ARTICLE BY
ADRIAN HORRIDGE
EMERITUS PROFESSOR
AUSTRALIAN NATIONAL UNIVERSITY

Bee Vision

IS TOTALLY DIFFERENT

"The amazing part of this story is that at the time von Frisch knew nothing about the types of receptors in the eyes of bees and was quite ignorant of mechanisms of colour vision. He openly assumed that bee colour vision would be like that in humans and designed experiments that supposedly proved it. Unfortunately for him, bee vision is totally different".
(The Australasian Beekeeper. 2017, Vol. 118, No.12, p.544).

This quotation, from my short contribution in the June 2017 issue of this Journal, provoked a couple of readers to ask for more evidence and detail, so let's begin.

Karl von Frisch was an assistant in Zoology at the University of Münich when he wrote a paper of 188 pages in 1914, describing in detail his experiments on bee vision of coloured and grey papers. Certainly, at the time, no-one had any knowledge of the variety or colour sensitivity of the visual receptors in bees' compound eyes, or, for that matter, in human eyes.

There was a test available that detected imperfections caused by genetic loss or alteration of the visual pigments in human colour vision, but no-one had tried it on bees. Karl von Frisch trained bees to go to a coloured or grey paper and then tested whether they could pick out the training paper placed among 15 different grey papers on a 4 by 4 panel (Figure 1A). The trained bees were successful when trained on a yellow, blue, black or white paper, but failed with several of the shades of green. This was his evidence for colour vision.

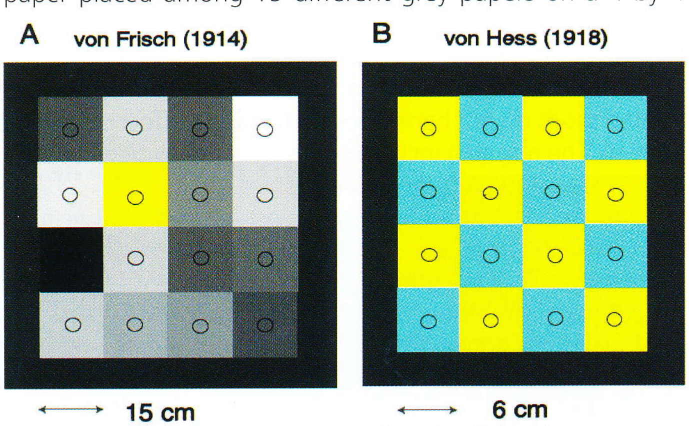

Figure 1. Test arrays. A. the von Frisch's test. B. the von Hess's training and test.

In response, in 1918, Carl von Hess, Professor of Ophthalmology at the same university used a 4 by 4 checkerboard of blue and yellow squares (Figure 1B) and found that bees trained on blue squares learned to distinguish blue from any other colour or grey level, but when trained on yellow, they failed every other test. This experiment is easily repeated; it excluded full colour vision but did not reveal what the bees detect. (We now know that they had learned to avoid the blue squares). The two experimenters could not agree. Neither repeated the method of the other, and in fact, neither understood their own result. Their papers, in German, were never critically analysed. Hess died in 1923 and von Frisch became a powerful Professor and Journal Editor, so his conclusion was never challenged, until in 2014-16 I published several papers using a different experimental design (Figure 2).

The new apparatus consists of a Y-shaped box (Figure 2) with a transparent top that excludes ultraviolet light. A small group of bees are trained to enter at the front into a choice chamber where they must pause at the baffles. They choose between two targets of coloured paper, each with a ½ inch hole in the centre. One of these holes leads to a reward box containing sugar solution, and the other leads nowhere. The targets are interchanged every five or ten minutes to force the bees to look at the targets, irrespective of their position. Within this apparatus, bees learn to distinguish any colour from any other really different colour or grey level.

Satisfactory learning takes 10-20 visits. It certainly looks like colour vision, but tests of what the bees learned reveals otherwise.

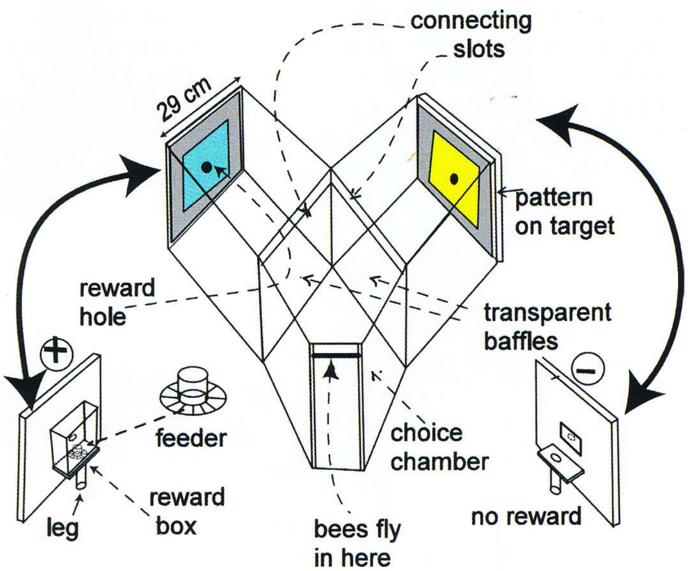

Figure 2. The Y-shaped box that creates a fixed choice with all variables controlled. The two targets, one rewarded (+), are interchanged every 5 or 10 min.

Thanks to patient recording directly from the receptor cells with a microelectrode, we now know that the worker bee has three colour types in each ommatidium of the compound eye (behind each facet); one cell sensitive to blue, six to green, and one to ultraviolet (UV) (Figure 3, left). The UV cells indicate for the bee the direction of the sky for escape and level flying, and have never been shown to be essential for foraging.

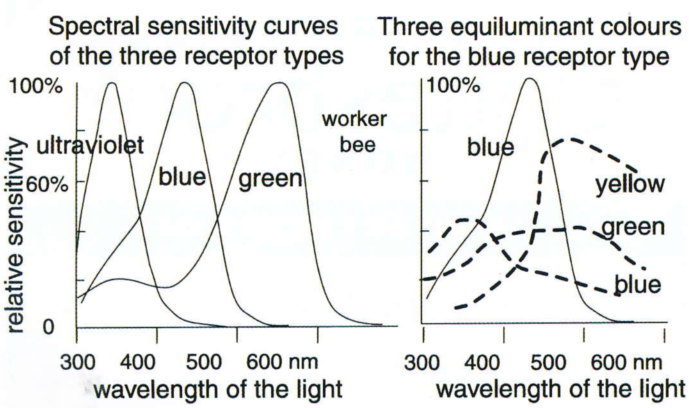

Figure 3. A. Spectral sensitivity curves reduced to 100%. B. Emission spectra of three coloured papers in sunlight on the same scale.

Sunlight reflected from each of the coloured papers is easily calibrated with a spectroscope, so we can find papers that give the same response of the blue- or of the green-sensitive receptors (Figure 3, right). They are called 'equiluminant'. For each receptor type, there are plenty of equiluminant pairs of standard colour papers available at artists' stores. As training targets, these pairs of papers make possible many informative experiments with known stimulus strength for each receptor type.

When trained to distinguish yellow (rewarded) from dark blue (unrewarded) targets with a similar stimulus to the blue receptors (Figure 4A), bees learn the task but cannot recognise the rewarded yellow colour Continued over...

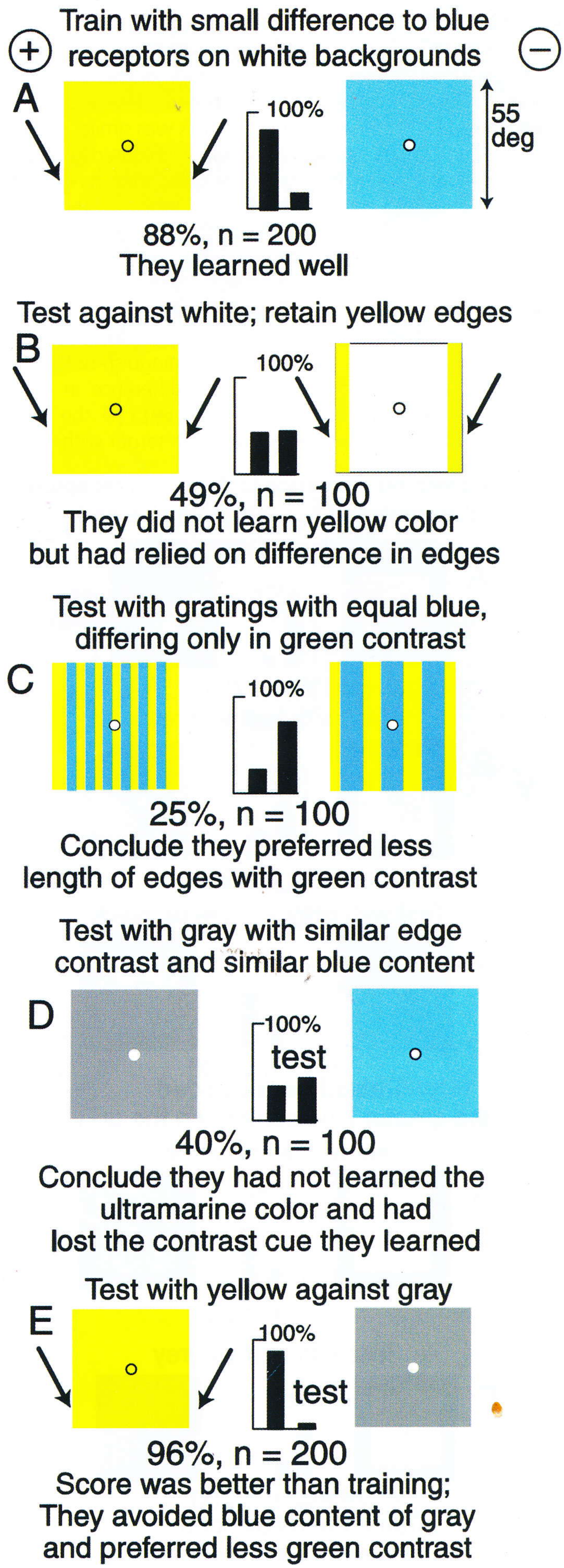

Figure 4. A. Training patterns. B - E. Tests with or without green edge contrast.

Continued... (Figure 4B). They learned nothing about blue, because there was no blue difference, and with the green receptors they learned only the contrast at the edges of yellow (arrows). The contrast must have been detected by the green receptors because the blue stimulus was similar on the two training targets. With two different coloured gratings with equal blue content the trained bees avoided the greater amount of green contrast (Figure 4C). When tested with grey versus dark blue with similar edge contrast and blue content, they failed (Figure 4D) because their familiar cues were the same on these targets. Tested with yellow versus the same grey (Figure 4E), they preferred the less green contrast against white at the edges of grey (arrows).

Next, a group of bees was trained to distinguish buff from blue, on a black background, with no difference in edge contrast to the green receptors (Figure 5A). All the tests showed that the bees learned to avoid the target with more blue content. They had not learned to look for a difference in green contrast and anyway they preferred blue (Figure 5B-E).

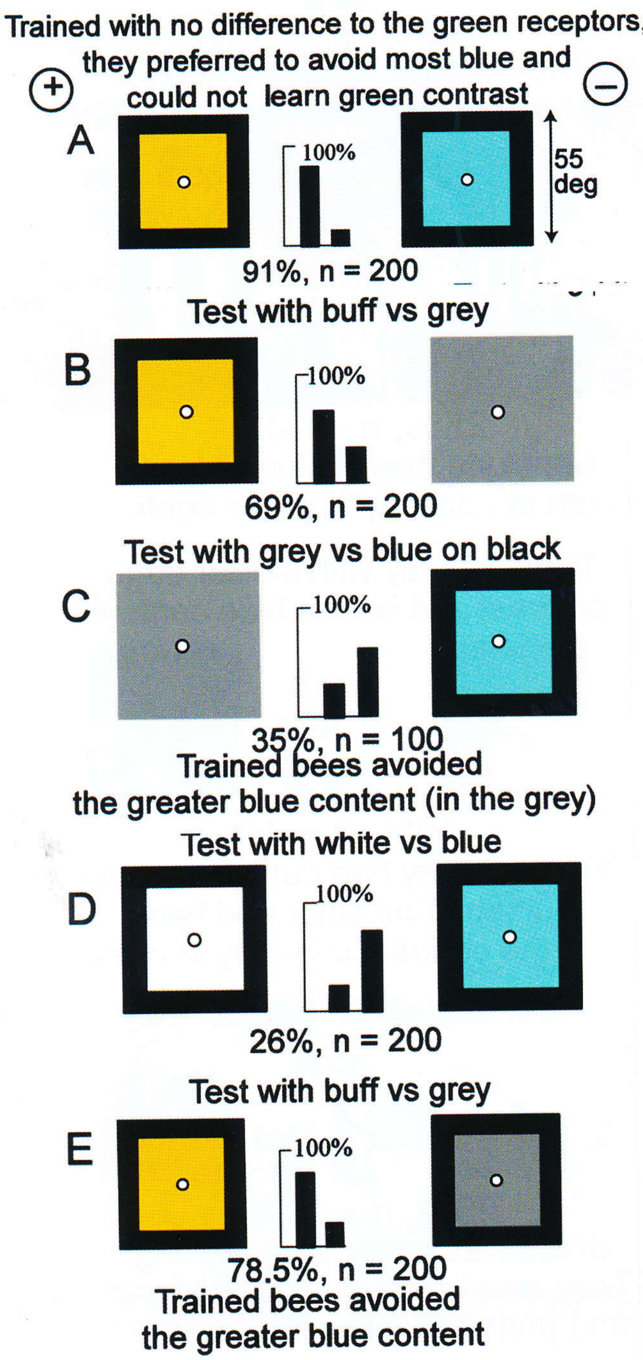

Figure 5. A. Train with no difference to green receptors. B – E. Tests for blue preference.

These experiments, and many more like them, demonstrate that bees have an entirely new kind of natural visual system. They do not see colours as we do. A century of text-book statements, and consequent belief that bees see flower colours, was an error, albeit a very plausible one.

Bees locate and measure amounts of blue in areas and, separately, quantities of green contrast at edges, and the angle between. They do not identify colours except by these features. To bees, white is an intense blue and black is zero blue with maximum edge contrast. Experimental science proceeds by demonstrating that old errors require revision, and by providing a new explanation that others should verify and build upon.

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Adrian Horridge began fundamental work on all aspects of insect vision in 1961. He has been a Fellow of the Royal Society since 1969 and of the Australian Academy of Science since 1974. His recent papers on bee vision of colour, are available free to download from his Web Page at: www. Adrian-Horridge.org