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Visual circuits in flies: beginning to see the whole picture

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Sensory signals are processed in the brain by dedicated neuronal circuits to form perceptions used to guide behavior. *Drosophila*, with its compact brain, amenability to genetic manipulations and sophisticated behaviors has emerged as a powerful model for investigating the neuronal circuits responsible for sensory perception. Vision in particular has been examined in detail. Light is detected in the eye by photoreceptors, specialized neurons containing light sensing Rhodopsin proteins. These photoreceptor signals are relayed to the optic lobes where they are processed to gain perceptions about different properties of the visual scene. In this review we describe recent advances in the characterization of neuronal circuits underlying four visual modalities in the fly brain: motion vision, phototaxis, color and polarized light vision.

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A fundamental goal in neuroscience is understanding how neuronal circuits interpret sensory signals in the brain to form behaviorally-relevant perception. The fly *Drosophila melanogaster*, a powerful model for developmental biologists, has recently emerged as a prolific system to elucidate complex problems in functional neuroscience, especially sensory perception. This 'simple' organism is capable of many sophisticated behaviors and combines the advantages of a rather compact brain (only 200 000 neurons) with a large toolbox for genetic manipulation. These attributes make the fly an attractive model for reaching a complete understanding of microcircuits underlying a given sensory modality — to link specific cell types to a given behavior.

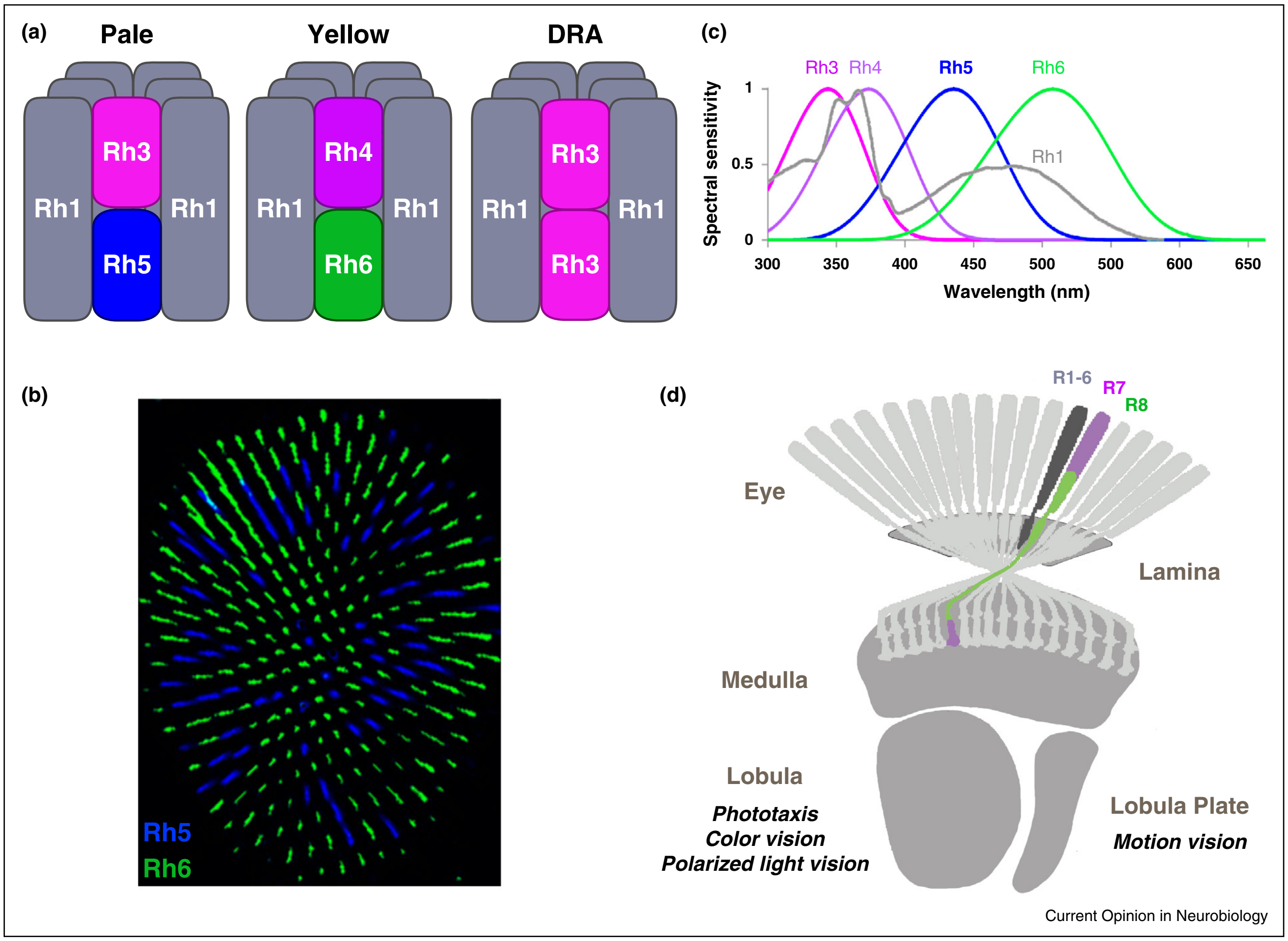
The visual system of the fly has been particularly well studied. While the development of the complex pattern of light-sensing photoreceptors in the eye has been elucidated in exquisite detail [1], the role of these sensory receptors and their downstream circuits in visual perception is emerging. In this review we will focus on recent advances in the identification and characterization of microcircuits underlying four different visual modalities: motion vision, phototaxis, color and polarized light vision.

The eye and the optic lobe

The fly eye contains about 800 independent unit eyes called ommatidia, corresponding to 800 pixels in the animal's visual field. Each ommatidium is composed of eight photoreceptor cells: six outers (R1–6) and two inners (R7 and R8) (for review on this section, see [1]) (Figure 1a). R1–6 photoreceptors, the equivalent of mammalian rods, all express the same broadband Rhodopsin Rh1. They are involved in dim light vision and the perception of motion [2]. Similar to mammalian cones, R7/R8 photoreceptors express different Rhodopsins in a pattern that defines two subtypes of stochastically distributed ommatidia (Figure 1b). These are involved in color vision [2,3•,4]: 'pale' ommatidia have the UV-sensitive Rhodopsin Rh3 in R7 and blue Rh5 in R8, while 'yellow' ommatidia have another UV Rhodopsin (Rh4) in R7 and the green-sensitive Rh6 in R8 (Figure 1a,c). The rhabdomeres (i.e. light gathering structures made of microvilli containing the Rhodopsins) of R7/R8 are staked one on top of the other and hence share the same light-path, providing the ideal configuration to compare their outputs. A third type of ommatidia is found in a narrow band of ommatidia in the dorsal rim area (DRA) of the eye, where both R7/R8 photoreceptors express the same UV Rhodopsin Rh3 (Figure 1a). These morphologically specialized ommatidia are involved in the detection of the e-vector of polarized skylight for navigation [5••]. Finally, both UV-Rhodopsins are co-expressed in R7 cells of the 'yellow' subset in the dorsal third of the eye, a region of the eye pointing towards the sky [6]. The function of these ommatidia remains elusive, although they have been proposed to be involved in the detection of solar versus anti-solar orientations.

Photoreceptors are sensory neurons that send their axons to the optic lobe, which is organized retinotopically (Figure 1d). The first level of neural integration of visual information is the lamina, where R1–6 photoreceptor axons terminate [7] (Figure 1d). Each pixel in the field of view of the fly corresponds to one column (or cartridge) in the lamina, as well as in the subsequent neuropil called the medulla, where R7/R8 photoreceptors terminate [8]. Each lamina cartridge contains 11 distinct classes of neurons [7]. The medulla is much more complex, with at least 70 different cell types being represented [7]. Lobula and lobula plate are higher level processing

Figure 1



The eye and the optic lobe of adult *Drosophila*. **(a)** A single ommatidium contains eight photoreceptors, six outers R1–6 (grey) and two inners R7–8 (colors). Outers express the Rh1 opsin, R7s express either Rh3 or Rh4 while R8s express Rh5 or Rh6. Four types of ommatida are found in the eye. 'Pale' and 'yellow' ommatidia are distributed stochastically in the main part of the eye. In the dorsal third, pale and specialized dorsal third yellow subtypes are found (not shown). In one to two rows of ommatidia in the dorsal rim area (DRA) of the retina, the remaining DRA subtype is found. **(b)** Stochastic distribution of Rh5 (blue) and Rh6 (green) expressing R8s in the main part of the eye. **(c)** Normalized spectral preference curves of the different rhodopsins expressed in the eye of the fly. Rh1 shows broad spectral sensitivity peaking in both the blue and the UV due to the presence of a sensitizing pigment (Modified from Ref. [3•]. **(d)** Photoreceptors project to the optic lobe. Outer photoreceptors send their axons to the lamina while R7/R8 photoreceptors send theirs to the medulla. The lobula is involved in spectral preference, color and polarized light vision. The lobula plate is a center for motion detection.

centers, with lobula thought to be involved in the processing of color vision [9], spectral preference [10••] and polarized light vision [11] while the lobula plate is the site of motion detection [12] (Figure 1d).

Motion detection

The perception of motion is by far the best-studied visual modality in the fly. It is critical for prey capture and mating, not to mention integration of the fly's own movement in the world. Mechanisms describing how neurons compute direction-selective signals by interpreting spatiotemporal changes in luminance have been studied extensively, starting with seminal work in other insects. In the 1950s, Hassentein and Reichardt developed their now famous, eponymous correlator model (Hassentein and Reichardt Correlator: HRC) by examining the optomotor response of the beetle *Chlorophanus*, that is, its tendency to rotate with the visual field to maintain a straight heading in its perceived environment [13]. *Drosophila* also displays a very robust optomotor behavior [12], which has been demonstrated to rely largely on R1–6 photoreceptors [2,14]. This behavior is typically measured using tethered flies that are either flying in a flight simulator, or walking on an air-suspended ball, while a motion stimulus is presented [15].