustrates the spatial distribution of a group of substances with like functional group but varying in chain length (after Chittka and Brockmann [19*], modified).

Figure 3



Stimulus generalization and peak shift in a color discrimination task. **(a)** Bees trained to a rewarding flower color (positive reinforced stimulus [S+]), respond most strongly to this same color when presented with a range of similar colors (blue curve). However, they also generalize these choices to other colors similar to S+, with the more similar colors chosen with higher probability (the typical generalization curve is bell shaped [blue curve]). If bees experience a similar color (S-) that they are penalized for choosing in addition to S+ during training, they will preferentially select a novel color when tested with a range of similar colors [26**]. This novel color is shifted from S+ in a direction away from S- (red curve). Thus, the peak response has shifted in response to experiencing S- during training (compare blue and red curves). (Note that generalization in color vision, in reality, is much less broad in bees than shown here for didactic purposes). **(b)** Color opponent space for bees, where axes correspond to excitation values of two types of color

coming from the sensory periphery. Consider the ‘cocktail party effect’, which allows you to focus on a single voice out of many talking in a room, or the young mother, who wakes at the slightest sound of her newborn while ignoring all other, even much louder, noises [30]. Do insects pay attention? Recent neurobiological [31] and behavioral findings [32**] indicate that, indeed, attention might be an important factor in determining how insects respond to visual stimuli. In terms of pollinators seeking out flowers of a particular species while ignoring others, it is essential to determine whether they can process all the stimuli that they encounter by means of parallel or serial processing. If information processing is serial (i.e. one ‘bit’ of incoming information is analyzed at a time) then the efficiency of finding a target flower will be constrained by how many other items (‘distractors’) are simultaneously present in a scene. If, however, processing is parallel, flowers of multiple species can be examined simultaneously.

Indeed, in a new study on honeybees, it was found that search for visual targets that differ in color (but not pattern, size, or movement) was strictly serial [32**]. This means that the accuracy and time with which a target was found depended on the number of distractors that were simultaneously presented in the target’s vicinity. This contrasts with human subjects who can examine stimuli in parallel if targets and distractors differ only in one stimulus dimension (e.g. color or shape). The target is said to ‘pop out’, and search time or accuracy are unaffected by the distractors that are also present in the scene [32**]. If bees are indeed limited to serial searching, this should have fundamental implications for flower search under natural conditions, because it means that the efficiency with which bees find flowers is not only constrained by parameters inherent to the target flowers (e.g. size, color and contrast to the background) but also by those of other (potentially competing) flowers in the same area. Common flowers could impair the fitness of rare flowers not just via mechanisms of optimal foraging but also because of the attentional limitations of pollinators.

Working memory dynamics

When foraging in a habitat that has several flower species, bees often make sequences of visits to flowers of one species, before switching to another species to which they will then stay temporarily faithful [33]. It has long been

opponent neurons. Hexagon corners correspond to maximum excitation of the UV (u: lower left), blue (b: top), and green (g: lower right) photoreceptors. Angular position in this space (as measured from the centre) corresponds to hue, whereas distance between color loci corresponds to perceived similarity. The training stimuli, S+ (white diamond) and S- (white triangle) differ only in the extent to which they excite the blue and green photoreceptors. The red circle illustrates the shifted peak response of bees exposed to both S+ and S- flower colors during training. These bees choose flowers that excite the green photoreceptors relatively more strongly than does S+.

hypothesized that such flower constancy might be based on the dynamics of working memory [34]. In contrast to the more durable and higher capacity storage of long-term (or reference) memory, working memories are short lived (usually from seconds to minutes) and volatile: they rapidly decay even without interference, and can be relatively easily erased by competing information. Your working memory is active when you read a new telephone number, dial it, and then forget it.

The early evidence that working memory dynamics govern foraging was circumstantial. In studies with natural flowers, bees showed highly stereotypical times when flying to flowers of the species just visited [34]. These flights were most commonly 2–4 sec in duration, almost never more than 8 sec, and surprisingly independent of the spatial distribution of flowers. Thus, it was conjectured that flight times were determined not by external factors, such as distances between flowers, but by working memory dynamics. It was thought that the signal of the previously encountered flower was held in working memory for a few seconds, and if newly incoming stimuli matched this signal, the bee would visit another flower of the same species. A few seconds later, after working memory has decayed, they might retrieve older memories for different flower species [34,35].

This theory has received recent support from experiments in which the distance, and hence flight time, between two sequentially encountered stimuli was rigorously controlled [36**]. Bees flying through a tunnel encountered a visual pattern *en route*. Later, when reaching the end of the tunnel, they had to remember which pattern they had seen to decide whether to steer left or right. The authors found almost exactly the same working memory dynamics as those recorded in the earlier study, where distances between food sources were not controlled. Recall was best in the first few seconds after encountering the first visual pattern, and working memory had largely decayed by 8 sec [36**] — precisely the same dynamics as in the field trials [34]! In those first few seconds, working memory was surprisingly robust to interference: bees didn't easily forget the first pattern before reaching the end of the tunnel, even if they encountered a second pattern *en route*. This could mean that some aspects of bee foraging behavior might be better explained by neural information processing dynamics than by optimality arguments [35].

Conclusions and future directions

Pollination systems are biological markets in which animals choose between 'products' (flower species) on the basis of quality (e.g. nectar sugar quantity), and in which plants might compete for 'customers' (pollinators) [37]. It is now clear that flower visitation (and therefore plant fitness) can be affected by multiple factors that are beyond the control of the individual plant or species.

Phenomena related to speed–accuracy tradeoffs, peak shift, attention and memory dynamics all mean that a particular plant's success will depend not only on the efficiency of its own signal but also on the efficiency of the signals of other species in the vicinity, as well as their relative abundance, distribution and degree of spatial intermixing. In view of this, it might not be surprising that the question of whether sympatric plant species have influenced each others' signal evolution has been difficult to answer [38], although there has been some success in linking the adaptive significance of flower signal evolution within species with pollinator sensory processes and cognition [39]. One promising avenue of research is the exploration of how bees integrate signals from different modalities, such as olfaction and vision, for adaptive foraging behavior [40,41]. With the advent of new methods to quantify similarity in these different sensory modalities, this should become increasingly feasible [10**].

There are good theoretical arguments to conjecture that common and rewarding plants should diverge in signal from sympatric plants, so as to facilitate memorization by pollinators [9]. Rare or non-rewarding plants, conversely, might fare better by converging on more common and rewarding species in the same habitat [9,10**,38]. Given recent advances in the tools used to quantitatively predict the similarity of two flowers in a bees' perception, we can now subject these hypotheses to rigorous testing. It has long been hypothesized that the flowers of some rewardless orchids have converged on local, rewarding plants, so that pollinators mistakenly visit the orchid 'mimic' after they have learnt that the model is rewarding [42]. Using state of the art technology, Galizia *et al.* [10**] have recently quantified the perceptual similarity between such a rewardless orchid, *Orchis israelitica*, and its putative model, the lily *Bellevalia flexuosa*, both in terms of color vision and olfaction. Despite the relatively crude similarity of the two species in terms of shape, limited similarity in terms of color (both species are white and UV absorbing), and no similarity of scent (on either the chemical level or the activation pattern of glomeruli in the antennal lobes), bees nevertheless switch between the two flower species [42].

It would perhaps be premature, however, to conclude that the orchid must have undergone evolutionary change to become more similar to the rewarding model [10**]. To show evolutionary adaptation, we must pit the measured similarity against that produced by a realistic null model — in other words, how likely is that the observed similarity might have been achieved by random pairing of species [9]? Indeed, white, UV-absorbing (typically bee blue-green) flowers are the most common in practically all temperate European and Mediterranean habitats [43]. Hence, wherever we place *Orchis israelitica*, we are likely to find a 'model' that is similar in terms of floral reflectance. But this would not, in fact, involve convergence by

the orchid on a model: an orchid with a common color can be fairly sure to find itself in the vicinity of other flowers with similar color.

This toolbox will be applicable to many aspects of how animals, including phytoparasites and herbivores, interact with plants. For example, there is a recent debate on whether 'bright' red and yellow autumn foliage colours might be signals to aphids, indicating the strength of defence mechanisms of trees [44]. This debate could substantially benefit from considering aphid visual perception, and the question of whether red leaf colours might in fact be cryptic, rather than 'bright', for aphids. Similarly, the methods by which herbivorous insects locate suitable targets by means of chemoreception, comparing complex bouquets of incoming sensory information with memorised or innate templates of rewarding targets' scents, would surely benefit from understanding olfactory attention and memory dynamics [45]. In conclusion, the toolbox of the neurobiologist must be paired with that of the evolutionary biologist if we are to successfully identify patterns of floral signal evolution.

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Free journals for developing countries

The WHO and six medical journal publishers have launched the Health InterNetwork Access to Research Initiative, which enables nearly 70 of the world's poorest countries to gain free access to biomedical literature through the internet.

The science publishers, Blackwell, Elsevier, Harcourt Worldwide STM group, Wolters Kluwer International Health and Science, Springer-Verlag and John Wiley, were approached by the WHO and the British Medical Journal in 2001. Initially, more than 1500 journals were made available for free or at significantly reduced prices to universities, medical schools, and research and public institutions in developing countries. In 2002, 22 additional publishers joined, and more than 2000 journals are now available. Currently more than 70 publishers are participating in the program.

Gro Harlem Brundtland, the former director-general of the WHO, said that this initiative was "perhaps the biggest step ever taken towards reducing the health information gap between rich and poor countries".

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