

Review

Insect visual perception and pest control: opportunities and challenges

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Humans and insects inhabit very different perceptual worlds, so human experimenters need to be aware of their perceptual biases when investigating insect behaviour. In applied entomology, human perceptual biases have been a barrier to the rational design, manufacture, and improvement of pest control devices that effectively exploit insect visual behaviour. This review describes how the influence of human perceptual bias on this area of applied entomology is being reduced by our expanding understanding of insect visual perception and use of visual modelling methods and highlights several important challenges that are yet to be overcome.

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Introduction

The diverse sensory systems of animals and the selective pressures on their neural machinery to drive appropriate behavioural responses to pertinent natural stimuli mean that different species inhabit unique perceptual worlds (“umwelten”) [1]. If the mismatch between the perceptual worlds of humans and non-human animals is not adequately recognised, the perceptual biases of human observers can mislead our understanding of animal behaviour [2,3,4•]. This issue is of great relevance to the applied biology underlying pest control, which often seeks to identify stimuli that influence insect behaviour.

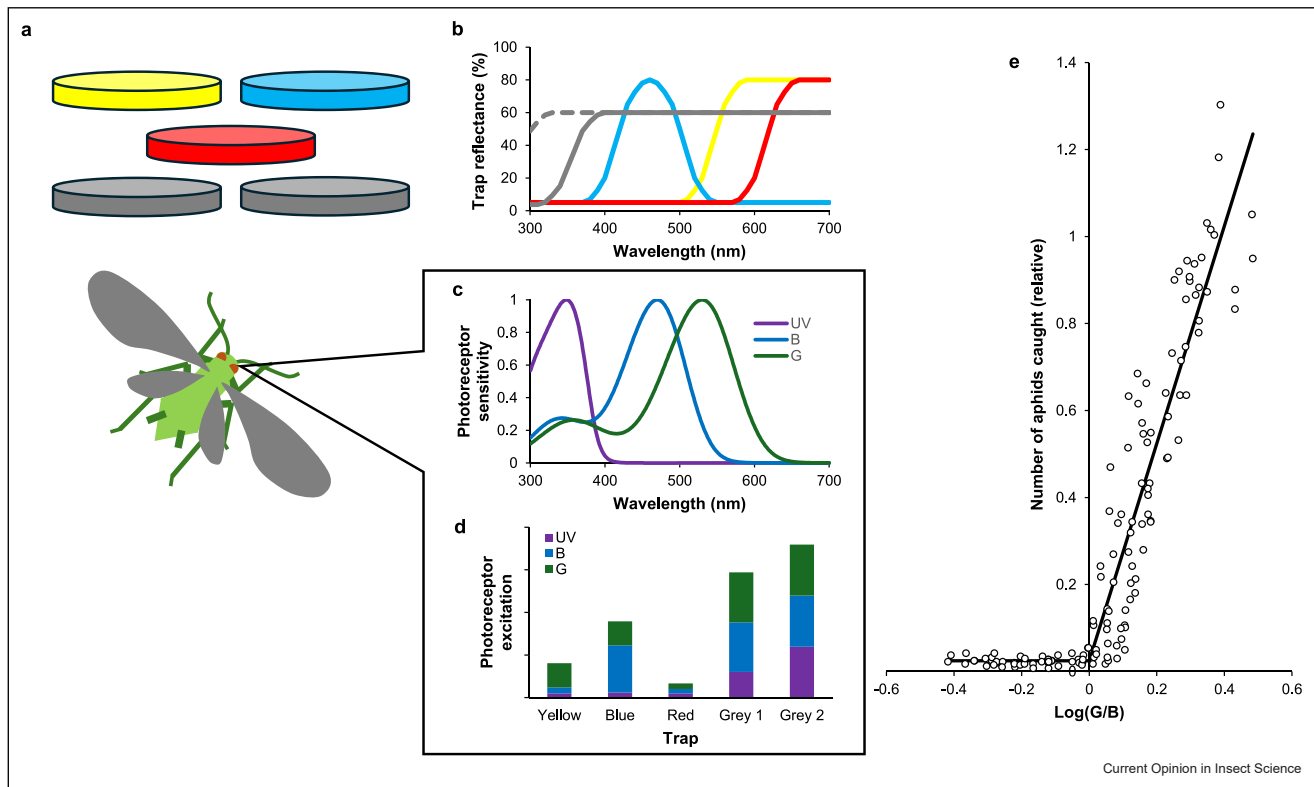
Caves et al. [3] propose that human perceptual biases cause us to (1) make assumptions about how an animal perceives sensory information due to the way we perceive or measure it, (2) assume that particular sensory features are significant to an animal just because they stand out to our perception, and (3) assume that the perceptual systems of animals categorise sensory stimuli in the same way we do when measuring them. The relevance of these biases to applied entomology is well illustrated by investigations into coloured stimuli to attract or repel insects. Such studies have regularly designed and reported visual stimuli exclusively using the language of human perception (e.g. ‘blue’, ‘green’, ‘red’, etc). Colour perceptions are generated by neural computations using the responses of two or more spectral types of photoreceptors as input. Whilst human colour perception derives from comparison of our short (‘blue’), medium (‘green’), and long (‘red’) wavelength-sensitive photoreceptor responses, insects often lack a red-sensitive photoreceptor and generally possess a UV-sensitive one, and the total number of photoreceptor spectral types can vary considerably between species [5]. Given this difference in sensory input, and the vastly different selective pressures on the neural mechanisms of human and insect behaviour, the perceptual worlds of these organisms must also be entirely different. Thus, human colour names do not adequately describe the visual perceptions that underlie insect behaviour (Figure 1a–d) [6]. A similar situation exists for other aspects of vision, including spatial and temporal acuity, field of view, and perception of polarised light.

In this review, we focus predominantly on colour vision, where methods from sensory ecology are now permitting applied entomologists to more effectively address some instances of human perceptual bias. As we gain more insight, other aspects of vision can be incorporated, and new perceptual problems emerge. Making progress on these challenges is critically important because without an understanding of how insects perceive a stimulus, we cannot understand why or how it affects their behaviour. This makes it impossible to efficiently design, correctly manufacture, and rationally improve control devices.

Colour modelling to overcome perceptual bias

Humans describe colour in terms of hue, saturation, and brightness, and these properties derive from different neural computations based on photoreceptor responses

Figure 1



Accounting for insect colour perception in applied entomology. **(a)** Applied entomological studies often investigate catches of insects at coloured traps, but describing those traps by their appearance to a human eye can be misleading. **(b)** The reflectance of light from a trap at different wavelengths can be objectively quantified (spectra shown are for illustration only). **(c)** Insect photoreceptors differ in sensitivity from those of humans. For example, aphids possess UV, blue, and green-sensitive photoreceptors. **(d)** It is the responses of those photoreceptors that provide the inputs to insect visual behaviour. Although the two grey traps are identical to a human eye, they elicit different responses in an aphid's photoreceptors due to its sensitivity to UV light (< 400 nm). Whilst the red trap might be striking to the human eye, it causes weak responses in an aphid's photoreceptors since it reflects most light outside of the aphid-visible range. Systematic investigation is required to determine whether and how such aspects affect the attractiveness of a trap to an aphid, e.g. [22•]. **(e)** Catches of migrant aphids at coloured water traps, expressed relative to the catches at yellow reference traps, could be explained by a colour opponent model comparing the responses in an aphid's green- and blue-sensitive photoreceptors [22•]. Such a model explains why yellow traps are highly attractive to aphids using colour metrics relevant to their behaviour. Mechanistic models of this kind provide a rational basis for selecting or optimising coloured traps.

(e) (figure adapted with permission from Ref. [22•], provided under CC BY 4.0. This panel is excluded from the CC BY license of the current work.).

to light reflected from a stimulus. Neural comparisons of photoreceptor responses extract chromatic information corresponding to hue and saturation, whilst neural sums provide achromatic information corresponding to brightness [7]. The sensory physiology of photoreceptors is well understood, and a photoreceptor's response scales with the number of photons absorbed. Spectral sensitivity functions describing the absorbance of a photopigment or electrical response of a photoreceptor with wavelength have been quantified experimentally for the photoreceptors of a large number of insect species [5] and can be modelled mathematically [8]. There has been considerable recent progress in predicting spectral sensitivity of vertebrate photopigments directly from their opsin sequences, and similar may soon be possible for insect photopigments [9,10]. Given spectral sensitivity functions, plus measured or assumed spectra for

the illuminating light, and reflectance spectra for stimuli of interest, the responses of insect photoreceptors to those stimuli can be calculated. Photoreceptor excitations can be used to position any visual stimulus within a receptor space with axes of each photoreceptor type or a chromaticity diagram with one less dimension that discounts achromatic (i.e. brightness) information [7,11]. Colour distances can also be calculated to determine the discriminability of any two colours based upon the levels of noise in each photoreceptor class [12]. In addition, photoreceptor-based models of behaviour can be created, wherein calculated photoreceptor responses are statistically related to measured behaviour [7,13,14]. Such approaches have great potential in applied entomology because they overcome our perceptual bias by quantifying colour according to the information that can be sensed by the insect [6].

Applied entomology has been relatively slow to adopt insect photoreceptor-based approaches to quantify colour, but they have now proved successful in several applications. To develop more attractive coloured polyester targets to control tsetse flies (Diptera: Glossinidae), statistical models were built to relate calculated photoreceptor signals to tsetse catches at a large number of differently coloured fabrics, creating a simple model of the perceptual mechanism that might drive their attraction [15,16]. A new fabric colour was engineered to more effectively activate the hypothesised mechanism and enhance attraction, and subsequent field tests verified its effectiveness in attracting tsetse [17,18]. Whilst the prevailing view was that tsetse targets needed to be 'blue', this fabric was purple to a human eye, demonstrating the need to focus on insect and not human perceptions. A similar approach to Western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), control hypothesised that an opponent response comparing 'blue'- and 'green'-sensitive photoreceptor outputs drove attraction to sticky traps, so this metric was modelled to select colours for greater attractiveness, and those expectations were confirmed by field tests [19]. Related photoreceptor-based metrics have also been used to model catches of aphids (Hemiptera: Aphididae) [20,21,22•] (see Figure 1e), and pollen beetles (Coleoptera: Nitidulidae) [23] at coloured water traps, with results explaining the effectiveness of the yellow traps currently employed for those species. In each case, photoreceptor-based metrics provide an appropriate, unbiased way to quantify coloured stimuli and a rational basis for improving them that avoids inefficient trial-and-error testing of colours unlikely to be effective based on calculated photoreceptor responses.

Challenges in the application of colour modelling

Despite the success of these approaches, there is still a need to carefully explore their application to a given problem, partly because an animal's perceptual world is not a simple and direct result of its sensory physiology. Many insects possess several different spectral types of photoreceptors [5], but the way these contribute to colour perception can vary. For example, the Japanese swallowtail butterfly, *Papilio xuthus* (Lepidoptera: Papilionidae), possesses eight spectral types of photoreceptor but is functionally tetrachromatic in conditioned colour discrimination [24]. Similarly, oviposition in several other butterfly species can be explained by tri- or tetra-chromatic mechanisms [13,14]. Thus, visual systems equipped with a large number of photoreceptor types might consist of subsystems serving different behavioural tasks, not all of which will necessarily involve chromatic mechanisms [25].

There may also be complexity in the way that colour perceptions are generated from photoreceptor signals. Visual modelling often uses colour spaces, which position stimuli using continuous colour coordinates derived from

photoreceptor signals, and the discriminability of stimuli can be estimated based upon their relative positions within that space (for a review, see Ref. [11]). In Japanese swallowtail butterflies, a population of neurons project to the mushroom bodies (sensory association areas of the brain) where individual neurons are sharply tuned to particular wavelengths across the range visible to the butterfly, potentially representing individual colour perceptions [26••,27•]. In contrast, behavioural evidence from *Lucilia* blowflies (Diptera: Calliphoridae) suggests that colours are perceived in a coarser way comprising just four colour categories [28], and recent research in *Drosophila* (Diptera: Drosophilidae) has identified only three or four types of hue-sensitive neuron within the optic lobe [29••]. Interestingly, categorical colour perception of this kind was not supported by behavioural experiments on hoverflies (Diptera: Syrphidae) [30]. Thus, the way in which a colour space built from sensory signals is translated into discrete colour perceptions may vary between species.

Beyond the traditional concept of 'colour'

The extent to which human subdivision of stimuli into chromatic (hue and saturation) and achromatic (brightness) components relates to insect perceptions of underlying behaviour is unclear (c.f. [3]). For example, achromatic and chromatic information interact to drive phototaxis in *Drosophila* [31]. Similarly, whilst the narrowband inner photoreceptors and broadband outer photoreceptors of flies were thought to serve chromatic and achromatic processing, respectively (e.g. [32]), mutant *Drosophila* with only outer photoreceptors and one class of inner photoreceptor functional can still discriminate blue and green stimuli independent of intensity [33], and neural circuits of the optic lobe previously presumed to underlie separate chromatic and achromatic processing have been found to interact whilst still achieving hue selectivity [34]. Thus, colour models that make incorrect assumptions about subdivisions within insect perception may give misleading results. In this context, artificial neural networks can extend photoreceptor-based models that have explained behaviour using a single linear interaction of photoreceptor signals [7,13,14] since they can incorporate parallel, nonlinear processing of photoreceptor signals using chromatic and/or achromatic mechanisms like those that occur in insect nervous systems and avoid the need to make assumptions about how those mechanisms might be subdivided [35]. Such models can provide working hypotheses for the mechanisms that may underlie behaviour [35], guiding future experimentation or trap development.

An extension of this problem is that the reflectance spectrum of a stimulus may not quantify a neat subdivision of sensory information for an insect (c.f. [3]). When light reflects from a shiny surface, it becomes partially linearly polarised. The response of an insect photoreceptor can be sensitive to the plane of polarised light due to regular

alignment of chromophores and microvilli within its rhabdomere, meaning that at the level of the receptor, polarisation plane and light intensity are confounded. Like many other insects, bees and flies have a dorsal rim region of their compound eyes where photoreceptor microvilli are aligned and the same visual pigment is expressed, providing a specialised region for sensing polarised light. Elsewhere in the compound eyes of bees, rhabdomeres twist to abolish polarisation sensitivity and preserve colour vision [36]. However, in *Papilio* butterflies [37], horseflies (Diptera: Tabanidae) [38], and stable flies (Diptera: Muscidae) [39], this is not the case since all possess photoreceptors that vary both in the wavelength and polarisation plane of light they are most sensitive to (see Figure 2). Consequently, underlying opponent mechanisms comparing photoreceptor responses can be activated by colour or polarisation, potentially resulting in false colour or false polarisation signals. Rather than confounding sensory perception, such

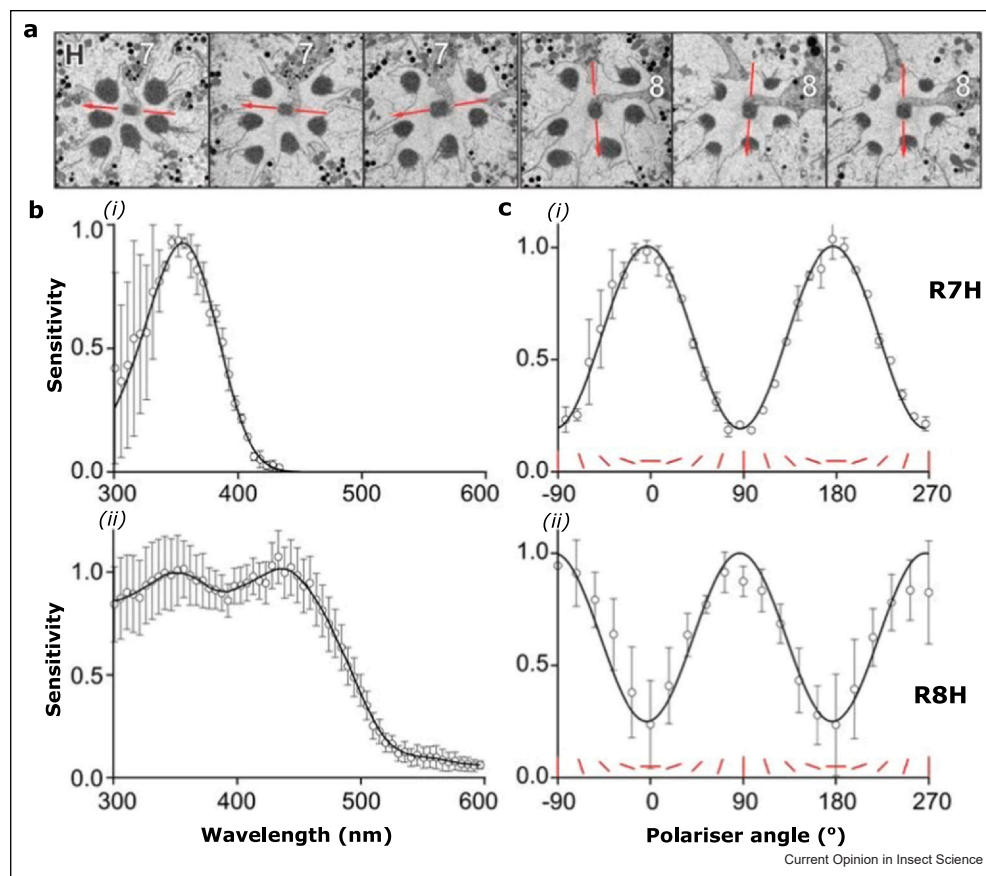
systems likely provide a matched filter relevant to behaviour, for example, a system that would be optimally activated by a leaf of the right colour, with the right surface texture, in the right orientation for oviposition by a butterfly [37].

Such issues are of potentially high relevance to pest control applications. This is because many traps have a slick glue coating, contain liquid, or have glossy plastic elements that may have unintended effects on insect perception and because combining different perceptual elements in the correct way could enhance trapping, as in horsefly traps that combine dark and highly polarising surfaces [40].

Modelling other aspects of vision

Humans can also bring their perceptual biases to other aspects of insect visual behaviour. The large eyes of humans have among the highest spatial acuity vision of all animals,

Figure 2



Complications to the modelling of insect vision in an applied context. Within fly ommatidia, the rhabdomeres of central photoreceptors R7 and R8 are stacked one on top of the other. (a) Successive sections through horsefly H-type ommatidia demonstrate that the microvilli of R7H and R8H photoreceptors are offset by approximately 90° (microvillar angle indicated by red line and photoreceptor identity indicated by number) [38]. (b) Due to possessing different visual pigments, the spectral sensitivity of R7H (i) and R8H (ii) differ. Data are mean \pm SD spectral sensitivities overlaid with a rhodopsin template (i) or smoothed (ii) [38]. (c) Due to the orientation of their microvilli, the polarisation sensitivity of R7H (i) and R8H (ii) also differ. Data are mean \pm SD responses over multiple runs in which a polariser was rotated relative to the eye equator [38]. Because polarisation angles range 0–180°, polariser angles separated by 180° are equivalent. Consequently, colour and polarisation sensations are confounded. Figure is a composite constructed with permission of the authors from Ref. [38], originally provided under CC BY-NC-ND. This figure is excluded from the CC BY license of the current work.

approximately 60 cycles per degree of visual angle (cpd), whereas the ability of arthropod pests to resolve spatial detail is poor to terrible in comparison [41,42]. For example, the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae), with good visual acuity for an arthropod, can resolve 0.33 cpd [43], while the cabbage aphid *Brevicoryne brassicae* (Hemiptera: Aphididae) can resolve just 0.06 cpd [44]. This is because higher sampling resolution in compound eyes requires larger lenses and smaller inter-ommatidial angles, resulting in a dramatic increase in eye size that could not be supported at small body size [45]. Spatial acuity affects the distance at which objects and spatial patterns can be resolved and therefore how visual traps will be perceived in ecologically relevant conditions. Acuity modelling [46] has not yet been applied to pest control but has great promise for reducing human biases in selecting the size, shape, internal pattern, and position of stimuli designed to influence insect behaviour, as well as understanding visual interactions with the environment more broadly. In the same vein, there are also opportunities to model the generally much wider field of view of arthropod pests compared to humans [47] and the temporal resolution of their photoreceptors, which in some species greatly exceeds that of humans and has implications for perception of optic flow and motion control [48], and flicker in light traps [49].

Concluding remarks

Human perceptual biases can impede progress in applied entomology (c.f. [3]), but visual modelling techniques can help overcome these biases and improve pest control. Such approaches have been applied successfully to improve trap colour and promise similar improvements to trap shape, pattern, and more. Whilst these methods allow significant advances in applied entomology, there is still a great deal more to be learnt about insect perception.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors have nothing to declare.

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