Wavelength Specific Behaviour
of the Whitefly *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae)*

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Summary. The visual behaviour of the whitefly *Trialeurodes vaporariorum* was investigated using a 'settling' response paradigm (Fig. 1) and a phototactic paradigm (Fig. 2).

1. Intensity response functions of the 'settling' response had different shapes at different wavelengths (Fig. 3).

2. Two forms of the 'settling' response paradigm gave markedly different results (Table 1). This showed that the whiteflies exhibited wavelength specific behaviour.

3. Using the phototactic paradigm, intensity response functions at 400 nm and 550 nm had opposite signs above threshold. There were no colour interaction effects (Figs. 5, 6, 7) and therefore no evidence for colour vision at least for that particular behavioural paradigm.

4. The phototactic paradigm at 400 nm and 550 nm probably measured two different antagonistic behavioural patterns, the visual inputs of which did not interact.

Introduction

True colour vision has been defined as the ability of an animal to distinguish spectral colours on the basis of wavelength differences only, independent of brightness differences or absolute spectral distribution of the stimulus (Menzel 1979). It involves central integration of the output of photoreceptors with different spectral sensitivities (Hu and Stark 1977). An animal with true colour vision can distinguish between a series of different wavelengths with a maximum discriminative ability falling between the peak sensitivities of the respective photoreceptors [e.g. ants (Kretz 1979), bees (von Helversen 1972)].

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On the other hand, wavelength specific behaviour occurs when different behavioural patterns of an animal have markedly different spectral sensitivities (Menzel 1979). This implies that photoreceptors with different spectral sensitivities may trigger or control different behavioural patterns but that the outputs of these receptors are not integrated in the central nervous system. It may be possible to demonstrate that a particular behavioural response is apparently intensity independent when the behavioural patterns controlled by the respective photoreceptors are antagonistic, but in contrast to true colour vision, wavelength specific behaviour cannot be independent of the absolute spectral distribution of the stimulus. An animal with colour vision may display wavelength specific behaviour, but demonstration of the presence of more than one photoreceptor with different spectral sensitivities, or wavelength specific behaviour, does not imply that an animal has colour vision. This has to be shown.

Among the insects the colour vision system of the honey-bee has been most studied (von Frisch 1914; Kühn 1927; Daumer 1956; von Helversen 1972; Neumeyer and von Helversen 1976; Neumeyer 1980). Only in the bee (von Helversen 1972) and the desert ant *Cataglyphis bicolor* (Kretz 1979), has colour vision been studied sufficiently to enable a spectral discrimination function to be constructed. In other insects, colour vision has been studied only qualitatively (reviewed by Burkhardt 1964; Mazokhin-Porshnyakov 1969; Autrum and Thomas 1973; Menzel 1975; Menzel 1979). Only a few have been shown to have true colour vision, despite the large number of species studied. This is probably because many species are difficult to train (Mazokhin-Porshnyakov 1964; Menzel 1979), training being the most powerful technique available. Nevertheless it is probable that true colour vision exists in, for example, *Papilio troilus* (Swihart 1971), *Paravespula germanica* (Beier and Menzel 1972) and *Formica polyctena* (Kiepenheuer

1968). All of these species have been successfully trained. *Drosophila melanogaster* has been conditioned to blue and yellow; according to Menne and Spatz (1977), the conditioning effect was largely independent of intensity, but Bicker and Reichert (1978) found that conditioning was wavelength and intensity dependent. Simultaneous and successive colour contrast has also been demonstrated in *Drosophila melanogaster* (Fischbach 1979).

The whitefly *Trialeurodes vaporariorum*, an important pest of glasshouse crops (reviewed by Vet et al. 1980), shows a spontaneous preference for yellow (Lloyd 1922; MacDowall 1972; Vaishampayan et al. 1975) and appeared to be a good candidate for true colour vision, since Moericke et al. (1966) found that the 'fall reflex' was apparently intensity independent. The fall reflex was a reaction that occurred to yellow and was characterised by cessation of wing movement of a flying whitefly, followed by downward movement of the abdomen, movement of the wings up and together and the legs close to the body with the femora pointing upwards and the tibiae and tarsae pointing downwards. The work of Moericke et al. (1966) and Vaishampayan et al. (1975) indicated that the behaviour of *T. vaporariorum* may be wavelength specific, but their results are difficult to interpret because the role of ultraviolet light was neglected and the intensities and spectral composition were not sufficiently controlled.

There are many examples of wavelength dependent behaviour, but relatively few well analysed cases of wavelength specific behaviour (reviewed by Menzel 1979). Wavelength specific behaviour patterns are especially interesting because they may help elucidate the sensory and interneuronal mechanisms of colour vision in invertebrates (Menzel 1979). This paper demonstrates wavelength specific behaviour in the whitefly *Trialeurodes vaporariorum,* using a 'settling' response analogous to landing on a host plant after a short flight, and also a form of phototaxis that probably conforms to the 'fast' phototaxis used by Menne and Spatz (1977).

Materials and Methods

Whiteflies

A culture of whiteflies was maintained on the bean *Phaseolus vulgaris* using a modified version of Scopes and Biggerstaff's (1971) mass-rearing technique for *Trialeurodes vaporariorum.* Adult whiteflies emerged in a growth-cabinet maintained at 21 °C ± 1 °C and were transferred to young bean plants soon after emergence by gently tapping them off one plant onto another. All whiteflies tested were one day old and were dark-adapted at 25 °C ± 1 °C for 15 min immediately before testing.
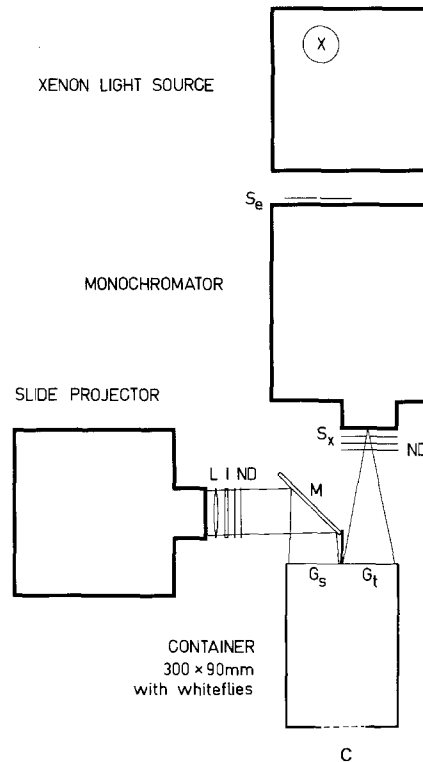

Fig. 1. Diagram of the apparatus used to measure the 'settling' response. *X* 150 W xenon lamp; S_e entrance slit; S_x exit slit; *L* lense; *I* 400 nm interference filter; *ND* neutral density filters; *M* aluminium surface coated mirror; G_s ground-glass screen illuminated by the standard 400 nm light; G_t ground-glass screen illuminated by the test light; *C* hole through which the whiteflies were introduced into the container and through which a photograph was taken of the whiteflies on ground-glass screens 2 min after the whiteflies were introduced

Test Paradigms and Experimental Procedures

Settling Response. The number of whiteflies that settled on an illuminated surface was used as the criteria for measuring the 'settling' response. The test container consisted of a clear plexiglass cylinder 300 mm × 90 mm diam. (Fig. 1). At one end were two vertical ground-glass surfaces, one illuminated with a constant intensity of 400 nm light (standard), the other with varying intensities and wavelengths (test). The two surfaces were separated by a vertical divider to prevent leakage of light from one surface to the other. The position of the standard and test surfaces were alternated and the container cleaned with distilled water between each trial. A black screen was placed around the container to eliminate a small amount of stray light from the light sources. All trials were carried out in a darkroom maintained at 25 °C ± 1 °C and a relative humidity of 50–60%.

Approximately 200 whiteflies were dark-adapted for 15 min in a polystyrene vial (8.3 × 3.5 cm) placed in a light-proof box; they were then introduced into the container, through a hole in the opposite end to the ground-glass, by gently tapping the vial containing the insects. The insects were introduced while the lights were on. The number of whiteflies on each surface was recorded photographically after 2 min. The 'settling' response (SR) was represented by a percentage –

$$SR = \frac{N_t}{N_s + N_t} \times 100$$

where N_s is the number of insects recorded on the standard (400 nm) surface and N_t the number recorded on the test surface.

AUTOMATIC SLIDE
PROJECTORS

L
I
ND

B
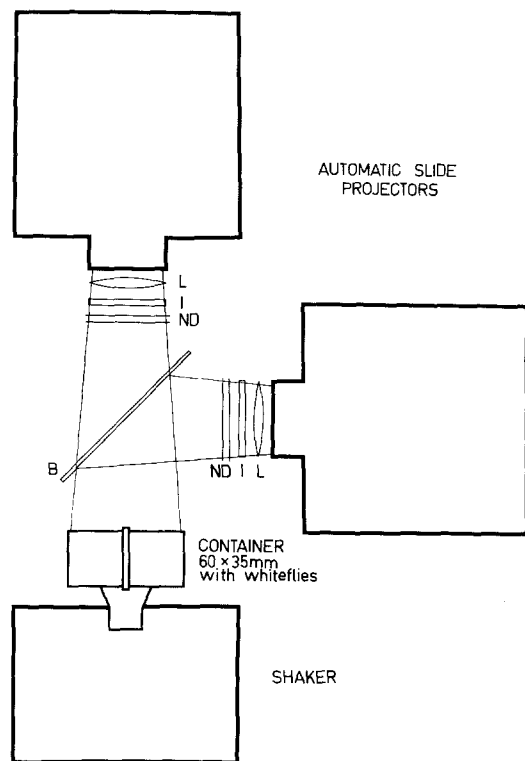
ND I L

CONTAINER
60 x 35mm
with whiteflies

SHAKER

Fig. 2. Diagram of the apparatus used to measure phototaxis. *L* lense; *I* interference filter; *ND* neutral density filters; *B* beam splitter. The projectors were focused on the container; slides, which were clear or blacked-out on one side, were exchanged in the projectors according to the illumination desired

Phototaxis. Here, the movement of whiteflies towards an illuminated region was used. The method used by Bicker and Reichert (1978) for *Drosophila melanogaster* was slightly modified, taking into account the small size of *T. vaporariorum* and the observation that *T. vaporariorum* is much less active than *Drosophila* under the same conditions.

The test container was a cylinder made from two polystyrene vials (20 × 35 mm diam.) joined lengthwise by a metal ring painted matt black (Fig. 2). The rear half of each vial was matt white, while the other half and the ends remained transparent. This design enabled rapid dismantling of the apparatus for cleaning or introduction of the insects. The apparatus was cleaned with distilled water before each trial and the orientation of each vial randomised. All trials were carried out in a darkroom at 25 °C ± 1 °C and a relative humidity of 50–60%.

Approximately one hundred whiteflies were dark-adapted for 15 min in the test container, after which the container was mounted on a vortex mixer. All manipulation was carried out under dim red light (Kodak safelight filter No. 1 A). The container was shaken vigorously on the mixer for 1 s in complete darkness; immediately it stopped shaking the projectors (see below) were turned on. After 2 min the number of whiteflies in each half of the container was counted under high intensity 550 nm light. The 400 nm light was turned off. Under this illumination the whiteflies moved very little and it is unlikely that it affected the final distribution of the insects. For the intensity response functions (Fig. 5), the response was recorded as a percentage of the total in the illuminated side; in the experiment involving a colour contrast (Fig. 6), the results were recorded as a percentage of the total in the side illuminated by the standard 400 nm light.

Optics

Settling Response (see Fig. 1). The light source for the standard light was a slide projector fitted with a 400 nm interference filter with a one-half bandwidth of 10 nm (Oriel G-572-4000). Monochromatic light from this projector was reflected onto the ground-glass via an aluminium surface-coated mirror. The light source for the test light was a Bausch and Lomb high intensity grating monochromator with a visible grating (33-86-02) and xenon lamp (except for the highest intensity at 660 nm, when the projector fitted with a 660 nm interference filter and a Wratten filter No. 25 was used as the test light source, with the monochromator as the standard light). The slit widths were adjusted to give a one-half bandwidth of 10 nm (except for the highest intensity at 350 nm when the bandwidth was 20 nm), and the monochromator was fitted with appropriate cut-off filters (Kodak Wratten filters Nos. 2B, 16 or 25) to eliminate higher order wavelengths. Light intensity was adjusted with Kodak Wratten neutral density filters. Both the cut-off filters and the neutral density filters were used with the gelatin film cemented between two pieces of glass. The flux of the standard light and higher intensities of the test light were measured 5 mm from the ground-glass, inside the testing container, with a Reeder thermopile and Keithley 249 milli-microvoltmeter. A separate measurement was made for each surface. Lower intensities, below the usable sensitivity of the thermopile, were calculated from the optical densities of the neutral density filters which had previously been calibrated at the appropriate wavelengths.

Phototaxis (see Fig. 2). Two automatic slide projectors, fitted with interference filters (400 nm and 550 nm, one-half bandwidths of 10 nm), were used as light sources. One projector, fitted with the 550 nm filter, was also fitted with Wratten filter No. 4 in order to eliminate higher order wavelengths. The projectors were focused on the test container; slides, which were clear or blacked-out on one side, were exchanged in the projectors according to the illumination desired. The difference in light intensity between the illuminated side of the test container compared with the non-illuminated side was of the order of 2 log units, due to reflections in the lenses of the projectors. Intensity was adjusted with the Wratten neutral density filters and was measured by placing the thermopile detector, covered with half a transparent polystyrene vial similar to those making up the test container, on the vortex mixer. Low intensities were calculated from the known optical densities of the neutral density filters.

Statistics

Means and standard errors are given. The action spectrum and the standard errors were calculated from a linear regression of the linear parts of the intensity response curves; except for 660 nm where the quantum flux level which produced a 50% response was read directly from the graph of means (Fig. 3). Analysis of the experiments on wavelength specific behaviour (Table 1) and the effect of light adaptation (Table 2) was by analysis of variance with a log transformation to stabilise the variance.

Results

Settling Response

The 'settling' response was measured by photographing the number of whiteflies on a ground-glass surface illuminated by a test monochromatic light against a standard 400 nm light, 2 min after the insects were introduced. Thus this response was related to flight
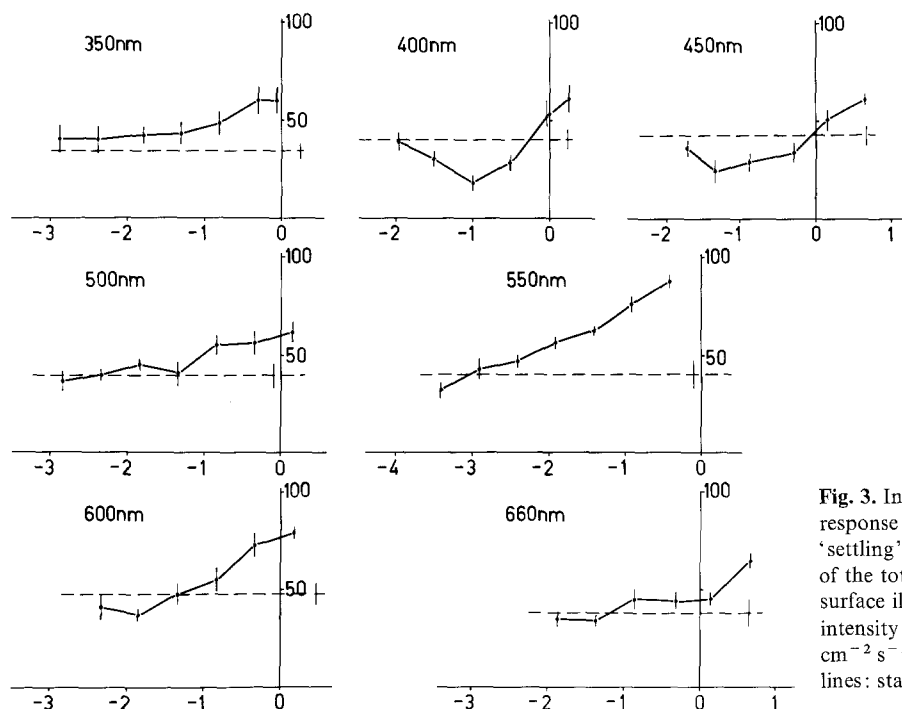
Fig. 3. Intensity-response functions. 'Settling' response plotted against log relative intensity. The 'settling' response was expressed as a percentage of the total number of whiteflies, recorded on the surface illuminated by the test light. Log intensity = zero represents 15.9×10^{13} quanta $cm^{-2} s^{-1}$. ———— Response to darkness. Vertical lines: standard errors of the mean of ten replicates
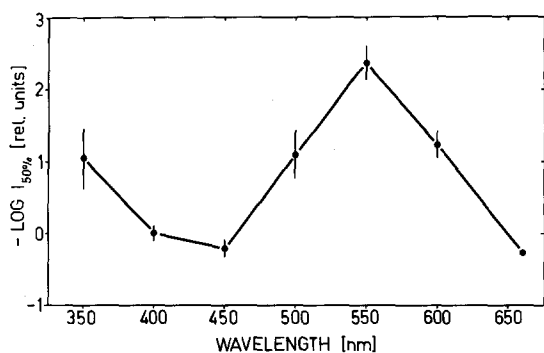

Fig. 4. Action spectrum of the 'settling' response. Minus the log of the intensity which produced a 50% response (from a regression of the linear parts of the intensity response functions; Fig. 3) plotted as a function of wavelength

towards the lights, and the amount of time spent on each surface after an initial landing. Intensity response functions were determined for seven wavelengths (Fig. 3). Since the shapes of the curves were different for different wavelengths, univariance (Naka and Rushton 1966; Rodieck 1973; Menzel 1979) could not be assumed for this behavioural response. The principle of univariance states that the response of a single photoreceptor is dependent on the number of quanta absorbed not the wavelength, and so if univariance holds for a given response (behavioural or otherwise), intensity response functions will be parallel. If univariance is to hold for single photoreceptors, at least two photoreceptors must be involved in this behavioural response. The action spectrum

for the 50% response level (Fig. 4) showed a peak at 550 nm, a minimum at 450 nm and rising values into the ultraviolet. MacDowall (1972) constructed a spectral efficiency function by measuring the number of whiteflies landing on a window illuminated with equal quanta of monochromatic light of various wavelengths. The action spectrum of the 'settling' response agrees with MacDowall's (1972) spectral efficiency function which peaked at 550 nm and closely followed the transmission spectrum of a tobacco leaf (475 nm to 625 nm), but since the 'settling' response was not univariant, the shape of the action spectrum changes with response level. Thus this experiment provides no evidence for colour vision *per se*, but does indicate that wavelength as well as intensity provide important behavioural cues. The whiteflies were probably exhibiting wavelength specific behaviour.

The behaviour patterns involved in the 'settling' response involved flight towards the lights, landing and take-off behaviour. It is likely that short wavelengths (≤ 400 nm) stimulate flight and inhibit landing of *T. vaporariorum*, while longer wavelengths stimulate landing and inhibit flight (Coombe 1981). To elucidate one of the possible behaviour patterns which may be involved in the 'settling' response, and also to show that *T. vaporariorum* shows wavelength specific behaviour according to Menzel's (1979) definition, the test paradigm was slightly modified. The ground-glass screen was smeared with a layer of paraffin oil which trapped all the whiteflies that landed on it. By comparing this method with the previous

Table 1. Photographic method vs trapping method

Wavelength	Percentage of the total on the test surface (mean of ten replicates)		
	Photographic method ('settling' response)	Trapping method	
350 nm	54.4	67.1	n.s.
450 nm	48.9	11.8	**
550 nm	50.0	20.2	**
	n.s.	**	

** Significant at the 1% level
n.s. Non significant

Table 2. Effect of light and dark-adaptation at 550 nm

	Percentage of the total on the test surface (mean of ten replicates)		
	Photographic method ('settling' response)	Trapping method	
Light-adapted	50.7	25.7	**
Dark-adapted	55.8	18.8	**
	n.s.	n.s.	

** Significant at the 1% level
n.s. Non significant

Fig. 5. Intensity-response functions of phototaxis for 550 nm (A) and 400 nm (B). The response, which was expressed as a percentage of the total number of whiteflies in the illuminated half of the container, is plotted as a function of log relative intensity where zero represents 8×10^{13} quanta cm^{-2} s^{-1}. Vertical lines: standard error of the mean of 10 replicates

photographic method which measured the 'settling' response, one possible behaviour pattern contributing to the overall 'settling' response could be separated; namely the initial attraction to an illuminated surface while the whiteflies were in motion.

At the intensity that gave a 50% 'settling' response (from Fig. 3), at 350 nm, 450 nm and 550 nm the response using the paraffin was markedly different from the 'settling' response measured by photography (Table 1). The response to 450 nm and 550 nm was much less when the trapping method was used and so the action spectrum for the trapping paradigm is different from the photographic paradigm. Therefore the underlying behaviour patterns must have different spectral sensitivities if the assumption can be made that adaptation levels were similar or had no effect. However, in the trapping paradigm many of the whiteflies were trapped soon after they were introduced and so were probably dark-adapted, but in the 'settling' response paradigm the whiteflies were probably light-adapted. Thus the above assumption could not be made. To test whether the adaptation levels could have influenced the observed responses, groups of whiteflies were either dark-adapted or light-adapted in a beam from a xenon arc lamp for 15 min before being tested with one or other of the paradigms. From Table 2, it can be seen that, at least
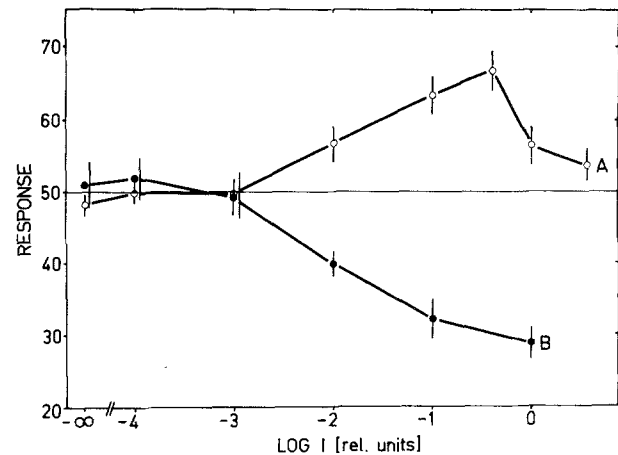
for the 550 nm light, light-adapted and dark-adapted whiteflies behaved similarly. T. vaporariorum clearly shows wavelength specific behaviour.

Colour Interaction

The previous experiments showed that T. vaporariorum exhibits wavelength specific behaviour but did not provide any indication of the complexity of the visual system controlling this behaviour. The following experiment was designed to test whether the system was a relatively simple wavelength specific system as postulated by Menzel (1979) or a more complex, highly developed colour vision system. The phototactic paradigm was originally used in an unsuccessful attempt to condition whiteflies to visual stimuli using shaking as an aversive conditioning stimulus [as used with Drosophila melanogaster (Menne and Spatz 1977; Bicker and Reichert 1978; Reichert and Bicker 1979)]. It proved to be much less tedious and more reliable than the 'settling' response paradigm and was thus used to investigate colour contrast.

The wavelengths 400 nm and 550 nm were selected because T. vaporariorum clearly exhibits wavelength specific behaviour with the 'settling' response at these wavelengths. T. vaporariorum also exhibits wavelength specific behaviour with phototaxis since the intensity response functions for phototaxis (Fig. 5) are different above threshold. The whiteflies were negatively phototactic to 400 nm light but positively phototactic to 550 nm light within the intensities used. Fischbach (1979) demonstrated simultaneous and suc-
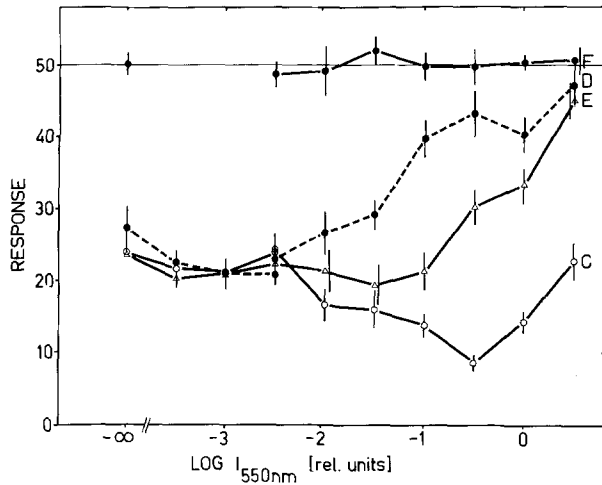
Fig. 6. Phototactic response of whiteflies to constant 400 nm light plotted as a function of log intensity of 550 nm light at the same and/or opposite side of the container. The response was expressed as a percentage of the total in the half of the container illuminated by the constant 400 nm light. The intensity of the 400 nm light (which is represented by zero on the intensity scale) was 8×10^{13} quanta $cm^{-2} s^{-1}$. (C) 400 nm vs 550 nm; (D) 400 nm + 550 nm vs darkness; (E) 400 nm + 550 nm vs 550 nm; (F) 550 nm vs 550 nm (control). The experiment was done in two sections ($I \leq 2.5$ and $I \geq 2.5$). The vertical lines are standard errors of the means of ten replicates. For the sake of clarity only the largest standard errors are shown at the lower intensities
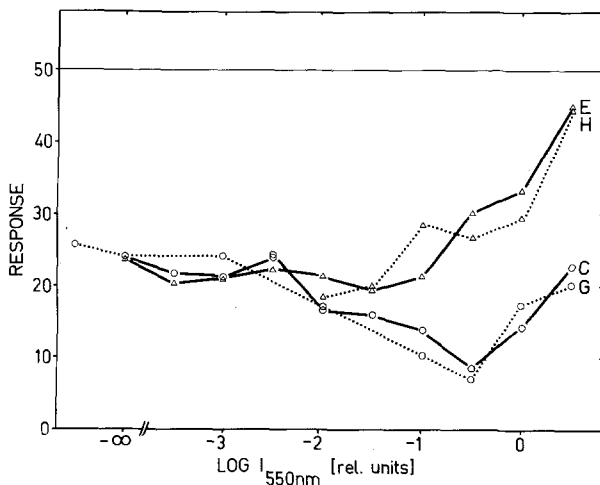

Fig. 7. (C) as in Fig. 6; (G) curve A (Fig. 5) superimposed on (C) by inverting (because of the way A is plotted) and superimposing the responses below threshold; (E) as in Fig. 6;(H) C+D minus the response to 400 nm presented alone. Intensities and response as in Fig. 6

cessive colour contrast in *Drosophila melanogaster* and the same method was used to test for colour contrast effects in *T. vaporariorum*. The results (Fig. 6) showed no colour contrast effects; in the presence of a wavelength contrast, the response was identical to the sum of the respective responses without

a wavelength contrast (Fig. 5), i.e. curve A (Fig. 5) can be closely superimposed on curve C (Fig. 6) by inverting and superimposing the respective responses below threshold (see Fig. 7). This compares with 'slow' phototaxis in *Drosophila* where it is not possible to predict the response in the presence of a wavelength contrast by a linear combination of the responses to the wavelengths presented alone (Fischbach 1979). In addition, the curves in Fig. 6 are as expected if there were no interactions of the outputs of the photoreceptors in the central nervous system. There is no shift in the threshold of curves D or C (Fig. 6) which differs from Fischbach's (1979) results, where he found a shift in threshold of the equivalent of curve D; but there is a shift in threshold of curve E, which is as expected if there were no interactions of the outputs of the photoreceptors. The curves are apparently additive, as Fischbach (1979) found, i.e. C+D minus the response to 400 nm alone = E (Fig. 7).

The intensity response functions (Fig. 5) show that at least two photoreceptors with different spectral sensitivities are involved in the phototactic response because the response is not univariant, but there are no colour contrast effects or interactions of the outputs of photoreceptor types in the central nervous system for these two wavelengths. Therefore there is no evidence for colour vision in the phototactic paradigm.

Discussion

Although the outputs of the different photoreceptors do not interact in the phototactic paradigm, they may interact in other behavioural responses such as food-plant selection, 'slow' phototaxis, the optomotor response, or the 'fall reflex' observed by Moericke et al. (1966). Fischbach (1979) tested 'slow' phototaxis in *Drosophila melanogaster* and it is possible that the difference between his results and those reported here may be due to the different behavioural paradigms used, rather than the different animals. The 'settling' response measured a response analogous to food-plant selection, namely, landing after a short flight, and is also related to the length of time spent on each surface after a landing. It is wavelength specific and may or may not involve colour vision. One other factor that must be considered is that the result may have been dependent on the wavelengths used, although it is doubtful that other wavelength pairs may have produced evidence of interactions of photoreceptor outputs, since the wavelengths used (400 nm and 550 nm) were chosen carefully, based not only on the results from the 'settling' response paradigm but

also on a number of preliminary trials using other wavelength pairs.

Moericke et al. (1966) found that the 'fall reflex' of *Trialeurodes vaporariorum* was apparently intensity independent and this has been taken as evidence of 'colour processing' by Schümperli (1973). However, although Moericke et al. showed that the 'fall reflex' occurred in response to yellow and not to any of a series of grey papers ranging from white to black, this does not mean that *T. vaporariorum* has true colour vision. This type of behaviour can occur when there is no interaction of photoreceptor outputs in the central nervous system. If, for example, there were two non-interacting photoreceptors, one controlling one behavioural pattern and the other controlling a different antagonistic behavioural pattern (e.g. if yellow stimulated landing and inhibited flight while ultraviolet inhibited landing and stimulated flight) the resultant behaviour would be apparently intensity independent because the behaviour would depend on the relative outputs of the photoreceptors and hence the absolute spectral distribution of the stimulus. This may have occurred in the phototactic paradigm of *T. vaporariorum*. The opposite phototactic responses to 550 nm and 400 nm (positive to 550 nm, negative to 400 nm) and the shapes of the curves in Fig. 6 support this supposition. If there were no interactions at all, both at the photoreceptor and also the behavioural level, one would expect D (Fig. 6) to be a mirror image of C, and E to remain at threshold (=response to 400 nm alone). However, what is observed is that D is the mirror image of C below a certain critical intensity, above which D probably tends towards A (Fig. 5), and E (Fig. 6) remains at threshold until this critical intensity is reached, above which it probably tends towards F. The fact that the curves behave as expected close to threshold [unlike *Drosophila* (Fischbach 1979)], coupled with the fact that there are no colour interaction effects, indicates that there are probably no interactions of photoreceptor outputs in the central nervous system. However, because the curves deviate from expectation at higher intensities (and in fact appear as if the behavioural pattern controlled by the 550 nm light is increasingly inhibiting the behavioural pattern controlled by the 400 nm light as intensity increases), the two behavioural patterns are probably antagonistic. This supports Menzel's (1979) hypothesis that early chromaticity-coding systems may have been antagonistically organised between behavioural patterns sensitive to short- and long-wavelengths.

Although *Drosophila* shows simultaneous and successive colour contrast effects in its 'slow' phototactic behaviour (Fischbach 1979), this does not necessarily mean that colour vision in flies is as highly developed as in ants, bees or humans and may not even fit the concept of 'true' colour vision, especially since Bicker and Reichert (1978) have shown that conditioning in *Drosophila* is wavelength- and intensity-dependent. Even so, their conditioning paradigm did not allow them to condition the flies to wavelength differences only. The results reported here, when compared with *Drosophila*, show the necessity to differentiate between wavelength specific behaviour without interactions of photoreceptor outputs (*T. vaporariorum*) and wavelength specific behaviour with interactions of photoreceptor outputs (*Drosophila melanogaster*). Such results also support Fischbach's (personal communication) concept of an evolutionary continuum towards 'true' colour vision, ranging from wavelength specific behaviour with no interactions between input channels to the central nervous system (i.e. photoreceptor outputs) through to variously highly developed 'true' colour vision systems.

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