Cover illustration

A backseat driver

Carnivorous, but mostly sanguivorous, leeches have been reviled for centuries even though they were used for bloodletting as medical treatment for perhaps 2000 years. Even today, these interesting annelids are used as medical adjuncts. In this regard, reducing the accumulation of tissue blood and venous congestion is accomplished better using leeches than by other methods, especially in confined areas such as the fingers or muscle flaps. Although voracious feeders when provided an opportunity, most leeches will dine only once every few months. Of course, when they do feed, they may increase in size by an order of magnitude. But, how do they locate their prey and what part does vision play?

The medicinal leech, *Hirudo medicinalis* (fig 1), among species of other leech, does have eyes and does see, albeit poorly, as sight is not its primary sensory modality. Nevertheless, these maligned creatures have a surprisingly sophisticated photoreceptive sensory system coupled with an ingenious and highly successful lifestyle.

Vision usually has a key role in predatorial lifestyles, although certainly this is not an exclusive criterion. Leeches prove the test as they are predators, although some might consider the appellation "parasite" more applicable.

The sensory system of leeches is somewhat of a mystery, but includes five pair of eyes on the head, as can be seen in the cover illustration. These eyes alone—in a leech—would be interesting enough, but there are more eyes—many more. These rapacious creatures have seven pairs or 14 sensilla (sensory units) distributed around each of their 21 mid-body segments, and others in the four head segments and seven tail segments, giving total of well over 300 "eyes" along various body surfaces.

Understanding the five dorsal pairs of more classical eyes and these sensilla receptors, however, requires some explanation.

The five paired cephalic eyes are eyecups and, as a result, do have some directional selectivity and may provide somewhat of a formed image. Some authorities have considered these eyes to be prototypical for the arthropod

Hirudo medicinalis.

compound eyes. Each one of these 10 eyes (five pairs) has approximately 50 photoreceptors, and each eye has a distinct visual field that does not overlap. Thus, each eye might correspond to a single ommatidium of the arthropod compound eye.

The sensillar sensory bulbs are not just "eyes" and may fall outside the definition some may have for eyes. These sensillar units contain distal mechanoreceptor cells with a cilium extending 3–12 μm beyond its body. Proximal to these mechanoreceptors are chemoreceptor cells, and, beneath (proximal to) all of these receptor cells are photoreceptor cells, buried approximately 100 μm , more or less, in a vertical unit. The sensillum is not primarily a visual sensory unit, but a mechanical one, and the cilium of each unit is sensitive to vibrations from water. The leech responds to small vibratory stimuli to find its prey. But these "buried" photoreceptors are backed by a melanocytic cup and are photoresponsive (Kretz JR *et al. J Comp Physiol* 1976;106:1–37).

So, what happens with these sensillar eyes and how does the leech use this information? We know that the visual pigment of all the photoreceptors has its maximal response to a wavelength of approximately 540 nm (essentially green), but is nearly insensitive to the more extreme ends of the visual spectrum (red and violet). Not surprisingly, this system is tuned to a moist semi-terrestrial freshwater environment. Although each of the five pairs of dorsal eyes on the "head" end is more or less directionally sensitive, the sensillar

photoreceptors are less so, and may not be directionally sensitive at all. The neurological input from the photoreceptors is incompletely understood, as there are inputs from each of the 300-plus sensilla into the single ventral nerve. The ventral sensilla are photophobic, and those on the dorsal surface, photophilic. The photoreceptor-generated signal travels to a segmental ganglion where the signal is integrated with signals from both the ipsilateral and contralateral sensillar photoreceptors from adjacent segments. The inputs from the contralateral sensilla are inhibitory. It is as if the eyes provide information that may be used as part of a reflex system to seek or shun light. This reflex system suggests that the sensory system is most satisfied when the creature is feeding with the ventral surface occluded by its prey and the dorsal surface stimulated by light. This seems akin to the reaction of other more "primitive" species—the jellyfish (BJO cover essay May 2003). Surprisingly, the leech will respond differently depending on the contents of its stomach. If sated, it will avoid light, but if hungry it will seek it. However, it is not quite that simple, either. The dorsal cephalic eyes probably function much like the eyes of other annelids, with the ability to sense light and movement and providing a poorly formed image. The sensillar photoreceptors probably respond to light and may be important for light perception, prey detection and circadian rhythm. But there may be more to this story, phylogenetically. This invertebrate illustrates that photoreceptors may sink into deeper tissue layers, taking a backseat to other sensory modalities. Yet, these photoreceptors still maintain the ability to respond to, or at least sense, light. Evolutionarily, something similar must have occurred to achieve the parietal eye of some fish, lizards, and eventually our own pineal—a backseat driver indeed.

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Photograph by Krista Todd. Thanks to Mark Siddall and William Kristan for comments.