St. Kilda Ho^P alleles are those that have been present since the island was first colonized or reflect subsequent, perhaps recent, admixture of sheep form elsewhere. For instance, coat colour polymorphisms in Soay sheep reflect admixture with modern breeds in the last 150 years [5]. So the Soay population might have been introgressed by superior Ho^P alleles that conceivably confer positive fitness effects through pleiotropy or close linkage with other genes. This view gains some support as over the last 20 years the Ho^P allele has been increasing in frequency in the population by ~20%. However, this rate of increase need not be the result of selection as it is not distinguishable from random fluctuations through drift [5].

The lesson from this study is simple. Pin-pointing the genetic basis of sexual traits in natural populations is likely to throw up challenging observations. It's too early to conclude that overdominance at single loci will play a large role in explaining the lek paradox, or that genic capture and sexual antagonism play no part. But, the vast diversity of bizarre and extravagant ornamentation and weaponry used in courtship is ripe for an unraveling of its genetic basis.

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Colour Vision: Parallel Pathways Intersect in *Drosophila*

In the last one hundred years, colour vision has been demonstrated in bees and many other insects. But the underlying neural wiring remained elusive. A new study on *Drosophila melanogaster* combining behavioural and genetic tools yields surprising insights.

Almut Kelber and Miriam J. Henze

Ninety-nine years after Nobel prize winner Karl von Frisch proved that honeybees see flowers in colour [1], bees are among the best-studied animals with respect to colour vision. Their eyes house photoreceptors sensitive to ultraviolet (UV), blue and green light. The signals from these three receptor types are compared neurally for very fine colour discrimination, limited only by receptor noise [2,3]. However, studies of the neural substrate of colour vision beyond the photoreceptor level have proven frustrating. Honeybee neurons were difficult to penetrate, signals were hard to interpret, and genetic tools are still unavailable. At this point, the fruit fly *Drosophila melanogaster* enters the colour vision scene. Flies, including *Drosophila*, have long been models for visual transduction and motion vision [4], but colour vision research rarely considered *Drosophila* a useful model species: fruit flies were thought to have an extremely derived colour vision system, and on top of that, they don't seem to care much about colour. Behavioural tests using phototaxis or aversive conditioning by electric shocks or heat [5,6] did not allow for studies of fine colour discrimination. Recently, however, the group of Hiromu Tanimoto and colleagues developed a method to train fruit flies to associate a light stimulus with a sugar reward [7]. In a new study [8], in this issue of *Current Biology*, they now combine the new behavioural method with genetic tools to unravel novel and important secrets of insect colour vision.

First, Schnaitmann, Tanimoto and colleagues [8] demonstrated that fruit flies learn to discriminate blue and green. In the critical test, they trained fruit flies with dark blue and light green and showed that the flies chose the correct colour even when intensities were inversed. Second, and more importantly, the authors asked which photoreceptor cells their flies used for this colour discrimination — with an astonishing result. To understand the importance of their finding, we have to take a closer look at the eyes of bees and flies and colour vision in general.

Colour vision — the ability to discriminate colour stimuli independent of intensity — requires at least two types of receptor with different, preferably narrow, spectral sensitivities. Signals from these receptors need to be compared in the colour vision pathway. By contrast, pattern, shape and motion vision rely on broadly tuned achromatic signals that do not include colour information. In humans, red and green cones contribute to both, the achromatic and the colour vision pathway. For achromatic vision, signals from red and green cones are summed in retinal ganglion cells. For colour vision, signals from red cones excite

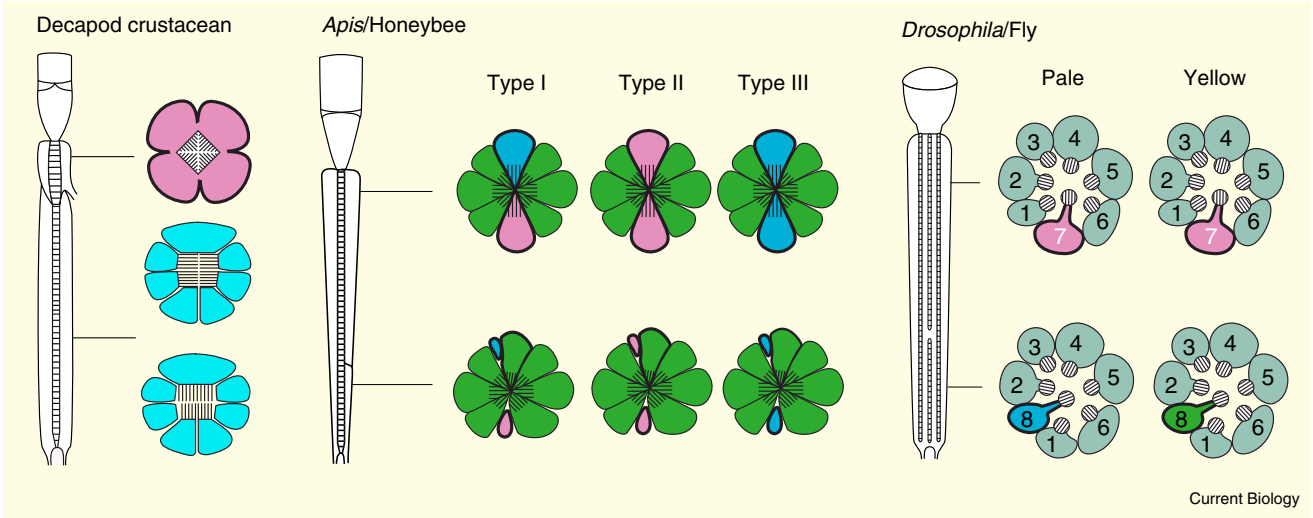

Figure 1. Crustacean, bee and fly ommatidia.

Cross and longitudinal sections reveal similarities between ommatidia types. Longitudinal sections show, from top to down, the optic apparatus and the receptor cells with the receptive structures, the rhabdoms (dashed). In cross sections, receptor cells are colour-coded according to their spectral sensitivity. Decapods have one UV receptor with distal rhabdom (pink) and seven LWS receptors (turquoise) with proximal rhabdoms. In three ommatidial types of bees, two UV receptrors (pink), two blue receptors (blue) or one of each contribute to the distal rhabdom, while six green receptors contribute to the entire rhabdom. An additional green receptor contributes only to the basal rhabdom. Flies have six broadly tuned receptors, R1–6 (grey), which have long rhabdomeres, and two narrowly tuned receptors (R7-8) in each rhabdom. R7 and R8 differ between 'pale' and 'yellow' ommatidia, being UV and blue-sensitive in 'pale' but UV- and green-sensitive in 'yellow' ommatidia. Receptors with long visual fibres projecting to the medulla are marked by bold surround lines, receptors with short visual fibres projecting to the lamina are marked by thin surround lines. As Schnaitmann and colleagues [8] now show, signals from the broadly tuned receptors R1–6 of *Drosophila* (which project to the lamina) are compared with signals from R7–8 (which project to the medulla), for colour vision. This implies that colour vision is more similar in crustaceans, flies and other insects than previously thought.

specific retinal ganglion cells, while signals from green cones inhibit them. In birds, both pathways are believed to be completely separated: achromatic vision uses signals from broadly tuned receptors, the double cones, while colour vision uses signals from four types of narrowly tuned single cones [9].

Insect Colour Vision

Crustacean and insect compound eyes share similarities (Figure 1) that give hints to the evolution of insect colour vision [10]. Their compound eyes consist of up to several thousand individual units, the ommatidia, each with a separate optic apparatus and several photoreceptor cells. Many crustaceans and most insects have two, three or more different spectral types of receptor cell [11]. In a decapod crustacean with basic colour vision, spectral sensitivity is linked to two anatomical classes of receptor cell. Seven long-wavelength-sensitive (LWS) receptors have proximal rhabdoms and short visual fibres projecting to the first ganglion of the visual pathway, the lamina. A single UV-sensitive receptor has a distal rhabdom and a long visual fibre projecting to the second visual ganglion, the medulla [12]. Colour vision must rely on comparing signals from these two types of receptors.

Insect ommatidia, as a rule, have six receptors with axons terminating in the lamina. In bees, they are LWS [13] and used as an input channel to their achromatic pathways analysing information on patterns, shape and motion [9]. The remaining photoreceptors project directly to the medulla. Two of these have distal rhabdoms and are short-wavelength-sensitive, just as the distal receptor in decapods. Their sensitivities differ between ommatidia [14–16], giving rise to a random array of three ommatidial types: ommatidial type one has one blue and one UV receptor, type two has two UV receptors and type three has two blue receptors. It is obvious that — just as in decapod crustaceans — colour vision depends on signals from receptor cells with axons terminating in the lamina *and* those with axons terminating in the medulla. LWS receptors with short visual fibres contribute to colour vision *and* achromatic pathways.

In flies, just as in other insects, six LWS receptors (R1–6) project to the lamina with short fibres. An additional UV-sensitive accessory pigment and the neural wiring result in broad spectral tuning and high sensitivity [4]. Just as in bees, these six receptors are the basis of achromatic vision [4]. Based on the remaining two receptors, R7 and R8, which have long visual fibres projecting to the medulla, flies have two types of ommatidia: in 'pale' ommatidia, R7 is UV-sensitive (335 nm) and R8 is blue-sensitive (460 nm). In 'yellow' ommatidia, R7 is also UV-sensitive but expresses a different opsin (355 nm), and R8 is green-sensitive (530 nm) [17].

At the time when the spectral sensitivity of fly receptors was first studied, it seemed most sensible to assume that fly colour vision builds exclusively on the spectral classes found in R7 and R8, without any contribution from the broadly tuned receptors R1–6. The highly sensitive achromatic pathway of flies, based on signals from R1–6, was assumed to be completely separated from the parallel colour vision pathway that uses signals from R7 and R8 [18]. This general belief — fly R1–6 and R7–8 being analogues to human rods and cones — has not been challenged for

decades. Only five years ago, a concise study [19] describing all medulla neurons connected to R7 and R8 could claim to list the entire colour vision pathway of *Drosophila*.

The new study by Schnaitmann and colleagues [8] now shows convincingly that, contrary to these expectations, photoreceptors R1–6 do indeed contribute to colour vision in *Drosophila*. Using a blind mutant and GAL4-drivers they generated flies with restricted sets of functional photoreceptors and tested their colour discrimination. Flies with functional 'yellow' ommatidia, but not those with 'pale' ommatidia, discriminated green and blue as well as normal flies, even with inversed intensities. As expected, flies which had no functional receptors except R7 and R8 in 'yellow' ommatidia also did well. However, even flies which only had functional receptors R8 and R1–6 in 'yellow' ommatidia could do the job.

This came as a surprise. It implies that the broadly tuned receptors R1–6 contribute to both the achromatic pathway *and* the colour vision pathway in flies. Schnaitmann *et al.* [8] went one step further and generated flies lacking neurons in the lamina. They showed that the colour vision pathway depends on neurons known as 'lamina monopolar cells' to convey the signals from R1–6 to the medulla, where they can be compared neurally with signals from R7 and R8. Further studies can now unravel the full colour vision pathway of *Drosophila*. The results by Schnaitmann and colleagues [8] strongly suggest that flies may have a rather conserved insect colour vision system. Thus, anything we learn from *Drosophila* will help us to understand colour vision not only in this tiny fly that did not seem to care much about colour, but even in bees and other insects.

More generally, we learn that flies use information more efficiently than previously thought. The analogy that fly receptors R1–6 serve a similar function as human rods, while fly receptors R7 and R8 are comparable to our cones, no longer holds. More adequately, flies use their receptors in a similar way as we use our cones: all receptors are involved in colour vision, and most — in flies six out of eight receptors in each ommatidium, in humans the red and green cones (93% of all cones) — are additionally used for achromatic vision, in a parallel pathway. Birds remain the challenge: why do the animals that have the sharpest vision of all use only half of their cones — the double cones — for high acuity achromatic vision? Or did we, just as in fruit flies, miss something? The new results on *Drosophila* [8] have challenged a paradigm: parallel visual pathways may share the same input more often than we thought.

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Nuclear Division: Giving Daughters Their Fair Share

How do nuclear components, apart from chromosomes, partition equally to daughter nuclei during mitosis? In *Schizosaccharomyces japonicus*, the conserved LEM-domain nuclear envelope protein Man1 ensures the formation of identical daughter nuclei by coupling nuclear pore complexes to the segregating chromosomes.

Alison D. Walters and Orna Cohen-Fix

When we consider what constitutes a successful mitosis, we immediately think of the correct segregation of chromosomes into two daughter nuclei. However, it takes more than chromosomes to make a nucleus. The integrity of the daughter nuclei and the organization of the chromatin within them rely on the presence of an intact nuclear envelope (NE). The NE is a double lipid bilayer, with an outer membrane that is continuous with the ER, and an inner nuclear membrane (INM) that contains proteins that interact with chromatin and other nuclear components. The NE is perforated by nuclear pore complexes (NPCs) that allow selective passage of proteins between the nucleoplasm and cytoplasm. In metazoans, a filamentous network,