

SEEING IN COLOUR: A HUNDRED YEARS OF STUDIES ON BEE VISION SINCE THE WORK OF THE NOBEL LAUREATE KARL VON FRISCH

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ABSTRACT: One hundred years ago it was often assumed that the capacity to perceive colour required a human brain. Then in 1914 a young Austrian researcher working at Munich University in Germany published evidence that honeybees could be trained to collect sugar water from a ‘blue’ coloured card, and find the colour among a number of different shades of achromatic grey. Von Frisch thus established honeybees as an important model of sensory processing in animals, and for work including his demonstration that bees used a symbolic dance language, won a Nobel Prize in 1973. This work led to the establishment of several research groups in Germany that developed a rich understanding of how bee vision has shaped flower colour evolution in the Northern Hemisphere. Applying these insights to Australian native bees offers great insights due to the long-term geological isolation of the continent. Australian bees have a phylogenetically ancient colour visual system and similar colour perception to honeybees. In Australia similar patterns of flower colour evolution have resulted and provide important evidence of parallel evolution, thanks to the pioneering work of Karl von Frisch 100 years ago.

Keywords: biogeography, climate, flower, photography, pollinator

The contribution of knowledge from German science has been instrumental in the development of many building blocks of the Australian scientific community, including the establishment of the Royal Botanical Gardens in Melbourne, Victoria, with key input from pioneers like Ferdinand von Mueller. Von Mueller was appointed Victoria’s first Government Botanist in 1853, and he established the National Herbarium of Victoria the same year before being appointed Director of the Royal Botanic Gardens in 1857. Until his retirement in 1896, his vision for the gardens as a centre for plant research led to the construction of a live plant house, including plantation of conifers and first giant water lily flowers in 1867 in Melbourne. The state botanical collection is historically and botanically a significant component for a majority of Australian material and also includes a considerable component of foreign collected material (Pescott 1982). Today, the fully established gardens provide a valuable resource for plant science research.

This resource has recently been instrumental in solving contemporary questions about flower evolution and allowing for continued research on what might happen in a rapidly changing world. Bee vision is currently the best understood model of how pollinators visually search for flowers, largely thanks to the seminal work of the Nobel laureate Karl von Frisch at the University of Munich in

Germany 100 years ago (von Frisch 1914, 1967). This work subsequently led to many investigations on bee vision over the past century (Dyer & Arikawa 2014) that serve as a solid basis for current advances in our understanding about flower evolution.

Seeing in colour is one of the most widely appreciated aspects of human perception, and indeed colour has been an important tool for scientific investigation for fields as diverse as physics, chemistry, biology and human communication (Hurvich 1981; Lee 2005). However, 100 years ago it was widely assumed that colour perception should not be possible for insects with constrained neural processing capabilities (von Hess 1913; Dyer & Arikawa 2014). Karl von Frisch trained honeybees to collect a sweet-tasting sugar solution associated with a coloured card. The bees then continued to choose the colour even if the appetitive sugar solution was removed, and the coloured card was presented beneath glass and among a variety of grey cards (Figure 1) that should present equivalent achromatic (‘brightness’) cues (von Frisch 1914); see Chittka et al. (2014) for a recent review. This experiment opened the eyes of the world to experiments with honeybees, and over the course of the twentieth century it was shown that bees can: (a) perceive ultraviolet wavelengths beyond our visual experience (Kühn 1927); (b) possess colour learning capacity (Menzel 1967; von Helversen 1972; Giurfa 2004;

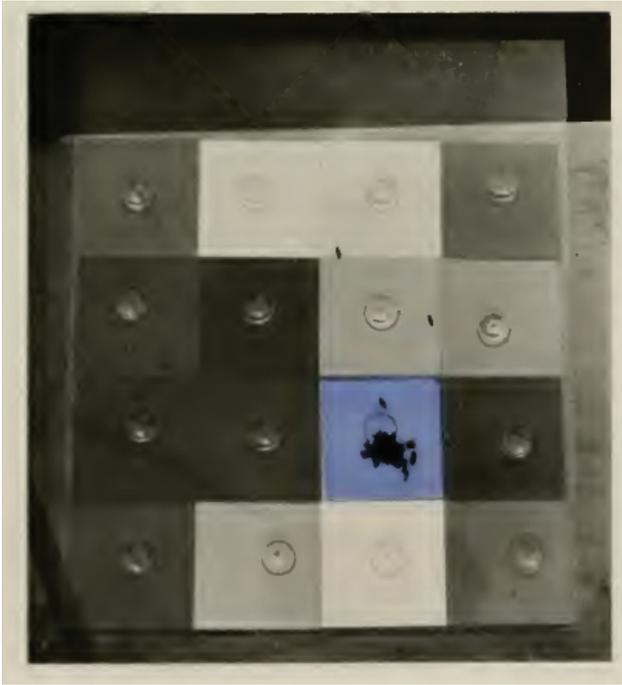


Figure 1: Example of one experimental test to show that bees could discriminate colour information independent of achromatic brightness cues. Bees were initially rewarded with sugar solution presented within an inverted watch glass dish, and then provided with a control transfer test where sugar solution was removed and cards were replaced by new stimuli to exclude olfactory cues. In other controls, glass was also used to cover stimuli to exclude olfactory or chemosensory cues. Modified versions of this experiment are still used to test whether different bee species or other animals have colour perception (Spaethe et al. 2014). Photograph reproduced from von Frisch (1914).

Avarguès-Weber et al. 2010; Reser et al. 2012); and (c) have a trichromatic colour experience based on ultraviolet, blue and green photoreceptors (Daumer 1956; Autrum & von Zwehl 1964; Peitsch et al. 1992), somewhat analogous to human trichromatic vision which is based on blue, green and red photoreceptors (Figure 2). Of particular importance was work by von Helversen (1972) who measured the capacity of honeybees to discriminate differences in the wavelength of electromagnetic radiation across their visual spectrum, and showed that bees best discriminate wavelengths at about 400 and 500 nm where the ultraviolet, blue and green photoreceptors overlap (e.g. Figure 3). The reflectance curve slope midpoints of flowers cluster in those ranges of wavelength for which discrimination is best, and this close fit is well explained by flowers' colours adapting their spectral signals to bee pollinator vision (Chittka & Menzel 1992; Dyer et al. 2012).

An important principle of studying signal-receiver interactions is visual ecology (Lythgoe 1979; Wolf 2002), where the characteristics of an animal's vision may influence, or be influenced by, the environment in which particular animals operate. Since flowering plants (angiosperms) often rely on animal vectors to facilitate

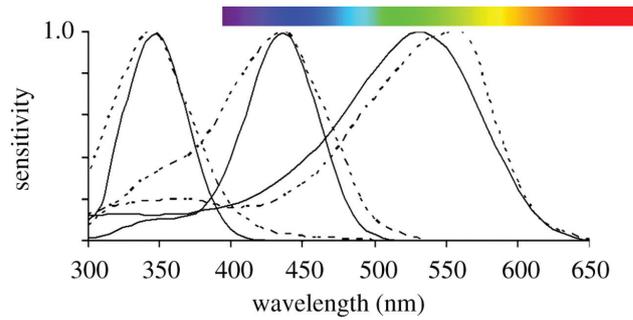


Figure 2: Electrophysiological recordings of the sensitivity of the bee eye to different wavelengths of radiation show most bees have a phylogenetically conserved set of three photoreceptors that contribute to colour perception (Peitsch et al. 1992). For example, the honeybee (*Apis mellifera*) [dotted line] and bumblebee (*Bombus terrestris*) [solid line] each have three photoreceptors maximally sensitive in the 'UV' at about 350 nm, the 'blue' at about 440 nm, and the 'green' at about 540 nm. Consistent findings for bumblebees have also been recently reported considering a larger sample size (Skorupski et al. 2007). For comparison, the horizontal bar represents how humans normally perceive spectral light (Lee 2005).

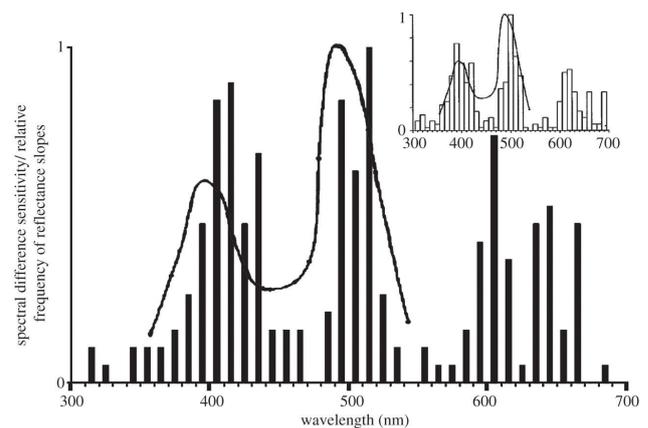


Figure 3: Relative frequency distribution of Australian native plant flowers having reflectance curve slope midpoints (black bars) compared with the inverse $\Delta\lambda/\lambda$ wavelength discrimination function (solid curve) of the honeybee (von Helversen 1972). The insert shows data for flowers from a previous study in Israel (Chittka & Menzel 1992). Australia is geologically well separated in space and time from the rest of the world and has a distinctive bee fauna. The data thus suggest parallel evolution of many angiosperm flower signals to suit the part of the spectrum that is best processed by hymenopteran trichromats (Dyer et al. 2012).

sexual reproduction through the transport of pollen between conspecific plants (Barth 1985), pollinators' vision may also exert a strong influence on signal evolution. For example, natural selection may favour the expression of signals that best attract the attention of the most efficient pollinators in an environment. The interpretation of colour signals by honeybees is one of the best studied models of animal perception, with sophisticated computer models to allow for interpretations of signal-receiver interactions

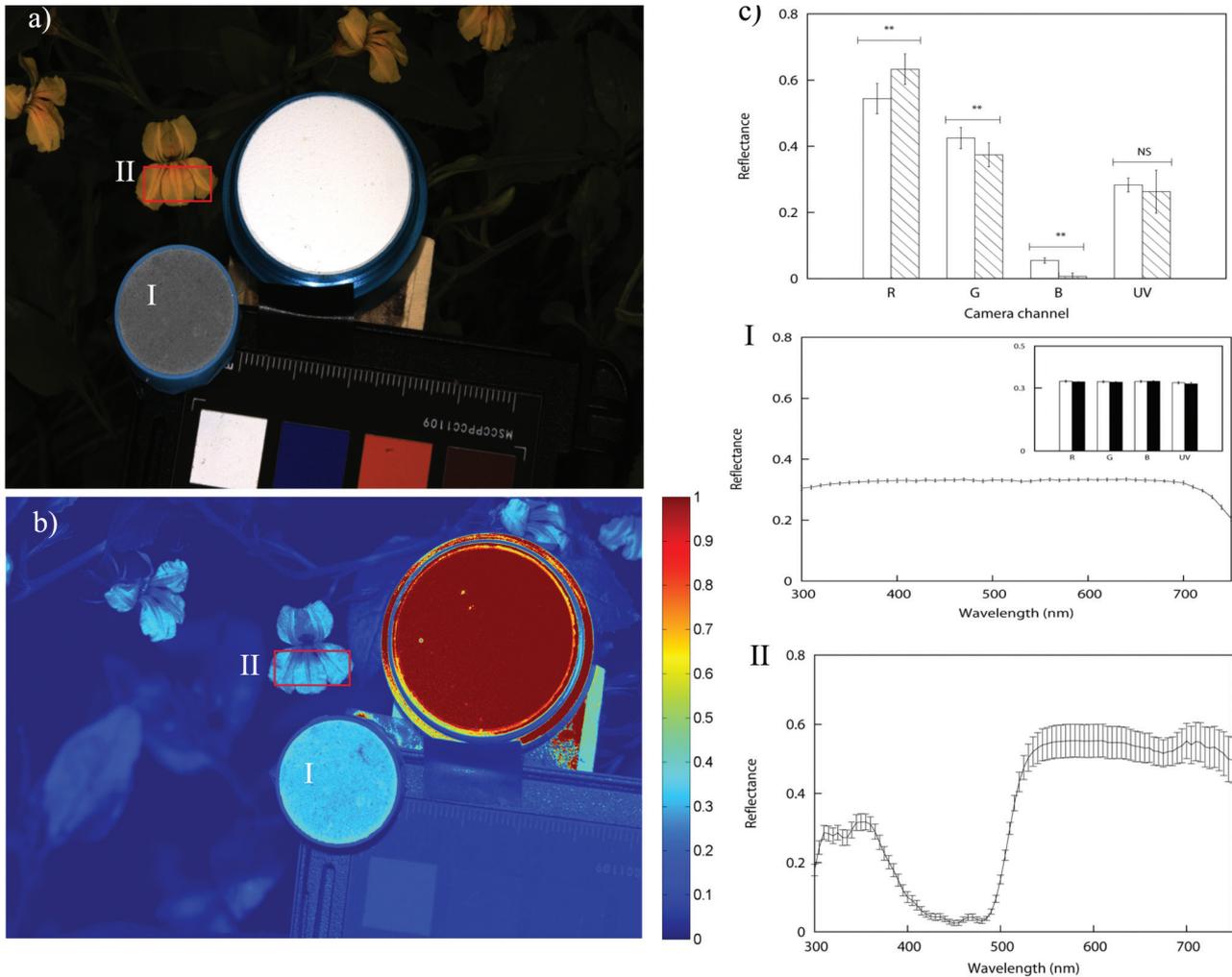


Figure 4: The spectral signals of flowers can be conveniently measured with a linearised camera sensor and/or spectrophotometer. (a) A consumer level RGB camera lens photograph of a yellow flower (*Goodenia ovata*) with calibrated 'white' and grey control scales. (b) Flower photograph imaged in the UV range with specialised sensor. (c) Comparative histograms of camera responses modelling the quantity of reflected radiation from a flower (hatched bars) show a close but significantly different result to data collected with a spectrophotometer (white bars; P-value significant at $\alpha = 0.05$). Panel (I) shows that for the control scales these respective measurement systems show almost identical results, and variability in flower pigmentation and structure explains differences recorded with a camera compared to a spectrophotometer. Panel (II) shows spectral reflectance of ($N=15$; Mean \pm S.E.M.) 'yellow' flower outer petal recordings. Flowers evolved these very specific spectral signals with sharp changes in reflection near 400 and 500 nm in relation to the colour discrimination abilities of bee pollinators. Reproduced from Garcia et al. (2014).

between angiosperms (flowering plants) and influential pollinators (Vorobyev & Brandt 1997). One reason for the strong research interest in honeybees is that foraging bees have a tendency to be 'flower constant' and continue to visit one type of flower while it remains rewarding (Chittka et al. 1999), and bees are of high economic and ecological value in understanding the pollination of plants, including crops (Klein et al. 2007). Specifically, about 35% of food currently consumed by humans comes as a result of insect pollination, for which bees are likely to be the major contributor (Klein et al. 2007). Moreover, imaging techniques using both film and digital sensors had provided an interesting insight into the way that honeybees perceive the world, and highlighted important differences between their and our visual appraisal of flowers (Figure 4) (Dyer 1996; Garcia et al. 2014). These imaging techniques

visualise within-flower colour patterns that visually guide bees towards the landing area on the flower (Pohl et al. 2008) that is inspected with the antennae preceding landing (Evangelista et al. 2010).

One of the most important discoveries about bees' colour perception is that nearly all bee species tested have a very similar set of three photoreceptors (Peitsch et al. 1992; Briscoe and Chittka 2001), and that flower colours in the Northern Hemisphere have evolved spectral signals that closely match (Figure 3) the regions of the electromagnetic spectrum (400 and 500nm) that bee colour vision discriminates best (Chittka & Menzel 1992). Importantly, the studies on colour receptors in different bee species around the world, like *Trigona cf. fuscipennis*, a stingless bee species from Costa Rica (Peitsch et al. 1992), now allow for robust modelling of behavioural

data collected using von Frisch principles (Spaethe et al. 2014). This research now potentially allows for some important bridges to be built between our understanding of bee physiology, and potential effects of biogeography on different environments around the world.

The study of biogeography began over two centuries ago following the voyage of Alexander von Humboldt to South America, laying a foundation for the beginning of modern ecology with his observations on the relationship between biological diversity and altitudinal gradients (von Humboldt 1807). Indeed this work strongly influenced the thinking of his contemporary naturalists such as Andrés Bello and Mariano Eduardo de Rivero y Ustariz, who led the scientific thinking of the nineteenth century in the Spanish colonies, constituting the role models for many modern Latin American scientists. Humboldt's recognition of the complex interactions between living organisms and their immediate physical environment was one of his greatest legacies to modern science (Bowler 2002), and now sets the scene for how our understanding of the challenges of plant pollination in a changing modern world may be addressed.

For example, since hymenopteran insects have highly conserved trichromatic vision (Briscoe & Chittka 2001), the pioneering work done in Germany and the Northern Hemisphere (Chittka & Menzel 1992; Chittka et al. 1994) lends itself for comparative studies on flower colour evolution in the island continent of Australia, as well as some other key study sites. Australia is an important case study since the continent has been separated from other major land masses by a significant sea barrier for over 34 million years, meaning it is an independent study site for understanding how flower colours evolved (McLoughlin 2001; Dyer et al. 2012). In Australia the honeybee is not native, but numerous stingless bee species exist that are likely to have the similar relative spectral discrimination to honeybees (Michener 2001; Spaethe et al. 2014). When flower data from the Maroon Botanical Gardens in Melbourne, which maintains a collection of typical Australian plant species, were collected and analysed with a spectrophotometer, there was a consistent distribution of flower spectra (Figure 3) compared to Northern Hemisphere flowers (Chittka & Menzel 1992; Dyer et al. 2012). An extension to this work in Australia was able to identify flowers as being either bee or bird pollinated, and could show that there was a large and statistically significant shift in the spectra of flowers depending upon the type of pollinator that visited the flowers of a plant, consistent with evidence that birds have a different colour visual system to bees. Birds can perceive long wavelength (red) colours in addition to UV, blue and green; and bird pollinated flowers show a shift to longer wavelength

red reflections (Shrestha et al. 2013). Other complex relationships exist; for example, the Australian spectacular crabspider, *Thomisus spectabilis*, takes advantage of the fact that honeybees are not native. While ambushing on flowers they successfully lure introduced honeybees by means of their white UV-reflective body colour (Heiling et al. 2003), whereas native Australian bees avoid their spider predators (Heiling & Herberstein 2004).

The importance of floral colour signals for communication with bees can hardly be overestimated. In fact each single flower colour provides various messages for bees. If the target colour is still far away and viewed under small visual angle, honeybees use only input from one photoreceptor type and orient colour blind by means of green contrast (Giurfa et al. 1996; Dyer et al. 2008). Naïve bumblebees respond to the colour contrast between flower and background and prefer colours of high colour purity (Lunau et al. 1996) which also potentially puts selective pressure on flower evolution. The colour pattern displayed by bee-pollinated flowers can guide inexperienced bumblebees towards the optimal landing site for the access to nectar as indicated by a central colour patch of superior colour purity guides (Lunau et al. 1996). Experienced bees use the different colour hues to constantly forage on flowers of the preferred food plant (Dyer et al. 2012), and some flowers may even exploit such preferences to gain visitations (Indsto et al. 2006). However, there is a need for much more research on colour vision of bees in different regions of the world to better understand if this coding of information in floral colours is present among all bee-pollinated flowers.

Other recent studies have also started to unlock the complex relationships between pollinator colour perception and how certain flower colours have evolved in specific environments. Hummingbird-pollinated flowers originating from South America have evolved distinctly different spectral signals to bee-pollinated flowers by altering the UV component of reflectance. The abundant red hummingbird-pollinated flowers absorb ultraviolet light in contrast to red bee-pollinated flowers. Preference tests show that the attractiveness of red colours for hummingbirds is independent of UV-reflectance, but bees strongly prefer red UV-reflecting colours over red UV-absorbing ones. By displaying red UV-absorbing colours hummingbird-pollinated flowers thus use a private communication channel to keep away potentially nectar-robbing bees and attract hummingbirds (Lunau et al. 2011).

In Nepal where the Himalayan mountains allow for a natural altitudinal experiment to test how flower colour might vary depending on climate and the distribution of pollinators, it has recently been possible to use the psychophysics colour discrimination principle of von

Helversen (1972) and compare sub-tropical regions where many bee species are numerous and sub-alpine regions where some bumblebee species are present, but flies are the most frequently observed insect (Shrestha et al. 2014). In such conditions it had been expected that the effect of bee colour vision on flower evolution should be diminished (Totland 1993; Totland et al. 2000), but, surprisingly, the recent study in Nepal found no significant difference between these different biogeographic regions. Indeed, consistent with data from Israel and Australia, bee vision best explained flower colour evolution in both the sub-tropical and sub-alpine regions of Nepal, and plants in Nepal have evolved these spectral signals independently as there was no significant phylogenetic relationship between species having similar colouration (Shrestha et al. 2014). Interestingly, a separate study conducted in the mountains of New Zealand (Bischoff et al. 2013) also observed a close fit of the flower spectra that have evolved and bee colour discrimination as described by the von Helversen function, thus showing that at a number of different biogeographic sites so far tested, trichromatic bees have been the most influential insect pollinator of flowering plants.

The potential to expand these techniques in many different countries and biogeographic areas in South America, Asia and Africa promises to reveal much about flowering plant biodiversity, and will provide important databases for mapping how distributions of plants/pollinators may affect environments due to spatial and/or temporal mismatching from effects like climate change (Hegland et al. 2009) and/or habitat fragmentation (Aguilar et al. 2006; Greenleaf & Kremen 2006; Aizen & Harder 2009). For example, a recent United Nations FAO report on climate change and plant pollination proposed useful methods for how surveys of the bee/insect species densities could be measured with coloured pan traps and/or transect walks, allowing for an understanding of what species currently exist in certain regions, and how this might change in the future (Kjøhl et al. 2011). Recent work (Spaethe et al. 2014) has confirmed that native bees in Australia and South America can be relatively easily trained and tested using principles first developed by von Frisch (von Frisch 1914), and there are opportunities to better understand plant pollination by different bee species at a global level, which will have important implications for the management of agriculture and the environment (Greenleaf & Kremen 2006; Ashworth et al. 2009).

If this can be achieved it will be a significant contribution to our understanding of a changing world, and we owe much thanks to seminal work done by the first researchers on bee colour vision like Karl von Frisch in 1914.

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