Ever since Morgan observed a mutant male with white eyes among the normally brilliant red-eyed specimens in his pedigree culture of fruit flies, *Drosophila* has been an inexhaustible source of scientific inspiration and discovery [1]. The regular, almost crystalline mosaic of the fruit fly eye has proved a powerful tool for unraveling genetic defects resulting in anatomical as well as functional modifications of normal physiological and/or behavioral patterns [2]. Developmental and cell biological studies in particular have greatly benefited from the clear and accessible organization of the fruit fly compound eye.

A *Drosophila* eye consists of roughly 800 anatomically identical units, called the ommatidia (Figure 1A). Each ommatidium contains eight photoreceptor cells (R1–R8) and is capped by a facet lens. The lens projects incident light into each photoreceptor’s rhabdomere—the specialized, light-sensitive organelle that functions as a light guide and contains the visual pigment molecules (called rhodopsins). Rhabdomeres also harbor the photoreceptor’s phototransduction machinery [3,4], which is made up of signaling components that capture and transform photons from light into an electrical signal, which conveys visual information to the brain. (All the rhabdomeres in an ommatidium are collectively known as the rhabdom.) The R1–R6 rhabdomeres stretch the full length of their photoreceptors, forming a trapezoid with the tandem of the R7 and R8 rhabdomeres in the center (Figure 1B and 1C).

Accordingly, the photoreceptors and their rhabdomeres can be classed as outer and inner (or peripheral and central), respectively [2,5], and these two classes serve different visual functions. R1–R6 mediate highly light-sensitive, broad spectral-band motion vision, and R7 and R8 underlie color vision, a capacity that is enabled by special optical and neural organizations [5]. The two classes of photoreceptors can be not only differentiated by the type of vision they mediate, but also by the route via which the visual information is conveyed. The different classes of visual information are collected in two consecutive optical ganglia—namely, the lamina, where information from R1–R6 is collated, and the medulla, where the R7 and R8 signals are transmitted. The specifics regarding further neural processing are unfortunately largely unknown.

Extensive studies on the larger housefly (*Musca*) and blowfly (*Calliphora*) have provided considerable insight into the workings of the fruit fly’s retinal organization. For example, transmission light microscopy has revealed two types of ommatidia, with the R7/R8 rhabdomeres of randomly distributed ommatidia appearing yellow, due to a blue-absorbing, photostable pigment (presumably zeaxanthin and/or lutein) concentrated in the R7 rhabdomere, and the rhabdomeres in the complementary set of ommatidia appearing pale [7]. The R7 and R8 photoreceptors of these ommatidia types, accordingly called y and p type, appear to have different rhodopsins [5].

*A long-standing general principle in vision research holds that single photoreceptors always contain a single type of rhodopsin, although occasional examples of co-expressed rhodopsins, as the authors have now demonstrated for *Drosophila*, have cropped up in both vertebrates and invertebrates. Röhlisch et al. [10], for example, investigated the retinae of the mouse, rabbit, and guinea pig, which are divided into a superior area dominated by green-sensitive (M) cones, and an inferior area in which cones possess practically only short wavelength-absorbing (S) rhodopsins. They found that the transitional zone between these retinal areas is populated by cones labeled by both M and S cone rhodopsin-specific antibodies. A related result was reported for the Syrian hamster [11]. Kitamoto et al. [12] studied the Japanese swallowtail butterfly, *Papilio xuthus*, and found...*
that the proximal photoreceptors of the so-called type II ommatidia co-express two mRNAs encoding long wavelength–absorbing rhodopsins. Recently, another example of co-expression of rhodopsins, resembling the Drosophila case, was discovered in a restricted area of the compound eye of the Small White butterfly, Pieris rapae crucivora. In a transition area—which is approximately six ommatidia wide—between the dorsal area and the main dorso-ventral area, the short-wavelength photoreceptors express two RNAs coding a UV-absorbing and a blue-absorbing rhodopsin (Omiya M and Arikawa K, unpublished data). The spatial area covered by these photoreceptors is similar to those of the co-expressing Drosophila photoreceptors discovered by Mazzoni et al. [9], suggesting that they fulfill a similar visual role (see below).

An obvious question is whether the co-expressed rhodopsins are both functional—that is, whether they are capable of triggering the phototransduction process, thus inducing a visual signal proportional to the absorbed photon flux. That question has been positively answered for the Papilio xuthus photoreceptors that co-express two rhodopsin mRNAs. Intracellular electrophysiological recordings of the spectral sensitivity of these photoreceptors yielded very broad-band sensitivity spectra, which could be interpreted with a computational model that assumed additive sensitivity of two phototransduction chains driven by the two rhodopsins [13].

We emphasize here that double expression of two rhodopsins does not produce an enhancement of absolute light sensitivity. Indeed, Mazzoni et al. [9] found that less Rh3 exists in R7 cells that co-express rh3 and rh4 than in R7 cells expressing only rh3. Assuming that the Rh3 and Rh4 expressed by the Drosophila R7 photoreceptors participate equally in the phototransduction process, the spectral sensitivity of the R7s will be proportional to the summed absorption spectra of the two UV rhodopsins. Because the absorption spectra of Rh3 and Rh4 are not widely spaced apart (Figure 2), the spectral sensitivity of the R7s will only be slightly broadened and still be restricted to the ultraviolet range. (Note that the spectral properties of the ommatidium’s integrated optics, consisting of the diffracting facet lens and the waveguiding rhabdomere, also contribute to the spectral sensitivity of a photoreceptor cell, although to a minor extent [14].)

Because double expression of the UV rhodopsins occurs in the R7s in the dorsal third of the compound eye, Mazzoni et al. [9] hypothesize that the R7 photoreceptors, together with the underlying R8s, function in analyzing the UV sky specifically to detect differences in the solar and nonsolar parts of the sky—that is, sky near the sun and away from it—which can differ considerably in short-wavelength light content. This skylight-discriminating ability may serve to help the fly orient for navigational purposes. Although testing this hypothesis will be difficult, because Drosophila is not well known for easy behavioral experiments, calculations of light capture of different sky areas based on detailed modeling of photoreceptor sensitivities will illuminate the tenability of the offered hypothesis. Alternatively, experiments on other species with similar expression patterns, like the butterflies, may provide behavioral evidence.
presumably ara and caup lift the blockade of the expression of Rh3 in the commonly Rh4-expressing y type R7.

It will be of great interest to see whether the dual expression of rhodopsins as found in the fruit fly is under similar genetic control, in butterfly as well as in vertebrate photoreceptors. This may further improve our insight into the evolution of rhodopsin expression patterns. Surveying different Drosophila species using the well-filled genetic toolbox now available for D. melanogaster will undoubtedly be of great value to further uncover the evolutionary history as well as the genetic mechanisms that break the one rhodopsin-per-photoreceptor rule.

References
1. Morgan TH (1910) Sex-limited inheritance in Drosophila. Science 32: 120-122.
2. Morante J, Desplan C, Celik A (2007) Generating patterned arrays of photoreceptors. Curr Opin Genet Dev 17: 314-319.
3. Minke B, Hardie RC (2000) Genetic dissection of Drosophila phototransduction. In: Molecular mechanisms in visual transduction. Handbook of Biological Physics, Vol. 3. Stavenga DG, DeGrip WJ, Pugh EN Jr, editors. Amsterdam: Elsevier. pp 449-525.
4. Hardie RC, Raugi P (2001) Visual transduction in Drosophila. Nature 413: 186-193.
5. Hardie RC (1985) Functional organization of the fly retina. Ottoson D, editor. Progr Sens Physiol 5:1-79.
6. Kirschfeld K (1967). Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexeauge von Musca. Exp Brain Res 3: 248-270.
7. Kirschfeld K, Feiler R, Franceschini N (1978) A photostable pigment within the rhabdomere of fly photoreceptors No. 7. J Comp Physiol 125: 275-284.
8. Salcedo E, Huber A, Heinrich S, Chadwell LV, Chou WH, et al. (1999) Blue- and green-absorbing rhodopsins of Drosophila ecotopic expression and physiological characterization of the R8 photoreceptor cell-specific Rh5 and Rh6 rhodopsins. J Neurosci 19: 10716-10726.
9. Mazzoni EOCA, Wernet MF, Vasiliauskas D, Johnston RJ, Cook TA, et al. (2008) Iroquois Complex genes induce co-expression of rhodopsins in Drosophila. PLoS Biol 6(4): e115. doi:10.1371/journal.pbio.0060115.g002
10. Röhlh P, Van Veen T, Szel A (1994) Two different rhodopsins in one retinal cone cell. Neuron 15: 1159-1166.
11. Glosmann M, Ahnelt PK (2002) A mouse-like retinal cone phenotype in the Syrian hamster: S opsin coexpressed with M opsin in a common cone photoreceptor. Brain Res 929: 139-146.
12. Kitamoto J, Sakamoto K, Ozaki K, Mishina Y, Arikawa K (1998) Two rhodopsins in one photoreceptor cell: identification and histological localization of three mRNAs encoding rhodopsin opsins in the retina of the butterfly Papilio xuthus. J Exp Biol 201: 1255-1261.
13. Arikawa K, Mizuno S, Kinoshita M, Stavenga DG (2003) Coexpression of two rhodopsins in a photoreceptor causes an abnormally broad spectral sensitivity in the eye of the butterfly Papilio xuthus. J Neurosci 23: 4527-4532.
14. Stavenga DG (2003) Angular and spectral sensitivity of fly photoreceptors. II. Dependence on facet lens F-number and rhabdomere type in Drosophila. J Comp Physiol A 189: 189-202.
15. Labhart T, Meyer EP (1999) Detectors for polarized skylight in insects: A survey of ommatidial specializations in the dorsal rim area of the compound eye. Micr Res Techn 47: 368-379.
16. Wernet MF, Labhart T, Baumann F, Mazzoni EO, Pichaud F, et al. (2003) Homothorax switches function of Drosophila photoreceptors from color to polarized light sensors. Cell 115: 267-279.
17. Cavodeassi F, Modolell J, Gómez-Skarmeta JL (2001) The Iroquois family of genes: from body building to neural patterning. Development 128: 2847-2855.
18. Cheng CW, Chow RL, Lebel W, Sakuma R, Cheung HOL, et al. (2005) The Iroquois homeobox gene, Iro5, is required for retinal cone bipolar cell development, Dev Biol 285: 48-60.
19. Cheng CW, Van CHM, Hui CC, Strahle U, Cheng SH (2006) The homeobox gene irx1a is required for the propagation of the neurogenic waves in the zebrafish retina. Mech Dev 123: 252-263.
20. Gómez-Skarmeta JL, Diez del Corral R, de la Calle-Mustienes E, Ferreis-Marcó D, Modolell J (1996) araucan and caspolican, two members of the novel Iroquois complex, encode homeoproteins that control pronuclear and vein-forming genes. Cell 85: 95-105.
21. Kehl BT, Cho KO, Choi KW (1998) mirror, a Drosophila homeobox gene in the iroquois complex, is required for sensory organ and alula formation. Development 125: 1217-1227.