

TO BE OR NOT TO BE A COLOUR-SEEING BEE

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ABSTRACT

Several different types of visually guided behaviour in the honeybee (*Apis mellifera*) are found to be colour-blind, although the bee certainly possesses colour vision, as demonstrated by the bee's performance in colour-discrimination tasks. The colour-blind behaviours are similar in that all of them involve movement. The evolutionary advantage of colour-blind motion perception is discussed.

KEY WORDS: Honeybee, behaviour, colour-vision, optomotor response, movement avoidance response, scanning, distance estimation, motion detection.

INTRODUCTION

To neurobiologists working on insect vision, the honeybee is a stroke of luck, comparable to what *Drosophila* is to geneticists. This is mainly due to the bee's remarkable capability of learning and memorizing visual cues associated with a food source or the home site which can easily be exploited in behavioural work' (rev. von Frisch, 1965; Menzel *et al.*, 1974). Since neither anatomical structures nor electrical potentials can reveal the final product of neural data processing, it is indeed in all cases the animal's behaviour that yields information about what and how well the animal sees.

This is also true in the case of colour vision. By definition, an animal possesses colour vision if it is able to distinguish between two spectrally different light stimuli regardless of their intensity. This definition implies that it is only the animal's performance in colour-discrimination tasks that can prove whether or not the animal perceives colours — even though, for colour vision to be possible, several physiological conditions must be met: First, there must exist in the retina at least two classes of photoreceptors differing from each other in their spectral sensitivities. Colour is coded as the ratio of excitations of the different types of photoreceptors (Rushton, 1970; Menzel, 1979). Second, the spectral sensitivity curves of the different receptor types must partly overlap, in order that every spectral colour (or mixture of colours) be

unambiguously defined by this ratio. And, clearly, the last condition is that a neural machinery exists which extracts the ratio. Correspondingly, the existence of different spectral types of receptors in the retina (even if their spectral sensitivity curves were found to overlap) does not yet prove that the owner of that retina can perceive colours.

Colour vision in bees had been demonstrated long before it could be shown that there exist different spectral types of photoreceptors in the bee's retina. The first electrical measurements from single cells were made in 1964 by Autrum and Zühlke, who found three classes of receptors possessing response maxima in ultra-violet (UV) (340 nm), blue (440 nm), and green (530 nm), respectively (see Fig. 17 in Discussion). At that time, behavioural work had already shown that bees possessed three spectral classes of receptors and that the spectrum visible to the bees included UV (see rev. in von Frisch, 1965, pp. 482-504).

The earliest evidence that the bee is a colour-seeing animal was provided by Karl von Frisch some 70 years ago (von Frisch, 1915). He trained bees to collect food on a blue piece of cardboard, and then tested the bees by offering them a choice between it and 15 differently shaded grey cardboards, one of which certainly must have possessed the same brightness as the previously rewarded blue cardboard. (At that time, it was not yet possible to calculate how bright a stimulus appeared to the eyes of the bee.) In this test, almost 100% of the bees' landings occurred on the blue cardboard. Obviously, to the bee, "blue" is a sensory modality that is independent of brightness. Since that experiment, von Frisch and many of his students have conducted many extensive investigations concerning the bee's colour vision, and they showed many times that bees distinguish well between a great variety of spectral colours and colour mixtures (von Frisch, 1919; Kühn 1927; Daumer, 1956; 1963; von Helversen, 1972; Menzel, 1967; 1968; 1969; Menzel *et al.*, 1974; Menzel and Erber, 1978).

Colour vision in honeybees and in many other insects certainly developed in co-evolution with the angiosperm plants which are, for this reason, also referred to as entomophil plants. The reasons for the evolution of both colour vision and the display of colours most probably lie in the fact that colour vision, since it is independent of intensity-contrast, improves the recognition of relevant objects, and colours, thus, increase the probability that their bearer will be recognized. Convincing examples of behaviourally functional colours are abundant: Species-specific colours, sex-specific colours, age- or season-specific colours, colours that serve for cheating (mimicry), and colours that serve as protection or camouflage. (Pogden and Pogden, 1974, provide a very vivid review of these fascinating phenomena.)

Recognition of relevant objects, however, is not the only task the visual system must cope with, and thus one cannot speculate that colour vision is advantageous under all circumstances. Indeed, if it were, there would not exist a single colour-seeing animal that, on some particular occasions, wishes to make no use of its ability to see colours. These particular occasions will be the topic of this article. Although my examples will be taken from the life of honeybees, their meaning might be understood in a much broader sense.

The first behavioural studies which suggested that colour vision is not always involved in a visual task were those done by Kaiser and Liske (1972; 1974) on the spectral sensitivity of the optomotor response. In this behaviour, the animal reacts to

movement of the visual panorama by turning in the direction of the movement, thus stabilizing the panorama's image on the retina. The optomotor response serves to compensate for involuntary deviations from the animal's course during locomotion (see excellent review by Wehner, 1981). This behaviour is mediated by innate reflexes, and is therefore independent of a learning process. Kaiser and Liske used individual tethered bees flying within a two-coloured vertically striped drum which rotated around them. The intensity of one of the colours was kept constant, while that of the other (termed "test-colour") was varied. The strength of the bee's torque in the direction of rotation of the grating was measured for a series of two-colour combinations. For each of them, a particular intensity of the test-colour was found at which the bee failed to respond to the rotation of the grating. Thus, the bee's optomotor response is driven by intensity-contrast, not by colour-contrast, and is therefore, by definition, a colour-blind behaviour. From the intensities of the test-colours at the point of zero response Kaiser and Liske have calculated that the optomotor response receives its input mainly from the green receptors. Using only one spectral class of receptors is the most obvious way of being colour-blind (see above), even though it is not the only one possible way (see Discussion).

In the present article I shall add evidence from my own work to show that the bee bypasses her capability to see colours whenever the task involves seeing objects that move relatively to the retina, and I will discuss the advantage of colour-blindness in such tasks. Unlike in the experiments of Kaiser and Liske described above, my bees are always freely flying bees which have been trained to visit the experimental apparatus and to associate the food reward with a visual stimulus. Since the experiments I shall describe differ greatly from each other, details concerning the rationale behind each of them and the different methods used will be given in context.

MOVEMENT-INDUCED BEHAVIOURS IN UNTETHERED BEES

In scientific work it often happens that one sets out to investigate one question, and ends up answering another. The first two of the three studies I shall describe below were originally designed to investigate questions involving neither motion perception nor colour vision. Their results later showed that they involved both. The third study, the preliminary results of which are described here for the first time, involves a behaviour which is well known to be guided by movement cues. Its spectral properties, however, have not been investigated before.

I. The Movement Avoidance Response

When, in 1982, Mandyam V. Srinivasan and I started to collaborate in behavioural work on honeybees, the first subject we were interested in was temporal acuity of honeybee's vision. Our question, precisely, was: How quickly (e.g., how many times per second) must two visual stimuli alternate in order that the bee no longer recognizes them as being two different stimuli? This particular temporal frequency would be the cut-off frequency of honeybee's vision.

One way of approaching this question could be to exploit the optomotor response (see Introduction), because, for each receptor viewing a rotating grating, two

stimuli alternate at a frequency that can be gradually increased, until, at a particular frequency, the optomotor response can no longer be elicited. This method has been applied many times (see Wehner, 1981, Table 2). Indeed, thanks to the existence of the optomotor response we know quite a lot about the visual systems of insects that cannot be trained to visual stimuli as readily as bees can. However, there is no reason to believe that the cut-off frequency of the optomotor response defines the temporal resolving power of the visual system as a whole. The optomotor system might be much slower than other visual subsystems, because if it were as fast it could interfere with other visually guided activities of the animal (see Srinivasan and Bernard, 1977; Collett, 1980). A fast flying bee, for example, would go into uncontrollable oscillations between the voluntary direction of her flight and the optomotor thrust in the opposite direction. Thus, in spite of the fact that the temporal properties of the bee's optomotor response had been investigated extensively (Wolf, 1933; Autrum and Stoecker, 1950; Kunze, 1961), Srinivasan and I needed additional methods for investigating our question.

We commenced by training bees to collect food on a circular piece of diffusing glass illuminated from below with a beam of light of constant intensity (Srinivasan and Lehrer, 1984a). After training, we tested the bees by offering them a choice between the steady light they had been trained to and a *flickering* test-light of the same spectral composition and mean intensity. Our criterion for the bees' discrimination between the two stimuli was the choice-frequency (CF), i.e., the percentage of landings on the previously rewarded (steady) light. The flicker frequency of the test-light was varied for the purpose of determining the cut-off frequency, i.e., the frequency at which the bees would choose indiscriminately (CF = 50%) between the flickering and the steady light.

The results of these experiments are summarized in Fig. 1 which shows the bees' choice-frequencies as a function of flicker-frequency of the test-lights. From these results we had to conclude that the bees took little notice of flicker. They landed on the flickering lights almost as often as on the steady light to which they had been trained.

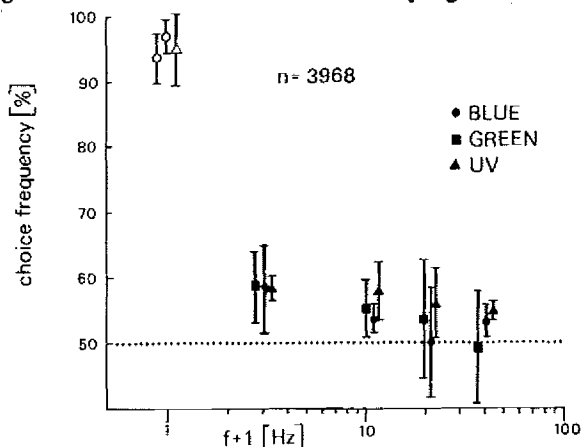


Fig. 1. Choice-frequencies in favour of a previously rewarded steady light in tests against flickering lights of the same colour and mean intensity. Here and also in Figs. 3 and 7, the temporal frequency of the test stimuli is plotted on a logarithmic scale and is calibrated ($f+1$) as to include $f=0$ Hz. n = total number of landings. After Srinivasan and Lehrer, 1984a.

This was the case at all flicker-frequencies tested, no matter what spectral composition we had used. (In three different experiments we used three different colours, see inset of Fig. 1). Control tests (empty symbols in Fig. 1) proved that the bees did learn the colour of the rewarded light: they could distinguish it very well from a steady light of a different colour, but not from a flickering light of the same colour.

Since it was not possible to determine cut-off frequencies from the results of the flicker experiments, Srinivasan and I decided to use stimuli that we modulated temporally in a different way: we made the stimuli move. We suspected no evil, because we did not intend to measure torque responses. All we planned to do was measure choice-frequencies in quite harmless binary-choice experiments, as in the flicker experiments before.

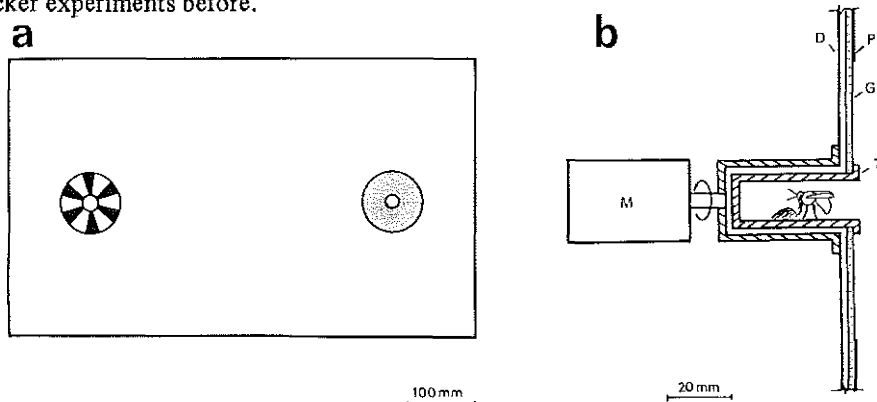


Fig. 2. Experimental apparatus used to examine temporal acuity of honeybee's vision. a: Front view, b: vertical cross-section along one of the pattern-carrying devices; M variable-speed motor; D metal disc carrying radial grating on front face; P black paper mask; G glass cover; T plexiglass tube penetrating the centre of the disc. From Srinivasan and Lehrer, 1984b.

Fig. 2 shows the experimental apparatus. During training as well as during the subsequent tests, two black-and-white radial gratings were offered simultaneously to the bees. The "grey" disc shown in Fig. 2a is in reality identical to the radial grating that is positioned next to it. However, it rotates at 50 revolutions per second. At this angular speed, since the grating exhibits a spatial period of 60° , it produces a temporal frequency of 300 Hz, at which the black and the white sectors fuse. To the human eye, this happens already at a much lower frequency (about 50 Hz). However, in the case of the bees, we wanted to be sure. From an earlier work using electrophysiological methods (Autrum and Stoecker, 1950) we knew that the response of the bee's photoreceptor cells to flicker cuts off at about 200 Hz, and, obviously, behaviour cannot be faster than the receptors.

The bees were rewarded with a drop of sugar solution when they landed on the tube in the centre of the disc. The tube was stationary even when the disc rotated (Fig. 2b), and thus the bees could feed there comfortably. The trained bees were then offered a choice between the grey disc and an identical radial grating that rotated at a series of various speeds and thus produced a variety of temporal frequencies. The idea again was to find the particular frequency at which the rotating grating and the grey disc look alike.

We conducted a series of experiments — also using gratings of other spatial periods than the one shown in Fig. 2 (see Srinivasan and Lehrer, 1984b) — and always obtained the same results. The curves shown in Fig. 3 were measured in three different experiments. In each case, the ordinate depicts the choice-frequencies in favour of the grey disc as a function of frequency of the alternative disc. From these curves it was now easy to determine the cut-off frequency: At 200 Hz, the bees can no longer resolve the black and the white sectors.

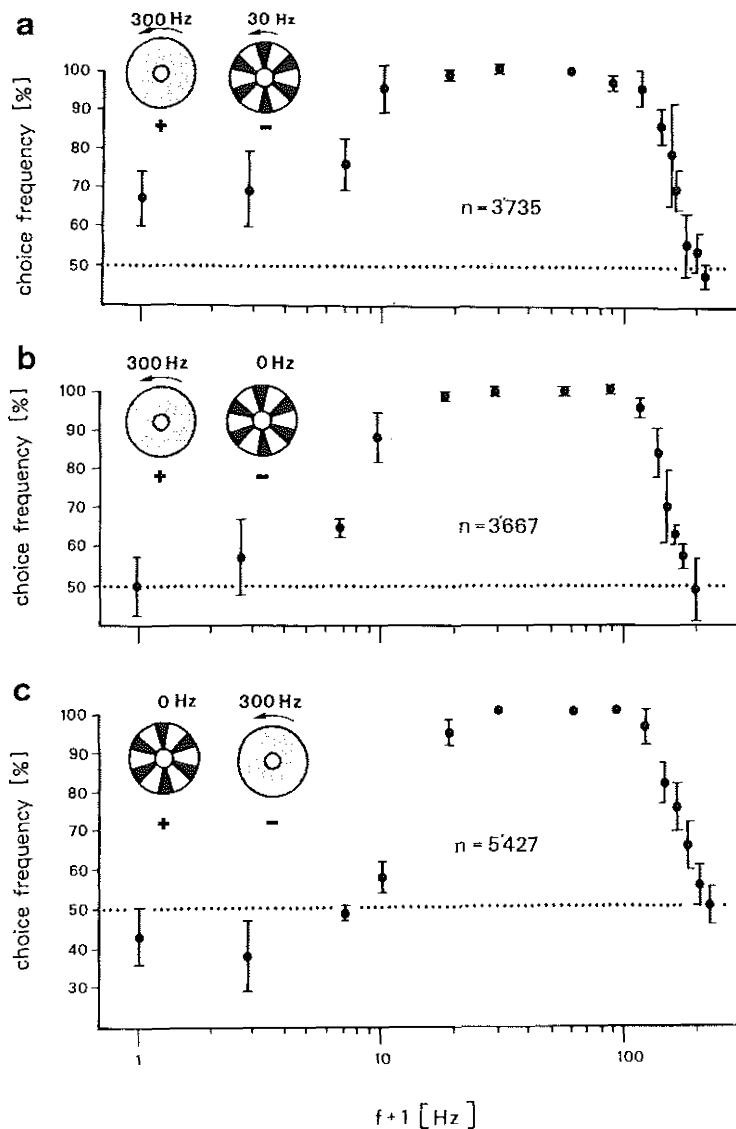


Fig. 3. Choice-frequencies in favour of the grey disc obtained in three experiments using three different training procedures. Plus and minus in the insets depict the rewarded and unrewarded stimulus, respectively. n = total number of choices. After Srinivasan and Lehrer, 1984b.

Surprisingly, however, this was not the only conclusion we were able to draw from these results. Another one was that the curves we obtained could not possibly be a consequence of the training procedure:

In Fig. 3b, the grey disc (300 Hz) was the rewarded one; the alternative disc during training was stationary (0 Hz). In Fig. 3c, the training procedure was reversed, with the stationary disc (0 Hz) rewarded. The choice-frequencies shown are those in favour of the grey disc. The bees' learning performance was miserable in both cases: look at the choice-frequencies obtained in the tests when 300 Hz was pitted against 0 Hz. The bees chose indiscriminately whether the grey or the sectored disc was rewarded. In Fig. 3a, the grey disc was rewarded against the 30 Hz grating. Here the bees performed beautifully: they exclusively chose the previously rewarded disc.

The results make sense when we look at frequencies lying between 18 Hz and 128 Hz in all of the three experiments: The bees avoid the rotating gratings and land on the grey disc irrespective of the training procedure. By using moving stimuli we had uncovered what was quite obviously a very sensitive movement-detection system, and what we measured was something we called "Movement Avoidance Response" (MAR). The cut-off frequency we have found for the temporal resolution of honeybee's vision is at the same time the cut-off frequency of the MAR.

Now, the shape of the curves (Fig. 3) strongly suggests that the MAR has a peak frequency as well, and Srinivasan and I were very curious to find it. It sits hidden somewhere in the saturated portion of the curves (CF = 100%). Binary choice experiments would never reveal it, and thus we had to find a different procedure. We placed ourselves behind a video-camera and recorded the flight-paths of individual bees flying in front of the rotating discs at all the frequencies we had tested before.

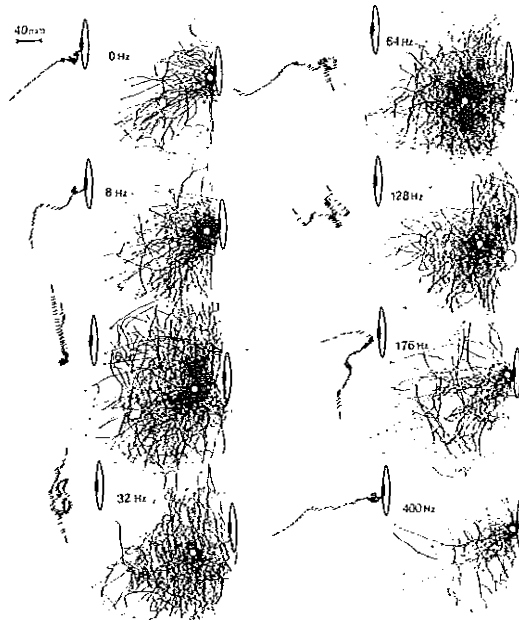


Fig. 4. Side view of flight-paths of bees approaching a rotating black-and-white grating which produces various temporal frequencies. From Srinivasan and Lehrer, 1984b.

Fig. 4 shows the flight-paths of bees, in this case filmed from the side. In each panel, the mouth of the tube in the centre of the disc can easily be discerned. At each frequency, one typical individual flight-path is shown (top left of each panel), and by its side are superimposed flight-paths of all the bees we had filmed at that particular frequency.

The searching bee behaves as if an invisible barrier existed between her and the rotating grating. The bee flies up to a certain point and no closer, then she retreats flying backwards, as if she has hit her head, only to repeat the manoeuvre. The superimposed paths can be thought of as describing a density function which specifies the probability of finding a bee at any given location. In every such "search cloud", a region of highest density can be recognized. In Fig. 4, the centre of this region is marked by a white dot. The distance of this dot from the tube, and also its position in the vertical plane with respect to the tube, obviously depends upon the frequency produced by the rotating grating.

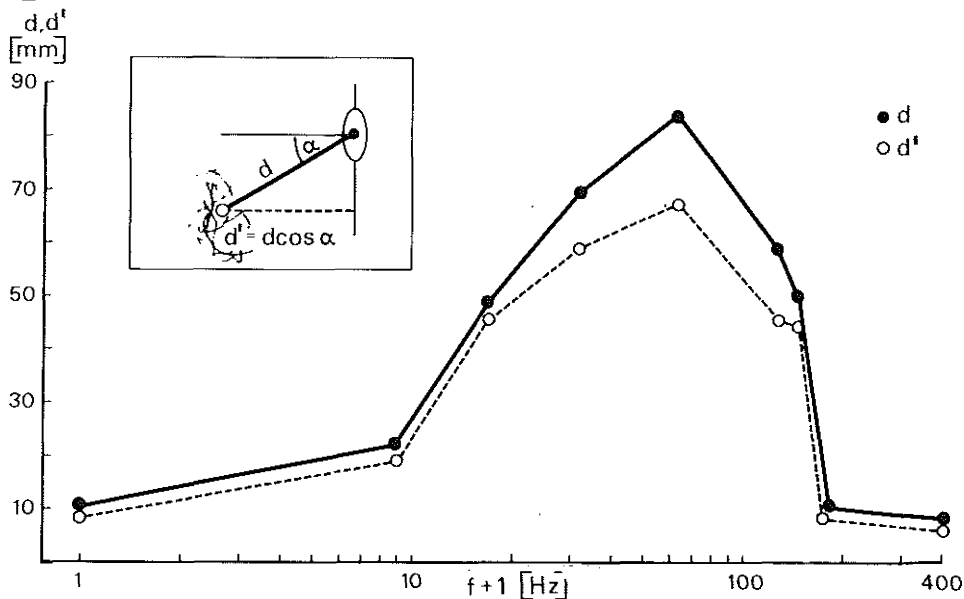


Fig. 5. Distance of the centre of highest density (white dots in Fig. 4) from the centre of the tube (d) and from the vertical surface of the apparatus (d') as a function of the temporal frequency of the rotating grating. From Srinivasan and Lehrer, 1984b.

Fig. 5 shows the distance of the point of highest density from the tube as a function of stimulus frequency (filled circles). If it is correct to assume that this distance is a good measure of the strength of the response, then, clearly, the peak of the MAR is to be found at around 65 Hz. The empty circles in Fig. 5 take into account, in addition, the angle α defined in the inset of the figure. One can see that the stronger the MAR is (Fig. 4), the more the bees avoid flying directly in front of the disc (Fig. 5).

This is also well documented in Fig. 6, which shows flight-paths recorded frontally (facing the disc): The camera has detected only very few bees in front of the 64 Hz disc. As one approaches 0 Hz and 400 Hz, more and more bees fly in front of the disc.

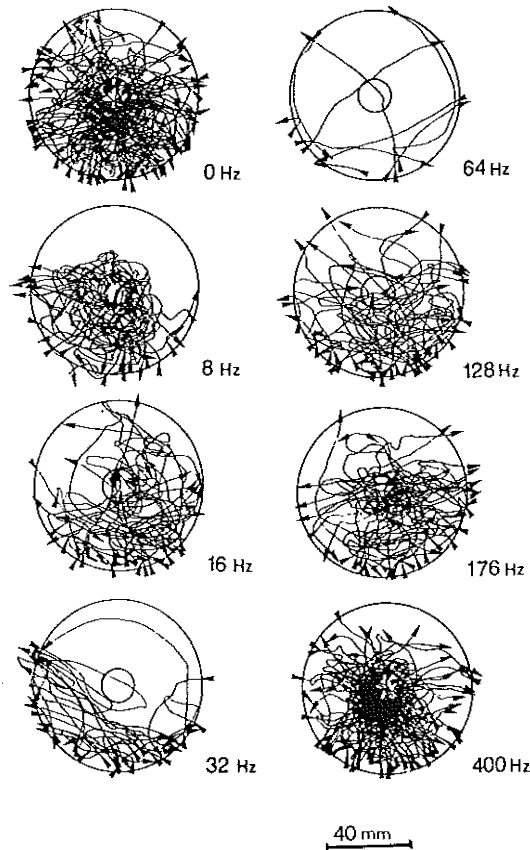


Fig. 6. Frontal view of the approach flights at the frequencies shown in Fig. 4. After Srinivasan and Lehrer, 1984b.

There are two arguments against classifying the MAR as being some type of optomotor response. First, its time course is very different. In bees, the optomotor response peaks at about 3 Hz to 8 Hz and cuts off between 50 Hz and 100 Hz (Wolf, 1933; Kunze, 1961; Menzel, 1973). The MAR, however, only starts to be active at about 10 Hz (Fig. 3). It peaks at about 65 Hz (Fig. 5) and has cut-off at 200 Hz, thus being altogether much quicker than the optomotor response. Second, as can be seen in Fig. 6, flight occurs in all directions and not mainly in the direction of rotation (which was counterclockwise), as would be the case for an optomotor response.

Here Srinivasan and I had a movement-induced reaction that was sensationally fast, actually as fast as the receptors (see above). In addition, as opposed to the very elaborate experiments that were needed for investigating the optomotor response (see above), the MAR promised to be very easy to examine with respect to its spectral

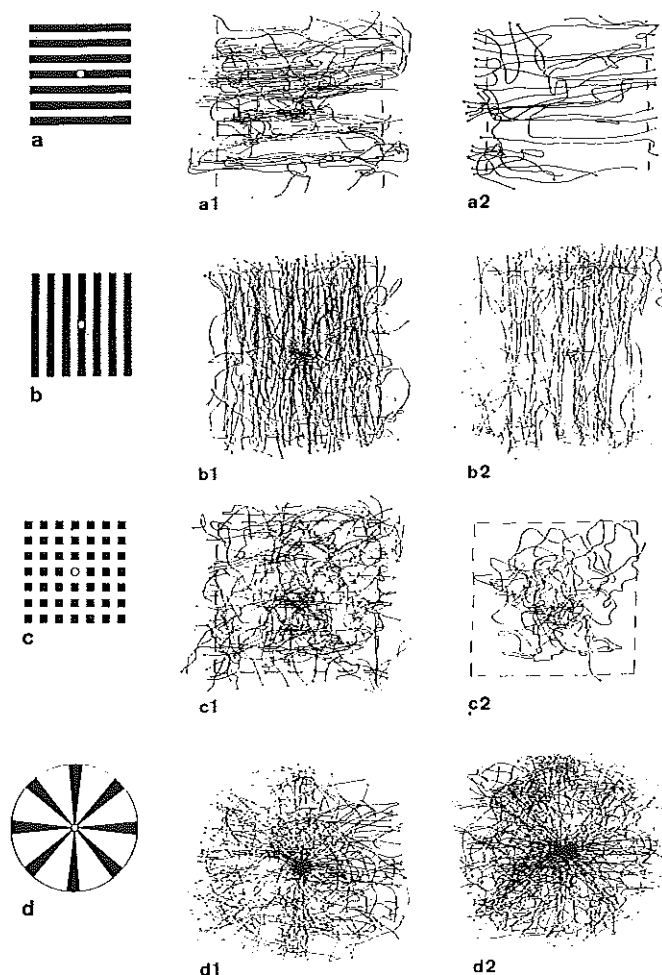


Fig. 9. Examples of flight-paths of bees recorded on each of the shapes shown on the left hand side. After Lehrer *et al.*, 1985.

The quantitative analysis of the flight paths (Fig. 10) confirms this finding. For each of the four shapes depicted in the insets, the mean values and standard deviations of the frequencies of four different types of flight elements are shown: straight flight sequents in (i) horizontal (ii) vertical and (iii) oblique direction, all of the same length, and (iv) curved elements, i.e., sudden changes of direction, U-turns and turns on the spot. The values are calculated from the six recordings done on each of the shapes after the six different training procedures, and one can see that, with one exception (explained in Lehrer *et al.*, 1985), the standard deviations (depicted by the height of the boxes in Fig. 10) are quite small. The distribution of the frequencies of the various

flight elements shows that the horizontal grating is mainly scanned in the horizontal direction, the vertical grating mainly in the vertical direction; oblique flight directions are most frequent on the radial grating (this shape is the only one that offers, among others, oblique contours), and the highest frequency of curved flight elements is found on the checkerboard-shape which, indeed, offers plenty of changes in direction of the contours.

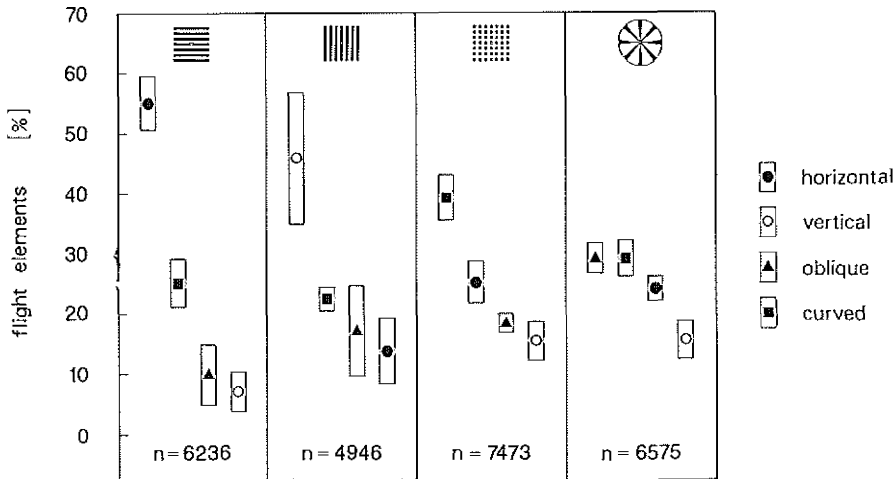


Fig. 10. Distribution of various flight elements recorded on each of the shapes shown in the insets. n = total number of flight elements. From Lehrer *et al.*, 1985.

Fig. 11 shows the results of the binary-choice tests. For each of the shapes (see insets) choice-frequencies obtained in its favour are shown for all of the tests in which this shape was presented to the bees simultaneously with another shape in the course of the six experiments. The previously rewarded shape and the alternative shape offered during the test are depicted along the abscissa (same symbols as in Fig. 8). For example, considering the horizontal grating in Fig. 11 a, "V:C" mean that it was tested against the vertical grating after having trained the bees to the checkerboard shape. Choice-frequencies obtained for each shape can take on every value between 0% and 100%. Obviously, the results of the binary choice tests are a consequence of a learning process: From each two alternative shapes the bees prefer the one that more closely resembles the geometry of the previously rewarded shape. In this task, choice behaviour can be manipulated by applying a particular training procedure, while scanning behaviour cannot (see Fig. 9). For the sake of comparison, the mean frequencies (\pm SD) of the horizontal and vertical flight elements from the quantification of the video-recordings (Fig. 10) are included in Fig. 11 (right ordinate and shaded bars). There is no correlation between the measured choice-frequencies and the measured proportions of various scanning elements obtained in the very same tests.

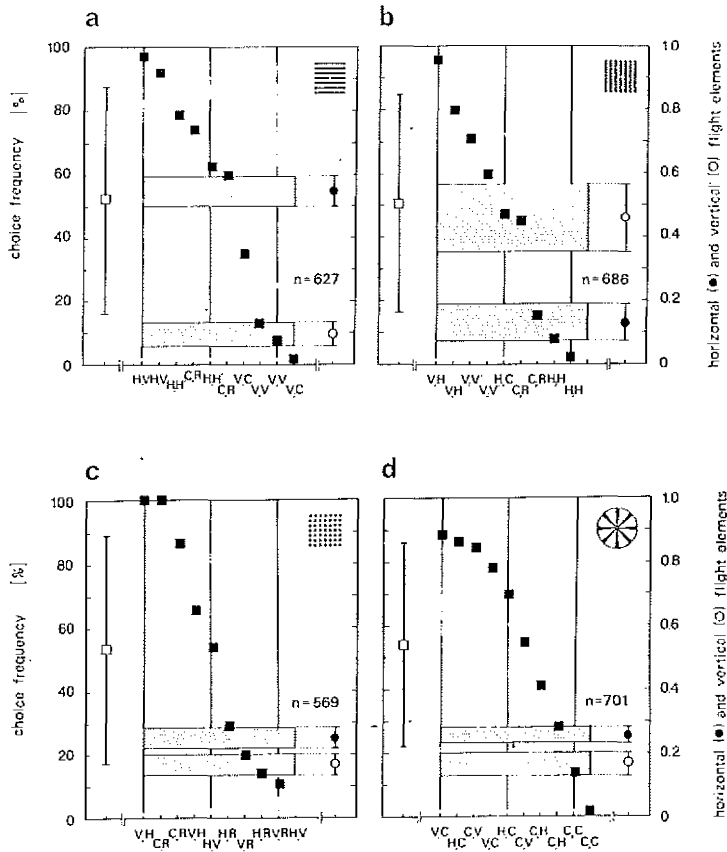


Fig. 11. Choice-frequencies obtained in binary-choice tests. Capital letters along the abscissa depict the rewarded shape (first letter) and the alternative shape used during test (second letter). (Symbols as in Fig. 8.) n = total number of choices. After Lehrer *et al.*, 1985.

From the above results it was not possible to conclude that scanning served pattern discrimination. However, neither was it possible to conclude that it did not: Since scanning behaviour could not be influenced by training, there was no way of finding out whether bees that scanned the patterns performed better in the discrimination task than bees that did not. Therefore, the large amount of data remained unpublished.

After the discovery of the MAR, however, Srinivasan, Wehner and I considered the scanning behaviour from a new perspective: Perhaps the bees followed the contours of the shape in order to avoid retinal movement while flying in front of it. Flight which takes the bee in a direction perpendicular to the contours would cause the contours to move across the retina, while flight along the contours or parallel to them would not. In addition, scanning behaviour has two important properties in common with both the optomotor response and the MAR: (i) It is independent of a learning process, and (ii) it does not habituate, i.e., no matter how often the bee is

confronted with the shape, she always follows the contours. These considerations made us decide to examine the spectral sensitivity of the scanning behaviour to see whether it was the same as the MAR and the optomotor response: This would indicate whether or not it was a movement-induced behaviour.

In Fig. 12 a and b, the bees flew in front of a horizontal and a vertical grating, respectively, which provided contrast only to the green receptor. In the horizontal and vertical gratings of Fig. 12 c and d, only contrast detectable by the blue receptor was present. (We used the same colour-combinations here as in the MAR experiments before.) The results are clear at first sight: Green-contrast elicits scanning, while blue-contrast does not. Consequently, the scanning behaviour is colour-blind.

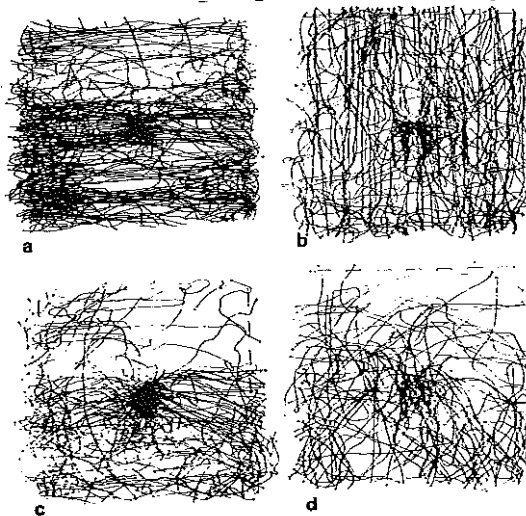


Fig. 12. Flight-paths of bees flying in front of horizontal (a,c) and vertical (b,d) gratings that offer either green-contrast (a,b) or blue-contrast (c,d). From Lehrer *et al.*, 1985.

There is no doubt that, in both colour-combinations, the orientation of contours was quite visible to the bees, because the bees were easily trained to discriminate between the vertical and the horizontal grating whether contrast was restricted to the green or the blue receptors (see Fig. 8 in Lehrer *et al.*, 1985), even though in the latter case they did not scan the gratings. Thus we at the same time have a tentative answer to our original question: Since bees that scan and bees that do not scan are equally successful in the discrimination task, scanning behaviour does obviously not serve pattern recognition.

III. Distance estimation

Bees are well known to use far and near visual marks to guide their return to a food source and to the home site (revs. von Frisch, 1965; Wehner, 1981). When offered a very unobscured feeding place and artificial marks, the bees can learn to localize the feeding place by using as cues the spatial relation and the distance between it and the visual marks (Anderson, 1977; Lehrer, 1980; Cartwright and Collett, 1982). Since bees do not possess stereoscopic vision (Horridge 1977), the question of how they estimate their distance from a mark has puzzled several workers. The results of

several studies show that the bees use two different types of cues in this task: (i) The retinal image size of the mark as viewed from the feeding site. (ii) Motion parallax, i.e., the speed at which the contours of the mark move across the retina when the animal moves a known distance or at a known speed: Nearer marks move faster than farther ones independent of their size. The first strategy predicts that when the mark is replaced by a smaller or a larger one, the bees would search at a nearer or a farther site, respectively (Cartwright and Collett, 1979; Maurer, 1980). The second predicts that altering the mark's size would not diminish the bee's performance in correctly localizing the feeding site (Cartwright and Collett, 1979; Lehrer 1980). Since in the above studies the bees were able to use either strategy or both of them simultaneously, no conclusive information could be obtained concerning the accuracy of distance estimation. In most cases, the bees seem to have applied some kind of compromise in the task, resulting in a rather mediocre performance.

In a recent study conducted at the Australian National University in Canberra during autumn 1986 (Lehrer *et al.*, in prep.), Srinivasan, Shao-wu Zhang and I set out to investigate the accuracy of the bees' distance estimation. Our ambition was to make sure that the bees used motion parallax and only that in the task, because in such a case, in the light of the findings described in the previous sections, it would be worthwhile to look at the spectral sensitivity of this performance.

We trained bees to enter the laboratory through a hole in the window and collect food on an artificial meadow. The meadow consisted of a horizontal surface (30cm x 40cm) lined with white paper and surrounded by a 12cm high wall lined with the same paper. The wall encouraged the bees to fly at a certain height above the meadow before landing on a flower. The flowers were black discs of various sizes, ranging between 20mm and 70mm in diameter. Six of them were placed flat on the meadow, each provided with a drop of water, and one was placed on a 70mm high nail and offered a drop of sugar solution. The size of the rewarded flower as well as its position was varied between each two rewards. The positions of the flowers lying on the ground, which were of six different sizes, were varied as well.

The bees' performance in localizing the correct flower was tested by offering them simultaneously three flowers of different sizes positioned on 70mm high nails (the training height), and three others on the ground, all flowers being unrewarded. In different tests, flowers of different sizes were offered at different positions within the meadow. As soon as at least 80% of the bees' landings occurred on the three high flowers, we commenced with critical tests. In these, the bees were offered a choice between five flowers of different sizes placed at five different heights, the highest at the training height, the lowest on the ground. Again, the sizes and the positions of the flowers were varied from one test to another.

Fig. 13 shows the distribution of the bees' landings on the five test flowers, summed over all tests and, normalized to the highest value. The bees' choices are strictly correlated with the flowers' height. Consequently, the bees' estimation of the height of the flowers is considerably accurate.

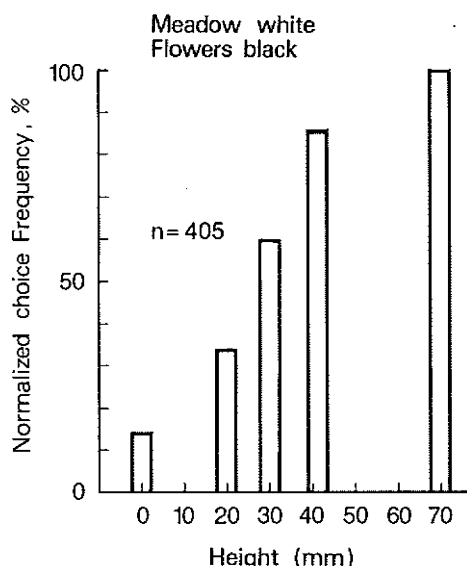


Fig. 13. Distribution of the bees' landings on five flowers of different heights after training to the highest flower. Flowers were black against a white background.

In this experiment the bees could neither learn a particular retinal size of the rewarded flower, since this varied from one reward to another, nor measure the vertical distance of the flower from the upper edge of the wall, since this varied with the flower's position and with the bee's location within the flying plane. The spatial relation between the different flowers offered no cues either, since it was not kept constant. Olfactory cues were excluded as well, since, during training, each of the flowers of different sizes was rewarded at one time or another. (Bees are in the habit of marking the feeding place with a particular pheromone.) In addition, the flowers were replaced by fresh ones prior to each test. The only information available to the bees in the task was motion parallax, and now we were ready to look at the spectral properties of this performance.

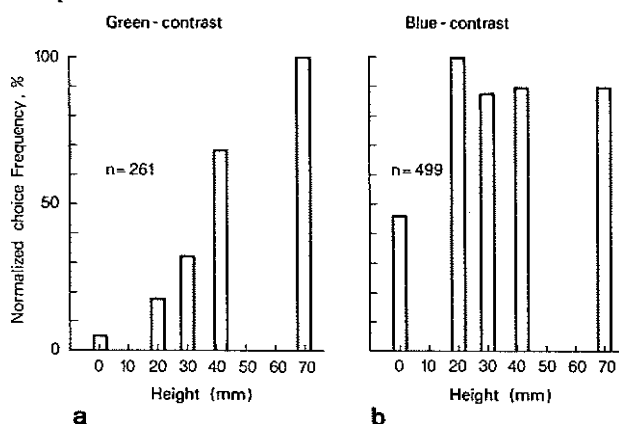


Fig. 14. As Fig. 13, but flowers and background offered either green-contrast (a) or blue-contrast (b)

In Fig. 14, the meadow was yellow and the flowers were blue. In (a), flowers and meadow offered exclusively green-contrast, while in (b) they produced exclusively blue-contrast. (We used the same pigment papers as in the MAR and the scanning experiments described above.) From the comparison of the results of the two experiments it is clear that distance estimation by means of motion parallax uses the input of the green channel and is therefore a colour-blind performance.

TO BE OR NOT TO BE A COLOUR-SEEING BEE

The four types of behaviours described in this article — the optomotor response, the movement avoidance response, the scanning behaviour, and distance estimation using motion parallax cues — are by all means four different types of behaviour. However, all four are clearly movement-induced behaviours. If the bee is again asked the original question, to be or not to be a colour-seeing bee, she will now insist that we specify whether we want her to look at stationary or at moving objects. I hope the reader is now convinced that the bee sees colours in images of stationary objects and is blind to the colours of images that move across the retina.

The reader would, however, be wrong. While it is true that in all of the four movement-induced responses I have described the bees do not use colour information, in spite of the fact that, physically, colours are present in the stimuli, Srinivasan, Wehner and I know that bees are capable of seeing colours in moving stimuli that, physically, contain no colours at all. The perception of movement-induced colour *illusions* will be the subject of our next publications (Srinivasan *et al.*, in press; Lehrer *et al.*, in prep.).

DISCUSSION

Bees are not the only insects to display a variety of movement-induced responses. Flies, for instance, track moving objects, chase other flies, land on approaching surfaces. (Tracking: Virsik and Reichardt, 1974; Land, 1975; Wehrhahn and Poggio, 1976. Chasing: Land and Collett, 1974; Collett and Land, 1975; Srinivasan and Bernard, 1977. Landing response: Braitenberg and Taddei-Ferretti, 1966; Perez de Talens and Taddei-Ferretti, 1970.) Although in the fly's retina there exist at least two (probably three) spectral classes of photoreceptors (rev. Menzel, 1979), it was not until recently that colour vision in a fly species could be proved behaviourally (Menne and Spatz, 1977). The fly's optomotor system has been shown to be colour-blind (Schlegel, 1934; Kaiser, 1968; Kirschfeld, 1972), but it remains to be seen whether the other movement-induced behaviours in the fly are colour-blind as well.

Motion-induced responses are also involved in the mating behaviour of butterflies and dragonflies (rev. Wehner, 1981, pp. 514-523), who are known to possess colour vision. However, the spectral sensitivity of these behaviours is not in all cases known. One very elaborate investigation done by Pajunen (1964) on mating behavior of the

dragonfly *Leucorrhinia dubia* shows that the cue involved is, indeed, movement, and that the male is blind to the colours of the female. The bee, however, is the only insect in which several different types of movement-induced behaviour have been not only found but in addition examined with respect to their spectral properties. In all of them, the bee behaves as if she possessed no colour vision.

Why should the bee who is famous for her excellent colour vision operate as if she were colour-blind whenever the task involves looking at moving objects?

To answer this question it is necessary to look at the neural mechanism of motion perception. Fig. 15 shows a model of a directionally-sensitive movement detector proposed by Srinivasan (1984). Although it is a very simplified model (for more sophisticated models see Hassenstein and Reichardt, 1956; Mimura, 1970; Wehner, 1981, Fig. 13), it possesses everything that is needed for detecting movement.

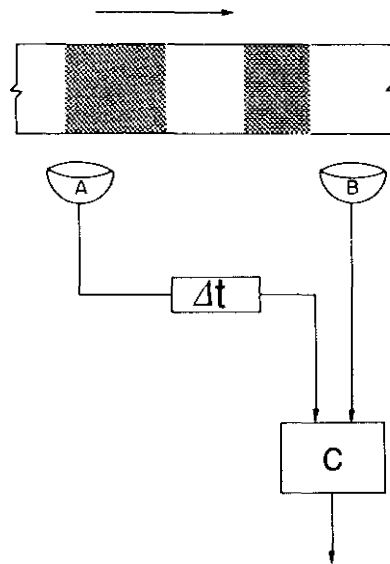


Fig. 15. Schematic representation of a directionally-selective movement detector. Arrow indicates direction of movement of the visual pattern. From Srinivasan, 1984.

It has two input channels, A and B, in a simple case they are two single photoreceptors in two neighbouring ommatidia. The visual pattern moving in the direction of the arrow will stimulate receptor A first, and then, with some delay, receptor B. Now all that has to be done is to compare the two inputs with each other. This is done at the Comparator (C in Fig. 15). If the input in A at time t has been the same as the input in B at time t plus Δt , then certainly movement has taken place. Movement detection can thus be done by means of correlation analysis, taking into account the time delay (Δt in the model). Whenever positive correlation is found, movement is registered and the system will in most cases respond to it. (For more detailed considerations see Hassenstein and Reichardt, 1956, Mimura, 1970, and Srinivasan, 1984. Summary in Wehner, 1981.)

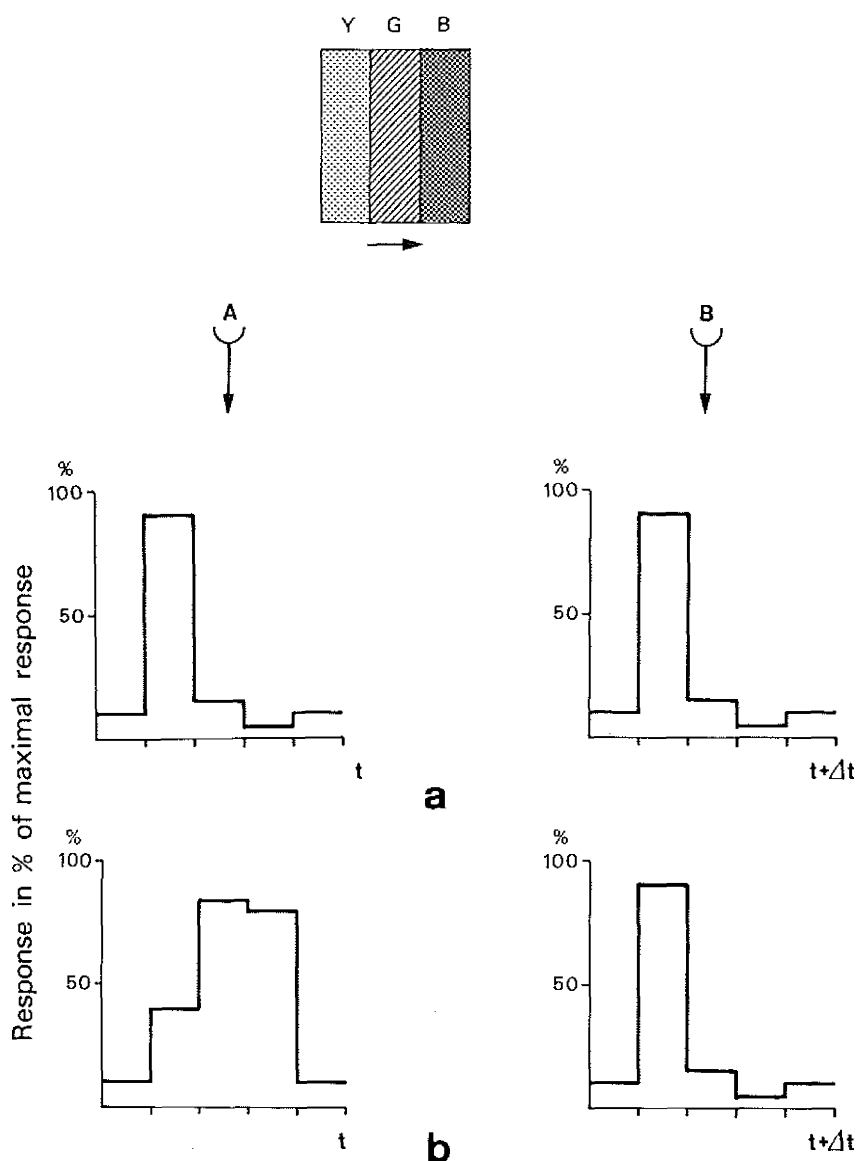


Fig. 16. Time course of excitation evoked by a three-coloured moving pattern in the two input channels A and B of the movement detector of Fig. 15. In (a), both A and B are blue channels; in (b), A is a green channel and B a blue channel. Calculations are based on the data shown in Fig. 17.

Since the bee's world is coloured, I have chosen, in Fig. 16, a coloured moving pattern constructed of pigment papers the reflectance curves of which are known. The colours are, from left to right, yellow, green, and blue. From the spectral sensitivity curves of the bee's photoreceptors (Fig. 17) and from the reflectance curves of these pigment papers (inset of Fig. 17) I have calculated the relative amount of excitation caused in each of the three spectral types of receptors by each of these three colours. Considering again the movement detector of Fig. 15, let us assume first that the inputs

of channels A and B are both of the same spectral type, say, both are blue receptors.

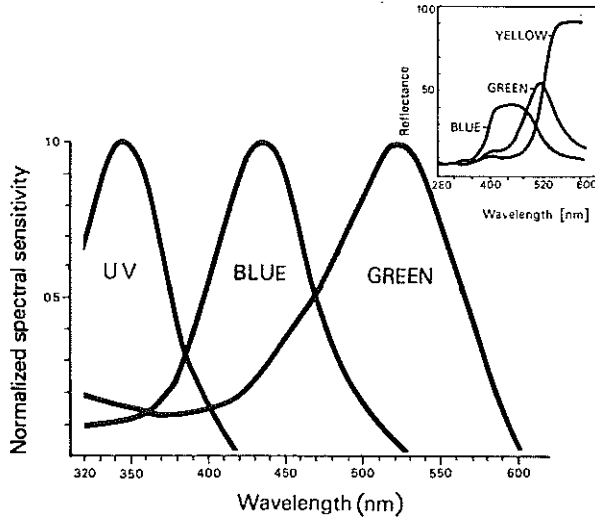


Fig. 17. Spectral sensitivity of the bee's three types of photoreceptors. After Srinivasan and Lehrer, 1985. Inset: Reflectance curves of the coloured papers used in the considerations of Fig. 16.

Such a case is assumed in Fig. 16a, which shows the time course of excitation in A and in B (from the calculations mentioned above) as the pattern moves relatively to the retina. Obviously, at time $(t + \Delta t)$, the excitation in B will be exactly the same as Δt before in A. The comparator will therefore announce maximal correlation. If A, however, were of a different spectral type, say, a green receptor, as is assumed in Fig. 16b, then the pattern of excitation in B will differ from the one in A. The comparator would have to cheat if it wanted to claim the two inputs were correlated. However,

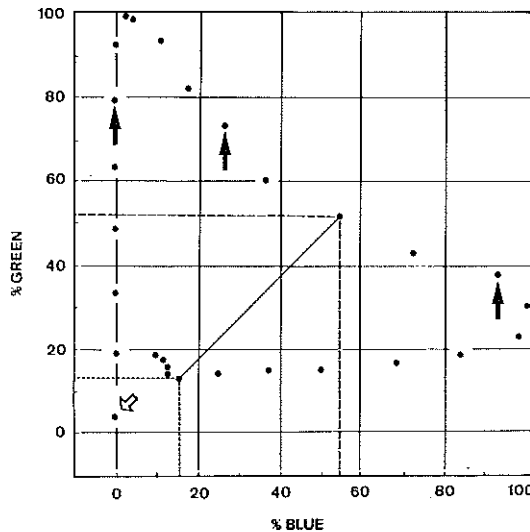


Fig. 18. Relative excitations evoked in the green (ordinate) and the blue receptor (abscissa) by individual spectral colours of the range 320nm-600nm (in 10nm intervals). Arrows depict the three colours used in the considerations of Fig. 16.

comparators are known to be honest guys. The bee is now in danger of not recognizing movement, although movement has, in fact, taken place.

While Fig. 16 represents only one particular example, in Fig. 18 I have tried to generalize the case. In this scatter diagram the spectral colours visible to the bee (in 10 nm-intervals) are placed under the assumption that A is a green receptor and B a blue receptor, as in Fig. 16b. The coordinates depict the relative amount of excitation in the two receptors caused by each of the colours. It is not easy to find two colours which, when offered one after the other, will cause a change of excitation in each of the two channels that is comparable in both magnitude and sign. One example is drawn in the figure. One may add one more colour (white arrow in the figure) and will then have a three-colour combination that would yield positive correlation. However, a great number of combinations are possible that would not. The black arrows in Fig. 18 depict the three colours I have used in the considerations of Fig. 16.

In Fig. 19 the same calculations were done as in Fig. 18, this time under the assumption that all three classes of photoreceptors deliver the input to B, while A relies, as before, on the green receptor only. Here we find perfect positive correlation for all wavelengths greater than 530 nm. This might not at all be a terribly bad solution: Such colours are, indeed, very well represented in terrestrial objects. However, if one adds to them just one colour from outside this spectral range, correlation will be gone. (The arrows again depict the three colours of Fig. 16). If the bee now were one of the many insects that are a potential meal of colourful birds, she would certainly risk her life with a movement detector of this kind. Or if she were a colourful dragonfly female starving for love and being well aware of the fact that all the male needs see is her gracious flight-style (Pajunen, 1964), there love would go.

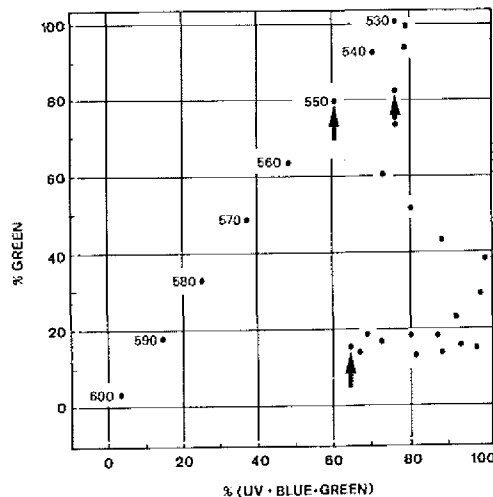


Fig. 19. As Fig. 18, but abscissa denotes summed excitations of all three spectral receptor types. Arrows as in Fig. 18.

Although we have considered only a few examples here, analyses of other cases (see Srinivasan, 1984) show that the problem does not disappear unless both A and B receive inputs from the same colour channels.

This can be done in several ways. Both A and B could use the UV channel, or the blue channel, or the green channel. In either case, the system would obviously be colour-blind. Other possibilities would be to use in both A and B any combination of two of the three channels, or all the three of them. Even in these cases, this will be at the cost of colour vision, since once summation has taken place no ratios can be extracted (see Introduction).

From the "neurotechnical" point of view, the easiest solution would probably be to pool the inputs of all three channels in both A and B — because, in the bee's retina, all three spectral types of photoreceptors contribute to the light-absorbing structure, the rhabdom, in every single ommatidium.

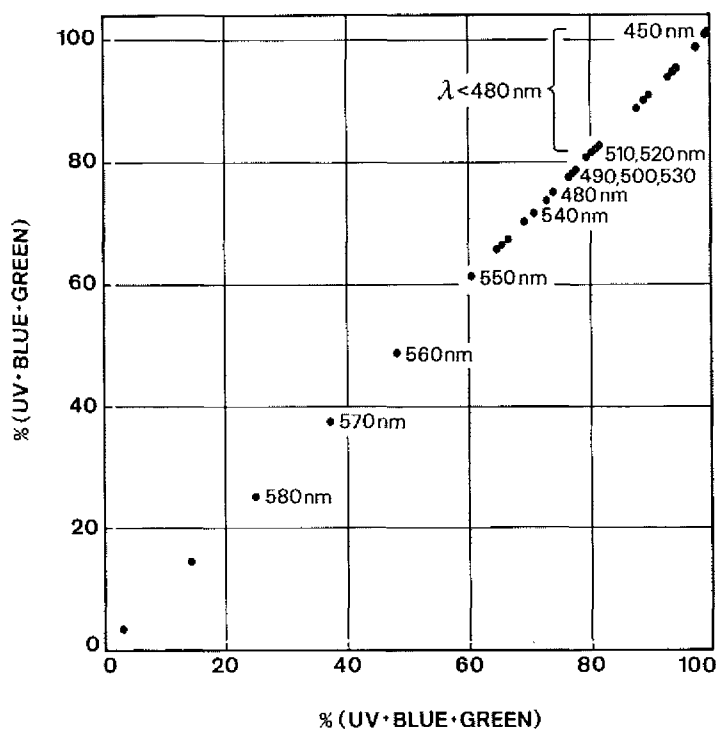


Fig. 20. As Fig. 19, but ordinate denotes summed excitations of all three receptor types.

In Fig. 20, the bee's motion detector indeed receives the summed input of all three channels. In this case, correlation is perfect, no matter which colours and how many of them one wishes to choose. For best results one would, of course, wish to choose colours to which the system is most sensitive. The system shown in Fig. 20 is most sensitive to very short-wavelength colours. However, these are colours that are hardly ever associated with moving images.

The best solution is now obvious (Fig. 21): The motion detector collects its input exclusively from the green channel. Now it can truthfully announce movement whenever movement occurs, and it is, in addition, most sensitive in that particular spectral range in which one finds the colours of objects the images of which move most frequently across the retina. In addition, as another glance at Fig. 17 will reveal, no one colour will leave this movement detector completely indifferent.

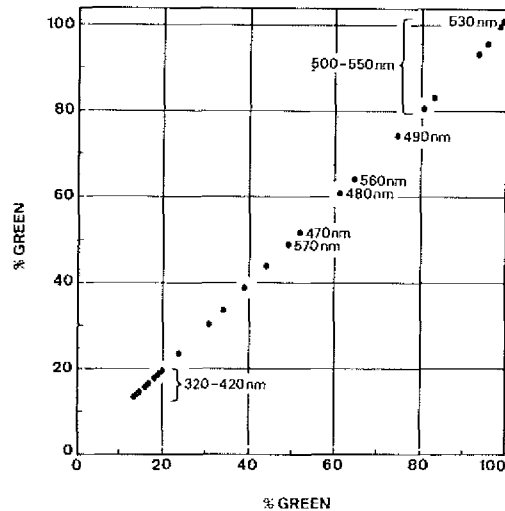


Fig. 21. As Fig. 20, but both ordinate and abscissa denote relative excitations of the green receptor.

The experiments described above show that, in the distal past, natural selection applied the same arguments to the bee's motion detection system.

While I am sure that the bees have solved the problem quite well, I do not doubt that other colour-seeing insects have as well. This could, perhaps, be shown behaviourally, but equally one might argue that the insects' mere existence is sufficient proof. One of the many adaptations that have made insects so successful might be their ability to be colour-blind when their way of life causes them to view a world that moves.

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