nisms of directional hearing in pigeons and mammals.

The two segregated frequency ranges of best localization performance in the pigeon (250–500 Hz and 2–4 kHz) could reflect the operational ranges of two distinct binaural mechanisms as proposed by the classic duplex theory of directional hearing [15]: the perception of interaural time (phase) differences at low frequencies and of interaural intensity disparities at high frequencies. The transitional zone between these mechanisms could correspond to the range of poor localization capabilities at 1–2 kHz determined by both, the physiological high-frequency limit for phase locking in the auditory nervous system [16] and the physical low-frequency limit for interaural level differences due to the acoustic shadow of the head.

Although this interpretation offers an explanation for the frequency dependence of auditory localization, it cannot, however, be completely excluded that the pigeon may use a pressure gradient system as suggested for the Japanese quail [17]. To solve this problem, measurements of the interaural intensity and phase difference thresholds are required. These behavioral experiments using heart-rate conditioning are in progress. First results are consistent with the hypothesis of combined binaural phase and intensity difference perception in sound localization.

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Pentachromatic Visual System in a Butterfly

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Since the first behavioral demonstration by von Frisch [1] of the ability of bees to discriminate colors, a number of reports have dealt with spectral sensitivity in insects [2]. Previous reports indicate that most insects have a color vision system based on three or four types of color receptor cells which cover the spectral region from UV (300 nm) to red (700 nm).

The existence of more than five different types of receptor cells with different spectral sensitivity in a compound eye has only been reported in some flies [3]. In the case of the flies, however, only three types can be recognized in terms of wavelength discrimination (UV, blue, and green): the color vision system of the flies is trichromatic. In this report we describe the first example of a pentachromatic color vision system in the Japanese yellow swallowtail butterfly, *Papilio xuthus* (Lepidoptera, Papilionidae) studied by intracellular electrophysiology. Matič [4] already reported that another butterfly species of the same genus, *Papilio aegeus* had four types of color receptors (peaks at 390, 450, 540, and 610 nm, respectively), but our results include an additional UV receptor which peaks at 360 nm.

Figure 1 shows the spectral sensitivity curves $S(\lambda)$ of five different color receptors found in *P. xuthus*. Their peak wavelengths are 360 nm (UV), 400 nm (violet), 460 nm (blue), 520 nm (green), and 600 nm (red), respectively. The most frequently recorded cell was the blue type (numbers are shown in Fig. 1). The violet receptor is probably comparable to Matič's UV cell which peaks at 390 nm [4]. Although these five types are functionally identifiable by electrophysiology, we have no direct evidence whether five different visual pigments exist in the eye or not. Width of the $S(\lambda)$ of the violet, blue, and red cells are relatively narrower than the predicted absorption spectra of respective rhodopsins from a nomogram [5]. In particular, the violet receptor has a very sharp $S(\lambda)$ whose band width at 50% sensitivity is only about 40 nm. Considering the fact that the visual pigment of *P. xuthus* is not rhodopsin but xanthopsin (Seki, personal communication), the occurrence of such differences between $S(\lambda)$ and theoretical absorption spectra of rhodopsins can be attributed to the chromophore differences. But the most plausible factor which narrows the $S(\lambda)$ is possibly the screening effect by cells surrounding a penetrated receptor. The butterfly re-

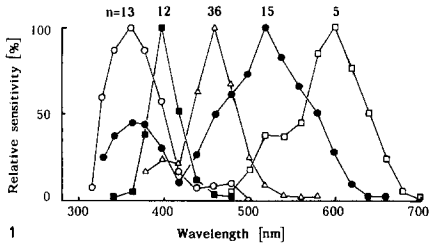

Fig. 1. Spectral sensitivity functions of five different types of photoreceptor in the compound eye of *P. xuthus*. Intracellular recordings were made by 3 *M* KCl-filled glass microelectrodes with resistances of 50–100 MΩ. Resting potentials were −50 to −70 mV. Only the cells whose V_{max} (maximum amplitude of receptor potential) over 40 mV were accepted as the results. Conventional flash method was used for stimulation. At very low light intensities discrete depolarizations (bumps) of 2–5 mV height could be recorded. Sensitivities at peak wavelengths were taken as 100%. *n* cell number

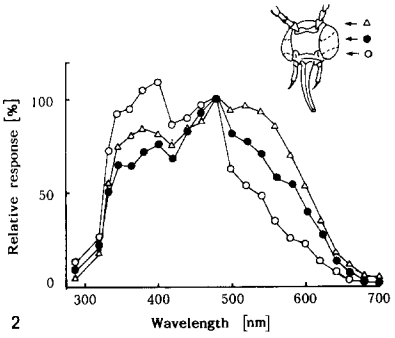

Fig. 2. Regional difference of spectral response function of the *P. xuthus* compound eye. ERG recordings were made by electrolytically sharpened tungsten wire. When recording the ERG from a part of the eye, rest of the eye was covered with water-soluble black paint. Responses at 480 nm (peak wavelength of dorsal and medial parts) were taken as 100%. The set of curves shown here is drawn from means of data from four individuals

tinula is of the so-called tiered type [6, 7]. Light received by proximal retinula cells is always filtered by substances contained within the distal retinula cells which lie directly above the proximal cells. Such filtering effects of distal retinula cells undoubtedly change the shape of the $S(\lambda)$ of the proximal photoreceptors. From our present results, it is most likely that UV and green cells whose $S(\lambda)$ almost fit the predicted spectra are distal retinula cells. Whether and how these five different types of color receptors are located within a single ommatidium is currently under investigation.

Large hyperpolarizing receptor potentials which have previously been reported as evidence of complex color opponency functions at the receptor level in *P. aegeus* [7] could not be recorded in *P. xuthus*. However, the relative height of the secondary peak of the green receptor at 360 nm varies between 0 and 80% of the primary peak at 520 nm from preparation to preparation. The existence of sensitizing pigment in the butterfly retinula is denied [8, 9], so that the large secondary peak observed in the green receptor is considered to be caused by positive electrical coupling with a UV receptor and/or a recording artefact.

Although five color receptors were demonstrated in the *P. xuthus* compound eye, only three types of photoreceptors were reported in the larval stemmata of the same species [10]. Each of them peaks at 370, 450, 530 nm, and they show almost similar $S(\lambda)$ of the adult UV, blue, and green receptors, respectively. This difference of the photoreceptor organization between the adult and the larva means that two types of receptors (violet and red) develop during the formation of the compound eyes in the pupal stage. By addition of the red receptors, butterflies can easily expand their "visible light" range. This corresponds well to their frequent visits to red flowers. On the other hand, the insertion of a violet receptor between the UV and the blue cells enhances color discrimination in the UV region.

To reveal the distribution pattern of the color receptors in the compound eye, regional recordings of the electroretinogram (ERG) were carried out. Figure 2 shows the spectral response curves recorded from dorsal, medial, and ventral parts of the compound eye. The relative heights of the peaks in the spectral response curves of the medial and dorsal parts of the eye show good correspondence with the numbers of encountered cells in the intracellular recordings (Fig. 1). However, the results clearly show that the ventral part is more sensitive to light of shorter wavelength: UV, violet, and blue receptors must be relatively abundant in the ventral part of the eye (Fig. 2). This situation of *P. xuthus* is the complete opposite of what has been reported on other insects [2] and is likely to be closely related to the behavior of the butterfly. Honeybees use UV receptors for the detection of polarized light in the sky, and, therefore, have the dorsal part of the eye more sensitive to UV light. In the case of butterflies, however, high sensitivity to UV and violet in the ventral region of the compound eye strongly suggests that reflected UV and violet light from below contain important information for them. Previous behavioral observation by Ilse [11] that papilionid butterflies preferentially visit blue and violet flowers can well be explained by the function of the compound eye since many flowers are known to possess so-called "nectar guides" which reflect UV light [12]. In addition, *P. xuthus* itself has UV-reflecting spots on the hind wings [13]. These reflections are not merely bright spots but also "colorful" patches for foraging butterflies and those in search of a mate.

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