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Visual Neuroscience: How Do Moths See to Fly at Night?

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A new study shows that moth vision trades speed and resolution for contrast sensitivity at night. These remarkable neural adaptations take place in the higher-order neurons of the hawkmoth motion vision pathway and allow the insects to see during night flights.

We spend most of our waking time in daylight or in the well-lit indoor spaces of modern life. Under these conditions vision provides us with a reliable representation of the world around us rich in colors and spatial details. But imagine being in the wilderness far from the city lights. Everything changes at sunset. The comfortable certainty of daytime vision is replaced by the uncertainty hidden in the deep shadows of twilight. As the sun's last rays create a faint golden rim on the horizon your visual experience becomes less dominant. The sounds of the night awaken your imagination and can cause even a slight sensation of fear of the invisible inhabitants of the wilderness hidden in the dark. Suddenly something passes you in the air flying — a hawkmoth! How on earth can a moth fly at these extremely low light levels? An answer to this question is provided in this issue of Current Biology: a new study by Stöckl et al. [1] shows that neural adaptations taking place in higher-order neurons of the moth motion vision pathway enable them to see 'on the wing' even in incredibly low light.

Seeing under very dim light poses a formidable challenge for the visual system. In these conditions, visual signals originating in a small number of photoreceptor cells have to be detected against neural noise originating in a much larger number of such cells, as well as in the neural circuitry processing these sparse signals. The randomness of rare photon arrivals makes it even harder to form reliable visual percepts in dim light. Yet many species show remarkable visual capabilities at extremely low light levels. The classic study by Selig Hecht and his colleagues [2] showed that dark-adapted humans can detect just a few light quanta absorbed on a small region of the peripheral retina. Dark-adapted toads can capture their prey easily in starlight [3]. Nocturnal Central American sweat bees can find their nest in the jungle at night [4]. Cockroaches show visually guided behaviour at light levels where only a few photons are captured among hundreds of photoreceptors [5]. Nocturnal African dung beetles can navigate with the aid of polarized moonlight [6]. In all of these cases, the striking behavioral performance of animals in dim light exceeds that of individual receptor cells at their visual inputs by orders of magnitude.

The basic trick for enhancing the quality of photos at night is well known to all photographers: pooling photons in space (increasing 'pixel size') and time (prolonging the exposure time) will boost the signals. There are mechanisms implementing similar pooling at multiple levels of the visual systems of both invertebrates and vertebrates. In our own retina, rod photoreceptors used mainly at low light levels have a longer integration time than cone photoreceptors that we use in daytime. This is one example of receptor-level temporal summation. Spatially, the visual circuits mediating rod signals in our own eyes pool signals from thousands of rods at the lowest light levels, whereas our highest resolution foveal cone vision relies on one-to-one connections between the cones and the midget ganglion cells at the retinal output. In many invertebrates, the migration of screening pigments allows dynamic control of the spatial summation at the receptor level [7]. It has also been proposed that the electrical coupling of rod photoreceptors in the vertebrate eye is more extensive at night time [8].
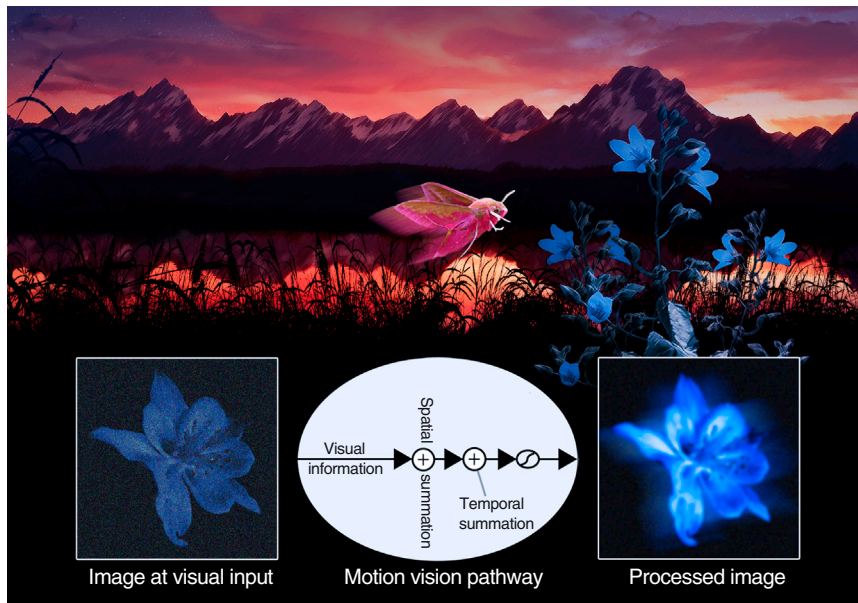
Figure 1. Visual processing in the motion vision pathway of a nocturnal hawkmoth.
The noisy image with low contrast present at the level of hawkmoth photoreceptors (inset, left) is enhanced in contrast (inset, right) by spatial and temporal summation taking place in the higher-order neurons. These neural computations are supralinear, producing higher contrast sensitivity than predicted by a simple linear model relying on spatial and temporal pooling only.

Unfortunately, there is no free lunch — especially not in biology. Pooling signals in space and time comes with fundamental limitations. First, although spatial pooling increases signals arising from photons, it also increases neural noise. Second, the more you pool in time and space the slower your vision is and the fewer fine spatial details you can see. These are especially hard problems for a flying insect. Their small body size will cause fast angular motions and thereby rapid changes in the visual scene during the flight. This would seem to require a fast visual system. Balancing sensitivity against acuity and speed is a trade-off problem where the optimal solution depends on light level and motion velocity.

So how can a moth then see at night? Stöckl et al. [1] took a novel and integrative approach to solve this fundamental problem by addressing it in a tractable model system in the motion vision pathway of the nocturnal elephant moth (*Deilephila elpenor*). They mastered demanding intracellular electrophysiological recordings both from photoreceptors at the visual input level and from the downstream neurons in the lobula plate of the motion vision pathway of the moth. The authors were able to quantify the spatial and temporal constraints set by the photoreceptors on contrast sensitivity and to compare these constraints to the contrast sensitivity measured at the level of the moth brain in the wide-field motion detecting neurons. This unique approach allowed them to quantify the amount of neural summation taking place in the visual pathway of the moth across a 10,000-fold range of light intensities comprising light levels from early sunset to dim moonlight.

Stöckl et al. [1] found that the postreceptoral neural circuits carry out extensive spatial and temporal summation at low light levels. Using a modeling approach the authors conclude that this summation enables hawkmoths to see at light levels 100 times dimmer than without such summation. Thus, the neural circuits of the moth motion vision pathway significantly trade speed and spatial resolution for contrast sensitivity, as illustrated in Figure 1.

But how far can the moth afford to sacrifice the speed of vision while flying at night? A recent behavioral study by another group of scientists brings an answer to this question. Sponberg et al. [9] showed that a closely-related hawkmoth species (*Manduca sexta*) slows down its behaviorally measured visual processing in perfect harmony to the speed of wind-blown flowers at night. Taking together the findings of these two beautiful studies, we now have a perfect answer. The Stöckel et al. [1] paper provides the neural account for this earlier behavioral result by directly showing that the moth brain slows down in the dark. These two studies [1,9] together suggest that the neural mechanisms of the moth visual system have been matched perfectly to the requirements of its environment.

What neural mechanisms underlie the spatial and temporal summation in the moth motion vision pathway? Stöckl et al. [1] do not give a direct answer to this question. However, their modeling predicts that the neural mechanism is supralinear, giving more advantage to contrast sensitivity than a simple linear summation of temporal and spatial effects would predict. This exciting prediction is in line with the idea that optimal performance at visual threshold relies on elegant nonlinear neural computations taking place in the visual circuits. Earlier literature in the vertebrate visual system showed that the detection of the weakest lights relies to a large extent on nonlinear noise filtering mechanisms at multiple levels of the neural circuit [10,11]. It remains to be seen in future studies how exactly the computations revealed by Stöckl et al. [1] are implemented and what noise sources truly limit detection under these conditions.

Similarly, it will be intriguing to understand the mechanisms that control the optimal tuning of spatial and temporal properties across multiple light levels in the moth. Recent studies [12,13] have unraveled neural circuit mechanisms underlying luminance-dependent changes in the spatial summation of the vertebrate retina. Further mechanistic understanding of evolution as an innovator at visual threshold might even help us to build more sensitive and efficient night vision devices in the future. Aside from these potential future innovations, this study reveals above all some of the key neural secrets underlying the night flight of a moth in the wilderness. This understanding as such is simply beautiful.

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Evolution: The End of an Ancient Asexual Scandal

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Bdelloid rotifers were believed to have persisted and diversified in the absence of sex. Two papers now show they exchange genes with each other, via horizontal gene transfers as known in bacteria and/or via other forms of non-canonical sex.

Asexual organisms are believed to be evolutionarily short-lived. Most asexual lineages occur on the tips of the tree of life and few have succeeded like their sexual counterparts. Only a handful of asexual lineages have diversified into different types considered as 'species' — sets of morphologically and ecologically distinct forms classified into different genera, or even families, of exclusively asexual organisms. The most prominent examples of lineages that have persisted and diversified over millions of years in the absence of sex include oribatid mites [1], darwinulid ostracods [2] (a group of freshwater Crustaceans) and, up to now, bdelloid rotifers [3] (Figure 1). These lineages have been referred to as 'ancient asexual scandals' as they appear to challenge the view that sex is a prerequisite for the long-term evolutionary success of a lineage [2,4]. They have also been considered a 'holy grail' for developing insights into one of the most notorious unresolved questions in evolutionary biology: why is sexual reproduction so universally favored in natural populations?

The idea is that if we can understand how ancient asexual scandals persisted and diversified in the absence of sex, we might develop insights into what the most fundamental benefits of sex are [5].

A new study in this issue of *Current Biology* by Debortoli *et al.* [6] shows that the answer to how bdelloid rotifers have persisted and diversified in the absence of sex might be that bdelloids engage in an unusual form of 'parasex' that allows for horizontal genetic exchange between individuals in the absence of regular meiosis and the production of gametes. The mechanisms mediating these horizontal gene transfers between individuals remain unknown. But the phenotype, horizontal gene transfer, brings an outstanding example of convergent evolution between bacteria and eukaryotes. Furthermore, elucidating the molecular details of horizontal gene transfer in bdelloids may open novel avenues to large-scale genome editing.

Bdelloid rotifers are abundant micro-invertebrates that occur in aqueous habitats throughout the world [7]. There

are 461 described species, distinguished from each other mainly on the basis of morphology [8,9]. Many species are able to survive dry, harsh conditions by entering a desiccation-induced state of dormancy from which they can emerge upon re-hydration [7]. The first hint for horizontal gene transfers in bdelloid rotifers was published in 2008 when Gladyshev and colleagues showed that bdelloid genomes harbor unusually many genes of bacterial, fungal, and plant origin [10]. Later work in the species *Adineta ricciae* then demonstrated that many of these foreign genes are expressed, and that as many as 8–10 % of all transcripts are of foreign origin [11]. The publication of the genome of a related species, *Adineta vaga* [12], revealed a similar level of foreign gene content, with 8 % of predicted genes of non-metazoan origin. Finally, foreign gene uptake is ongoing in bdelloids and has contributed to functional differences among species [13] and therefore to adaptive evolution in bdelloids.

Given the evidence that bdelloid rotifers acquire and use genes from

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