Butterfly Color Vision - Another View of Our World

Kentaro Arikawa

Laboratory of Neuroethology, SOKENDAI-Graduate University for Advanced Studies, Hayama, 240-0193, Japan

ABSTRACT

Butterflies often feed on nectar of colorful flowers. How do they find flowers? Do they discriminate flowers by color? We found a swallowtail butterfly uses sophisticated color vision when searching for food. Surprisingly, color vision system appears to be very much different among animals, even among butterflies. I will overview the current understanding of insect color vision from the evolutionary point of view: each animal has its own visual world. Study of insect vision should also contribute designing novel "visual" devices and to manage insect pests for the crop without using chemical insecticides.

1. INTRODUCTION

Color vision is the ability of discriminating visual stimuli based on their spectral (wavelength) contents irrespective of the intensity. We have a trichromatic system based on the blue (B), green (G) and red (R) light sensitive sensors (photoreceptor cells) in the eye (Fig. 1A). Color vision appears to be rather common among animals, some of which in fact exhibit surprisingly good performance in discriminating colors. For example, a swallowtail butterfly *Papilio xuthus* can detect only 1 nm difference in wavelength, which rivals our performance. But *Papilio*'s performance is even better because their visible light expands deeply into the ultraviolet range that we cannot see. We now know that *Papilio* has a tetrachromatic system based on the UV, B, G and R sensitive photoreceptor cells in the compound eye. We have also demonstrated that *Papilio* exhibits color constancy and simultaneous color as well as brightness contrast. Here I first summarize our current understanding about the color vision mechanism of *Papilio*, and then will compare color vision among animals.

2. COMPOUND EYES

2.1 Photoreceptor spectral sensitivities

Compound eyes are composed of multiple units called ommatidia. The ommatidial array is visible from outside as a number of hexagonally-packed facets. The diameter of a facet is about 25 μm in most insects, which makes the number of ommatidia roughly proportional to the size of compound eyes. An ommatidium is a long structure, which are tightly packed to each other making the compound eye a dome-shaped structure. A compound eye of *Papilio xuthus* is made up with about 12,000 ommatidia.

An ommatidium of *Papilio* contains nine photoreceptor cells. Each photoreceptor bears numerous microvilli containing photosensitive protein, rhodopsin, forming a single rhabdom along the ommatidial longitudinal axis. The rhabdom is surrounded by red or yellow pigment, which act as spectral filters for the photoreceptors. A subset of red-pigmented ommatidia has UV-absorbing fluorescence pigment at the top of the rhabdom. Distribution of the red, yellow and fluorescing ommatidia appears random: the *Papilio* eye is a random mesh of 3 types of ommatidia.

Spectral properties of rhodopsin and the filter pigments determine photoreceptors' spectral sensitivity, which can be determined by measuring electrical responses of them. We thus identified UV, violet (V), B, G, R and broad-band (BB) receptors (Fig. 1B). The receptors are embedded in 3 types of ommatidia in 3 fixed combinations [1]. The spectral heterogeneity of butterfly eyes is a particularly pronounced case among insects [2].

3. COLOR VISION OF *PAPILIO*

3.1 Color vision with color constancy

To demonstrate color vision in *Papilio*, we trained naïve *Papilio* to take nectar on a colored disk, simulating their flower-visiting behavior in the field (Fig. 1D). *Papilio* readily becomes able to visit the colored disk even if it is presented with disks of other colors. *Papilio* really used chromatic cue of the disk, not the brightness, because they could select the colored disk among the disks of different shades of greys.

Perceived colors of objects basically remain constant irrespective of spectral contents of the illumination. This property is known as color constancy, which is important for animals that assess object quality by color. We confirmed that *Papilio* has color constancy by testing them under differently colored illuminations [3].

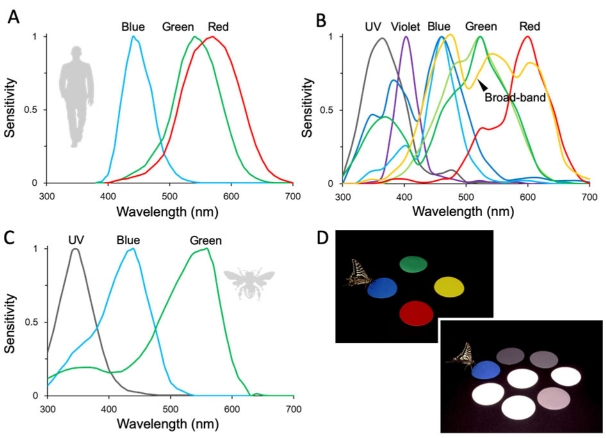

Fig. 1: Photoreceptor spectral sensitivities of humans (A), the Japanese yellow swallowtail, *Papilio xuthus* (B), and honeybee *Apis mellifera* (C). D) Color vision test in *Papilio xuthus*.

3.2 Wavelength discrimination

Dimension of color vision (tri- or tetra-chromacy, etc) can be studied by measuring wavelength discrimination ability. We can discriminate about 1 nm difference ($\Delta\lambda \doteqdot 1$ nm) in two wavelength regions, which are around 500 nm and 600 nm (see Fig. 2B). These regions respectively correspond to where the sensitivities of B and G receptors, and G and R receptors overlap. Existence of two highly sensitive wavelength regions is because the system is trichromatic.

We measured wavelength discrimination in *Papilio* using its feeding response. We trained butterflies to extend their coiled mouth towards light of certain wavelength. When shown the training light with another light of different wavelength at the same intensity, the butterfly extends its mouth towards the training light if two lights are discriminable. We thus found that *Papilio* can detect 1-2 nm difference at around 430, 480 and 560 nm, indicating that their color vision system is tetrachromatic. Model calculation well reproduced the behavioral results when we assumed the UV, B, G and R receptors contribute the discrimination (Fig. 2A).

Figure 2B shows the wavelength discrimination of some animals including humans. Honeybees and humans are trichromatic, while goldfish and *Papilio* are tetrachromatic. *Papilio*'s performance is indeed the best among them [4].

4. COMPARATIVE ASPECTS

4.1 Photoreceptor diversity

As shown in Figs 1C and 2B, color vision of honeybees and butterflies are different. Even among butterflies, color vision properties appear to be different. Because behavioral experiments are not easy to perform, this has not been convincingly demonstrated at the behavioral level. However, we see a clue of the variability at the photoreceptor level.

Some butterflies have only 3 receptor classes (UV, B and G) in their eyes as honeybees do, suggesting their trichromacy. Some have 6 or more. The cabbage white, *Pieris rapae*, has 6 as in *Papilio*, but the sensitivity profiles are different: they are UV, V, B, G, R and dark red. In addition, the V receptors are found only in females. They are replaced by double-peaked B (dB) receptors in males. Sexual dimorphism is even more pronounced in the Eastern pale clouded yellow, *Colias erate*, where males have one class of R receptors, while females have 3 classes of them. Multiple R receptors would make females capable of discriminating subtle differences in greenish, yellowish, and reddish colors. This is probably beneficial in assessing quality of leaves on which to lay eggs [5].

In terms of the number of receptor classes in butterflies, the Common bluebottle, *Graphium sarpedon*, has the record at this stage, which is 15 [6]. How does *Graphium* use these 15 classes of receptors? It seems unlikely that they are "pentadeca-" chromatic. *Papilio* uses 4 out of 6 for

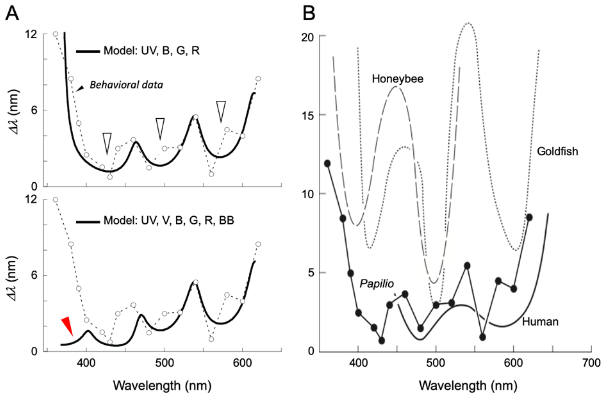

Fig. 2: (A) Wavelength discrimination (Δλ) function of *Papilio.* Troughs (open arrowheads) indicate high-sensitive regions. Behavioral data (dotted line) are well explained by the model with inputs from UV, B, G and R receptors (upper), but not by all six receptors (lower), where significant deviation is observed in the UV region (red arrowhead). (B) Comparison of wavelength discrimination of animals.

color vision. If this is also the case of *Graphium*, other 11 receptors may be useful for detecting specific stimuli, for example, fast-moving objects against the sky, or particular light wavelengths reflected from potential mates or enemies.

4.2 Perspectives

We of course cannot see the world as butterflies do, because our eyes and brains are designed differently. It is however still exciting to try to understand how the world of butterflies looks like by combining evidence from various kinds of experiments. We are currently studying hard to understand how the wavelength information is processed in their tiny brains to produce "colors" as their own experience. We are also interested in how color vision systems have evolved over time by comparing the eyes and brains of many different insects.

In this process, we may even discover principles for designing new artificial "visual" systems. It would be fantastic if we could program drones to use their "eyes" to control themselves as skillfully as insects do. Another possible application of insect vision research is to control insect pests. Excess use of chemical insecticides damages environment. Perhaps we can safely keep pest insects away from crops by using light instead of chemicals. For this, we first have to understand how insect visual systems work.

5. REFERENCES

[1] Arikawa, ***J Comp Physiol A***, 189, 791-800 (2003)
[2] Perry, Kinoshita, Saldi, Huo, Arikawa, Desplan, ***Nature***, 535, 280–4 (2016)
[3] Kinoshita, Arikawa, ***J Comp Physiol A***, 200, 513-26 (2014)
[4] Koshitaka, Kinoshita, Vorobyev, Arikawa, ***Proc Biol Sci***, 275, 947-54 (2008)
[5] Marshall, Arikawa, ***Curr Biol***, 24, R1150-4 (2014)
[6] Chen, Awata, Matsushita, Yang, Arikawa, ***Front Ecol Evol***, 4, 1-12 (2016)