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your head up looking for predators and your head down looking for food at the same time. Humans have recently been referred to as a 'super-predator' and many animals are most terrified of humans with potential repercussions on prey demography and trophic cascades. Because animals across all taxa engage in some sort of anti-predator defense, the ecology of fear may be widely applicable. Experimental manipulations provide the clearest evidence of fear operating, and many experiments in mesocosms on invertebrates and aquatic species demonstrate that fear is powerful enough to affect prey populations and communities. Manipulations in terrestrial vertebrate systems are relatively scarce but experiments thus far are revealing the importance of fear. More manipulations, especially in terrestrial vertebrate systems, are necessary to assess whether and how fear operates across animal taxa, and within taxa, across species.

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The mirror-based eyes of scallops demonstrate a light-evoked pupillary response

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Light levels in terrestrial and shallow-water environments can vary by ten orders of magnitude between clear days and overcast nights. Light-evoked pupillary responses help the eyes of animals perform optimally under these variable light conditions by balancing trade-offs between sensitivity and resolution [1]. Here, we document that the mirror-based eyes of the bay scallop *Argopecten irradians* and the sea scallop *Placopecten magellanicus* have pupils that constrict to ~60% of their fully dilated areas within several minutes of light exposure. The eyes of scallops contain two separate retinas and our ray-tracing model indicates that, compared to eyes with fully constricted pupils, eyes from *A. irradians* with fully dilated pupils provide approximately three times the sensitivity and half the spatial resolution at the distal retina and five times the sensitivity and one third the spatial resolution at the proximal retina. We also identify radial and circular actin fibers associated with the corneas of *A. irradians* that may represent muscles whose contractions dilate and constrict the pupil, respectively.

Positioned along the edges of their valves, scallops (Mollusca; Bivalvia) have dozens of eyes, each measuring ~400–800 μm in diameter. Like camera-type eyes, these eyes are single-chambered and have both a lens and a cornea. Unlike camera-type eyes, the eyes of scallops primarily use a concave mirror to focus light; they also contain two separate retinas, the proximal retina that lies close to the mirror at the back of the eye and the distal retina that lies between the proximal retina and the lens [2]. These eyes provide scallops with spatial vision that is surprisingly acute for a bivalve: behavioral trials [3], electrophysiological experiments [4], and ray-tracing models [5] all indicate that the eyes of scallops have angular resolutions of ~2°. In 1886, it was reported that scallops can constrict the pupils of their eyes to half of their maximum diameters through the coordinated activities of radial and circular muscle fibers [6]; however, this report was challenged in 1910 [7] and pupillary responses in scallops were not explored again until now.

Using time-lapse imaging, we documented that the onset of light causes pupils from the eyes of intact, un-anesthetized specimens of *A. irradians* and *P. magellanicus* to constrict to 50–60% of their fully dilated areas within several minutes (Figure 1A). After ten minutes of exposure to light, the pupils of *A. irradians* and *P. magellanicus* dilated fully after 45 and 15 minutes in the dark, respectively. Light intensity influenced the magnitudes of the pupillary responses of scallops (Figure 1A). The pupils of *A. irradians* constricted the most under the brightest conditions we tested, which were similar to an overcast day (~1,000 lux) and constricted the least under the dimmest conditions we tested, which were similar to late civil twilight (~1 lux). Compared to other pupillary responses, such as those of vertebrates and cephalopods [8], those of scallops are small in magnitude and slow in action. The pupillary responses of scallops most closely resemble those of the camera-type eyes of box jellyfish, in which a minute of light exposure causes pupils to constrict to half of their fully dilated areas [9].

To test how pupillary responses may impact visual performance in scallops, we used a ray-tracing model to predict the sensitivity and resolution at both retinas in the eyes of *A. irradians*. Across the full range of pupil apertures we observed in our trials (200–400 μm), we found that the sensitivity of the proximal retina (3–15 μm^2 sr) was consistently higher than that of the distal retina (1–3 μm^2 sr) and that the resolution at the proximal retina (30°–100°) was always coarser than the resolution at the distal retina (~2°); further, we found that aperture has a more pronounced effect on the function of the proximal retina than the distal retina (Figures 1B,C, and S1 in Supplemental Information, published with this article online).

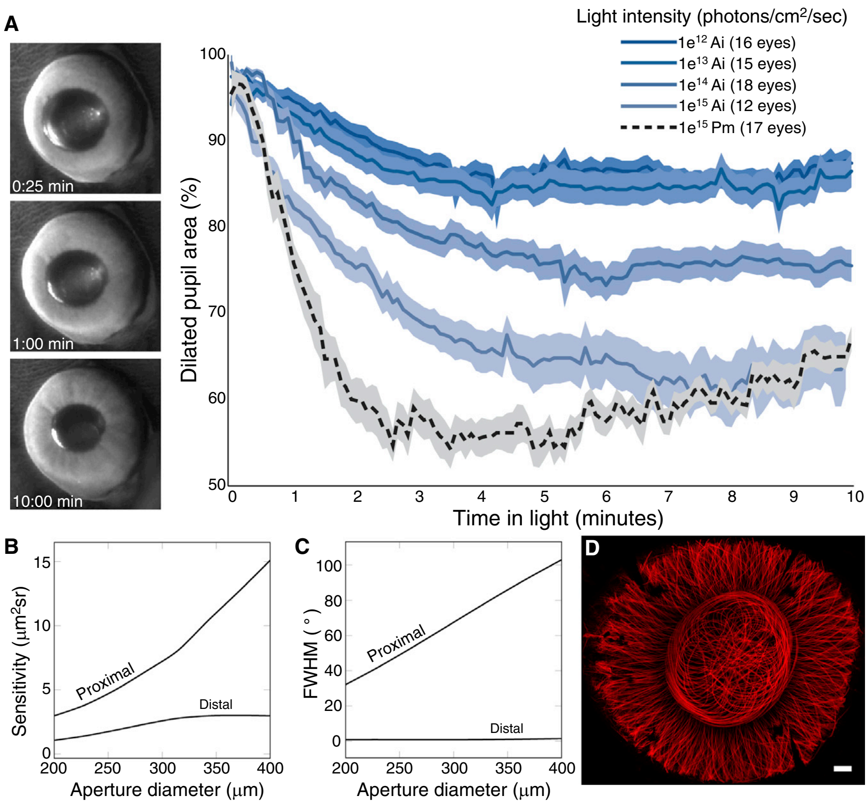

Figure 1. Light-evoked pupillary constriction in scallops.
(A) Time courses of pupil constriction in *A. irradians* (solid blue lines) and *Placopecten magellanicus* (dashed black line). Shading represents +/- 1 standard error around the mean value. Light levels (in photons/cm^2/sec) and sample sizes for each experiment are indicated. Panels to the left are time-lapse images of an eye from *A. irradians* undergoing pupil constriction, with the time after the onset of light marked at the bottom of each image. (B) The sensitivities of the proximal and distal retinas in the eyes of *A. irradians* as functions of aperture diameter; here, for the distal retina, note that wider pupils improve sensitivity up to the point at which increased optical aberrations counteract the benefits of additional light. (C) The angular resolutions — described as full width at half maximum (FWHM) in degrees — at the proximal and distal retinas in the eyes of *A. irradians* as functions of aperture diameter. (D) Phalloidin labelling of the inside surface of a cornea from *A. irradians* in which the circular structure is the cornea, the surrounding tissue is the inside of the pigmented layer that surrounds the eye, and the scale bar is 50 um.

We find that a retina's proximity to the light-focusing mirror explains the effect that the aperture of the pupil has on its performance. The resolution at the distal retina, the further of the two retinas from the mirror, was primarily influenced by longitudinal spherical aberration (LSA): rays entering the eye through the periphery of the pupil intersect the distal retina at locations different from those of rays entering through the pupil's center (Video S1). The resolution at the proximal retina was influenced to a lesser degree by LSA because the proximal retina lies further away from the focal point of the eye. Instead, resolution at the proximal retina improves when the aperture narrows for the same reason that narrower apertures are associated with sharper images in eyes and cameras based on pinhole optics.

Next, we asked how scallops control the widths of their pupils. In corneas from the eyes of *A. irradians*, counterstaining with phalloidin revealed radial and circular actin fibers that may represent muscle fibers whose contractions control, respectively, the dilation and constriction of the pupils (Figure 1D). The radial fibers travel up the interior surface of the optic chamber and intermingle with loops of actin fibers in the center of the cornea. The circular fibers ring the cornea's periphery and contribute to the loops of fibers in its center. The eyes of scallops lack an iris (the pigmented cells that surround the eyes are part of a continuous sheet of epithelial cells that includes the transparent cells of the cornea), so we hypothesize that coordinated activities between radial and circular muscles dilate and constrict the pupil by altering the dimensions of the cornea.

By demonstrating pupillary responses in two species of scallop that are ecologically distinct — *A. irradians* prefer to live in beds of eelgrass (*Zostera*) in warm, shallow water (<12 m), whereas *P. magellanicus* prefer open seafloor environments in colder, deeper (18–110 m) water [10] — our work indicates that mobile pupils may be widespread across scallops. Evidence for a pupillary response in scallops highlights the optical refinements of their mirror-based eyes and the ecological importance of vision to these mobile, jet-propelled bivalves.

SUPPLEMENTAL INFORMATION

Supplemental Information contains one figure, experimental procedures, and one video, all of which can be found with this article online at https://doi.org/10.1016/j.cub.2019.03.053.

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