Correspondences

Range-finding in squid using retinal deformation and image blur

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Squid and other cephalopods catch prey with remarkable speed and precision [1]. Before the strike occurs, they encounter the difficult task of judging an object's distance and size in the contrast-poor world of the mid-water environment [1–4]. Here we describe a solution to this common problem underwater, where a large portion of a squid's dorso-temporal retina is intentionally blurred. This apparently counter-adaptive 'retinal bump' is combined with a vertical bobbing behavior that scans objects of interest from focused to defocused retinal regions. The image focus differential changes sharply at precisely the distance equivalent to tentacle length and enables the squid, *Sepioteuthis lessoniana*, to capture prey. This unique range-finding mechanism is an adaptation to hunting, defense, and object size identification in an environment where the depth cues found on land are less reliable.

The range finding hypothesis presented here has grown from the surprise discovery of a retinal bump that forces much of the temporal retina in the squid *S. lessoniana* out of focus. In the featureless ocean, the crucial determination of small objects that may be worth eating versus large, potentially threatening objects has driven the evolution of this unique monocular range-finding adaptation.

Firstly, the possibility that the retinal deformation of the retinal bump might be an artifact in this soft-bodied animal was eliminated, both *in vivo* and *in vitro*. A combination of techniques was used, including transmitted illumination in small transparent individuals, dissection, standard histology, magnetic resolution imagery (MRI), ultrasonic *in vivo* imaging and *in vivo* infra-red retinoscopy (Figure 1A–H). The retinal bump is formed by the optic lobe pressing into the back of the retina in the dorso-temporal region. Optically, the result of the retinal bump is severe hyperopic blur over around a quarter of the visual field (Figure 1H). Having a large part of the frontal visual field defocused may seem counter-adaptive for survival. However, the retinal bump is combined with unique head-bobbing movements (See the Supplemental Movie 1 available on-line with this issue for further detail), resulting in dynamic eye positioning that places the image in and out of the retinal bump (Figure 1J). Hence, this bobbing behavior produces the focus differential (δ) between the focused retinal region and the bump. We argue that this is a novel mechanism for determining distance in an environment where parallax is not possible and both stereopsis and vergence cues may be degraded by the featureless waters [3,5].

We calculated the resulting theoretical changes of focus of the object as it moved over the retina during head bobbing and found a strong correlation between tentacular length and the focus differential (δ) (see the Supplemental Information available on-line with this issue for further details). Using this simple cue at different object distances, the squid could easily determine when a small object came in range and entered the 'strike zone' (Figure 1J,K). Large objects would never reach this differential threshold and could be categorized accordingly.

Given the degree of defocus of this retinal bump (Δ 40–170D), we also examined the squid's spherical lens to see if there were different focal points in different directions. Laser ray tracing confirmed that the graded-refraction lens formed a focused image at a single distance (around Matthiessen's ratio) in all directions, and that corresponds well to the distance to the non-retinal bump part of the retina (Figure 1K). In all cases, with the exception of very large animals, ray tracing results place the focused image far behind the retina of the retinal bump, resulting in an extremely blurred image [6].

Other ways to partially compensate for this defocus would be lens accommodation or pupillary constriction [4,7]. However, our retinoscopic reflex images in *S. lessoniana* showed no obvious dynamic accommodation, though they did demonstrate the permanent presence of the retinal bump (Figure 1G). In addition, even if both mechanisms were combined, they could not compensate for this degree of defocus.

Interestingly, the size of the retinal bump is age dependent and in fact disappears in the last months of the squid's life (see Supplemental Figure S1). This may be due to the relative morphology of a larger cephalic region and differential growth of eye versus optic lobe. This change, having all retina areas in focus, coincides with a behavioral switch from hunting and growing rapidly, to reproduction and mate selection. The sorts of close-range decisions needed during mate choice and reproduction may require sharp focus and may not benefit from the distinctly long-distance predatory or defensive range-finding mechanism described here.

Differentially focused or 'ramp' retinae are known in a number of fish and are linked by static accommodation mechanisms and simultaneous matches with areas of interest that are both close and far away [8]. In the stingray, for example, the dorsal portion of the retina is located further away from the lens than the medial and ventral areas and the resulting myopic sight there (–3D) has been proposed to view the receptive field directed towards the substrate. The eye can therefore be focused on objects at close range ventrally and further away laterally with minimal lens accommodation.

A different retinal defocus mechanism, aiding distance judgment, has recently been proposed in spiders [9]. This adaptation uses the chromatic aberration of the lenses of the principle eyes together with retinal regions at different focal depths to achieve the result, but in common with the hypothesis we present here, it also relies on a comparison of one retinal area with another. Thus, while it may seem initially surprising that squid apparently throw away precision and focus, as with other invertebrate systems they have

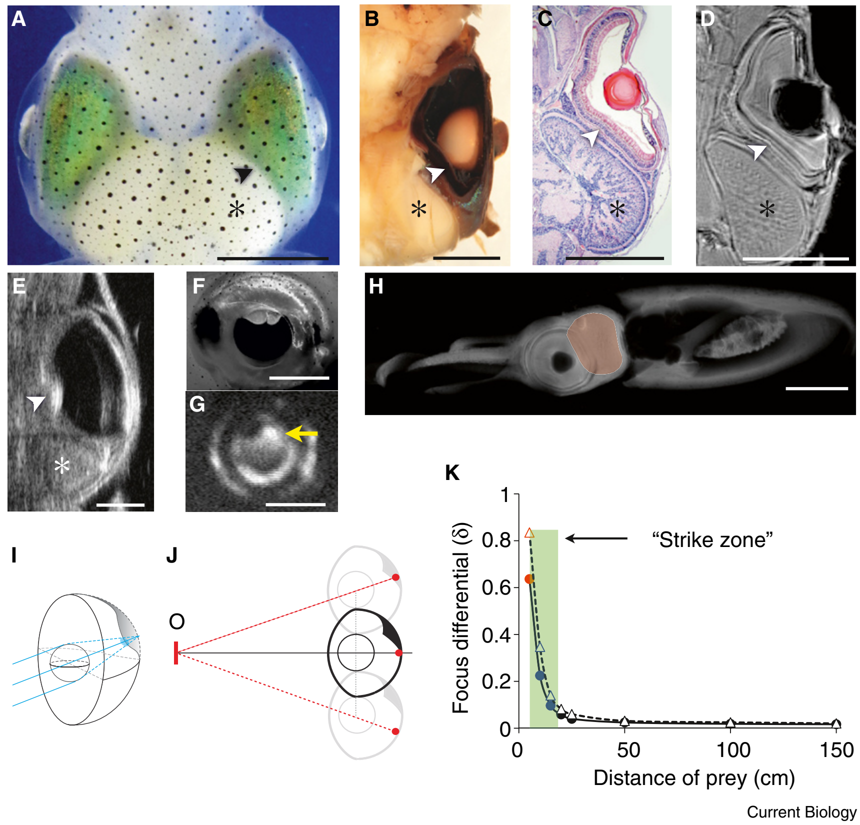

Figure 1. The non-hemispherical eye resulting in a new form of range-finding in *Sepioteuthis lessoniana.*

(A–H) The retinal deformation of squid permanently appears using a combination of techniques. (A) The live specimen. (B) Dissection of the rapidly fixed eye and brain using perfusion. (C) Histological cryosection of an unfixed, fresh specimen (12 μm thickness). (D) High resolution contrast-enhanced MRI of a lightly preserved specimen. (E) High resolution ultrasound imaging of an anesthetized specimen. The retinal bump (RB) (arrowheads) and optic lobe (OPL) (stars) are indicated. (F) The dilated pupil under red illumination. (G) Retinoscopic imaging of free swimming squid. The bright reflection on the upper area indicates hyperopic defocus (arrow). (H) MRI sagittal section. The shaded area (pink) shows that the OPL intrudes into the back of the retina at the dorso-temporal region, causing the frontal and downward (approximately 35º) view to be defocused. Scale bars: 5 mm. (I–K) Object distance estimation using retinal bump and head bobbing behavior. (I) Schematic drawing of the anatomical model of the deformation of the eye and the resulting defocus on the retinal bump (blue circles). (J) Dynamic eye positioning places the object's image (O) in and out of the retinal bump, resulting in changes of the focal quality (see Supplemental Information for further details). (K) The curves show focus differentials of a particular object over distance for both a constricted pupil (diffraction-limited condition; solid line) and a dilated pupil (diffraction-free condition; dashed line) (see Supplemental information for further details). In both conditions, the focus differential remains low for distant objects until 15 cm (blue circle), the point just within tentacle range (specimen mantle length, ML): 5 cm, tentacle projecting up to 2 MLs).

found a simple solution to a specific problem that their environment imposes.

Finally it is worth commenting that similarities in the anatomy of fish eyes and the cephalopod eye are often heralded as an example of convergence in evolution [10]. While this remains true in terms of the basic building blocks, deformed eye shapes present in squid are a good indication of the differences in optics and visual strategy between two distantly related groups inhabiting the same aquatic world. Food density in the mid-water environment that squid inhabit is usually low and the ability to determine the proximity of an object and rapidly decide whether to eat it or avoid it would be both advantageous and conserve energy.

Supplemental information

Supplemental information includes experimental procedures, two figures and a movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.11.058.

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