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SCANNING EYE MOVEMENTS IN A HETEROPOD MOLLUSC

BY M. F. LAND
School of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QG, U.K.

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The eyes of the heteropod molluscs are unusually large and complex, compared with those of other gastropods (Hesse, 1900). They have a basic design not unlike fish eyes, with a large spherical lens of short focal length that forms an image on a retina of highly ciliated photoreceptors (Dilly, 1969). Perhaps the strangest feature of the eyes is the shape of the retina. It is not a hemispherical cup as in fish, cephalopods and alciopid worms, but a long narrow ribbon only a few receptors wide (6 in *Pterotrachea coronata*, only 3 in *Oxygyrus*). The ribbon is several hundred receptors long and in some species it is straight whilst in others it is curved into a horseshoe configuration. In either case this means that the field of view of the eye is a narrow strip of space a few degrees high and 80–180° long. Most of the surroundings are therefore not seen by the animal at any given time. In this paper I show that the problem of the narrow field of view is solved in one heteropod species at least by systematic scanning movements of the eyes, in which each retina 'sweeps' through a 90° arc.

Oxygyrus keraudreni is a small epi-pelagic carnivorous heteropod. Several specimens were caught in neuston nets or plankton tows during cruise 105 of the R.R.S. *Discovery* in the vicinity of the Canary Islands. They were studied alive in a long vertical tube of sea water to see their normal orientation during swimming (Fig. 1). Eye movements, which can easily be seen with the unaided eye, were recorded on video tape using a Sanyo portable camera and recorder (VTC 7100), with the animals in a small dish. The tapes were later analysed frame by frame to provide a record of eye orientation versus time. The eyes were later sectioned (1 μm) to obtain the dimensions of the retinal elements.

Oxygyrus normally swim with the shell pointing downwards as shown in Fig. 1. They maintain their position in the water by repeated bouts of swimming involving flapping movements of the dorsally directed foot. Oddly, these drive the animal upwards. Each bout lasts 1–2 s, with longer intervals in between (mean 10·1 s) during which the animal sinks a few centimetres. Every 3 minutes or so the animal moves its proboscis around and cleans the keel of the shell with its radula for a few seconds. Presumably the keel is sticky and functions as a sort of net. When the eyes are not actively scanning they have a rest position in which the retinae are directed laterally, i.e. the retinal band is horizontal, and so is the plane containing the retina and the centre of the lens. When

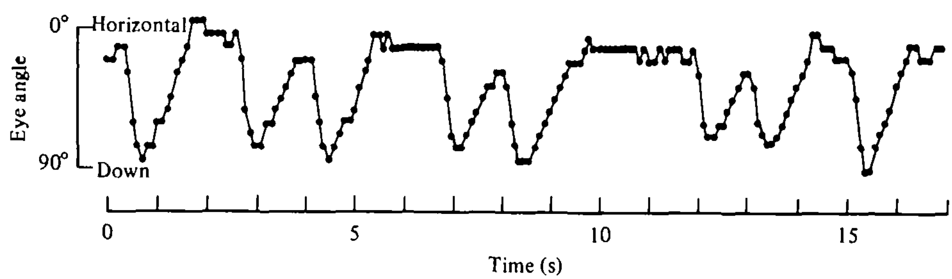

Fig. 2. Record of eight consecutive scanning eye movements, made by measuring the vertical width of the black retinal strip on successive video frames, and later converting these to angular measurements.

the animal rocks slightly about a transverse axis, as it often does after a bout of swimming, the retina remains horizontal, and this is presumably a compensatory reflex mediated by the statocysts. Imposed pitching movements of up to 30° seem to be accurately compensated.

Scanning eye movements occur during the periods between swimming bouts, and consist of a rapid downward rotation of each eye lasting 0·2–0·3 s, followed immediately by a much slower return to the horizontal rest position. This takes 0·6–1·1 s (Fig. 2). During the fast phase of these rotations the retina moves up and the lens down, so that the retinal field of view sweeps downwards through the upwelling light. It then sweeps slowly upwards. The total excursion is about 100°, so that the whole of the quarter-sphere from just above the horizontal to directly below the animal is scanned. The maximum angular velocities of the eye are 250° s^{-1} during the downward phase, and 80° s^{-1} in the upward phase. In *Oxygyrus* the two eyes sometimes scan synchronously, but by no means always. In some *Atlanta* species, on the other hand, where the eyes are directed frontally rather than laterally, and probably have considerable binocular overlap, the eye movements are always conjugate. *Oxygyrus* spend most of the time scanning: during a 2 min period the average time between the starts of scanning movements was 2·5 s (S.D. 1·3) with the scanning movements themselves lasting 1·3 s (S.D., 0·2), meaning that the eyes were moving 52% of the time.

In a living specimen of *Oxygyrus* with a shell 4·2 mm across at the widest point (excluding the keel) the eye had a maximum width of 1·2 mm. The lens diameter was 550 μm, and the distance from the centre of the lens to the back of the pigment layer in the living animal was 575 μm. The pigment layer is about 10 μm thick, and the receptors are 25 μm long, so that the focal length of the lens, assuming the retina to be in focus, will be 540 μm. The ratio of focal length to lens radius (Matthiessen's ratio) is thus 1·96, which is lower than in fish (2·5–2·6), and implies that the lens must be optically inhomogeneous and also that it has a high central refractive index (~1·58) (Pumphrey, 1961; Land, 1980). In the retina the receptors are stacked in 3 horizontal rows. They are wider vertically than horizontally, so that the face that each receptor presents to the lens is about 10 μm by 3·9 μm. The receptors are contiguous, and the whole retinal strip is only 30 μm high. This corresponds to an angle

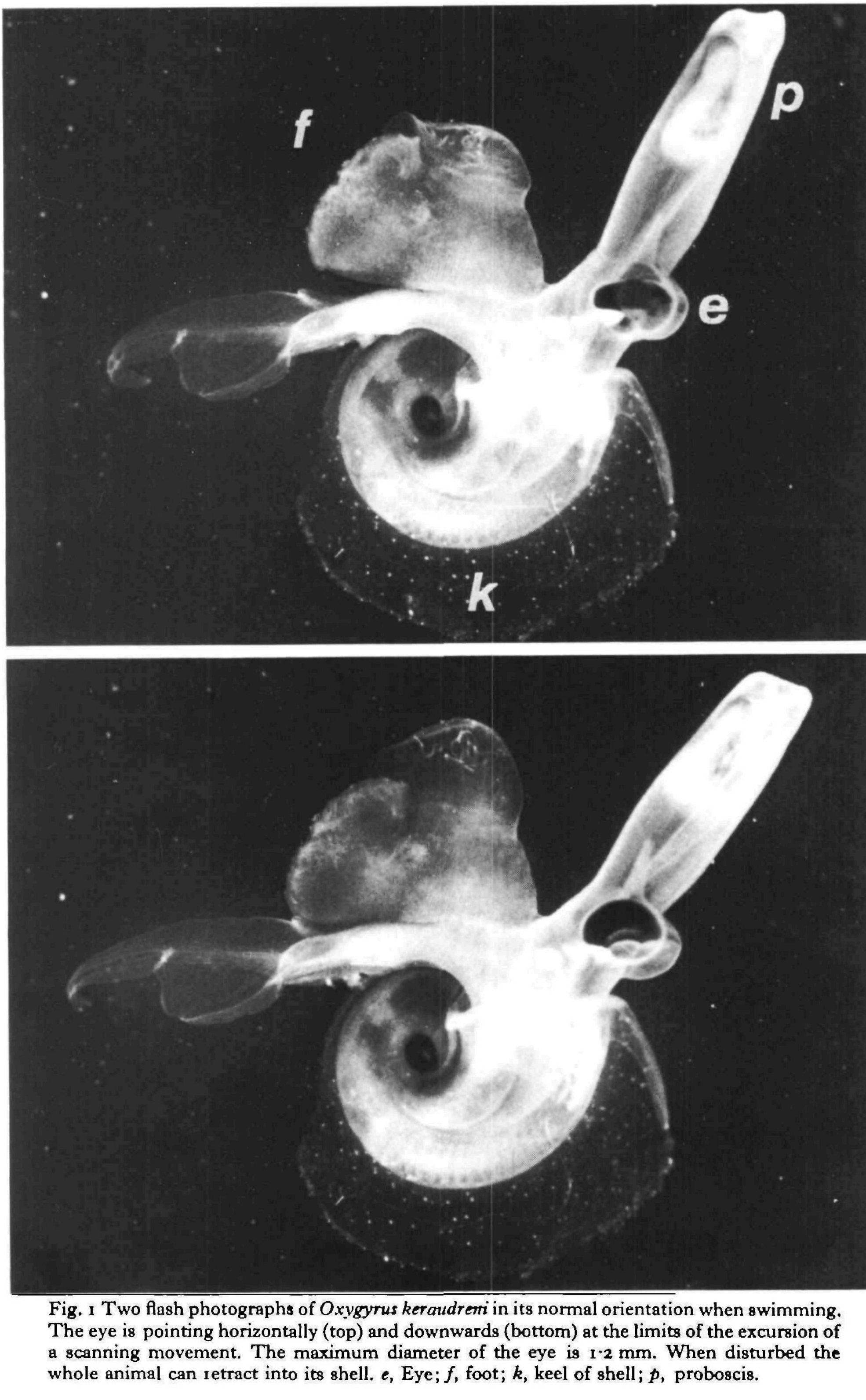

Fig. 1 Two flash photographs of *Oxygyrus keraudreni* in its normal orientation when swimming. The eye is pointing horizontally (top) and downwards (bottom) at the limits of the excursion of a scanning movement. The maximum diameter of the eye is 1·2 mm. When disturbed the whole animal can retract into its shell. *e*, Eye; *f*, foot; *k*, keel of shell; *p*, proboscis.

in visual space of 3·2°, with individual receptors subtending angles of 1·1° (vertically) by 0·4° along the row. Horizontally, the retina has a length of 1·6 mm and covers an angle of about 160°. There will thus be approximately 410 receptors in each row. If the retina is scanning at 80° s^{-1} (the lower figure) a receptor of vertical extent 1·1° will take 14 ms to pass through the image of a point source, and the whole retina will have a 'shutter time' of 42 ms. This is presumably long enough to register the presence of a stationary object in the water.

In a wide range of animals, from insects to man, one finds a repertoire of eye movements whose principal functions are concerned with the stabilization of the image on the retina (Land, 1975). Thus when we 'scan' the surroundings we do this in small discreet jumps (saccades) with stationary pauses between them, the eyes being protected against rotation by the vestibulo-ocular reflex and optokinetic nystagmus. In *Oxygyrus* the situation appears very different. The eyes are programmed to make smooth scanning movements, and it seems likely that the function of the movements is to enable the animal to detect stationary objects in the surrounding water. Since the eyes scan the lower, dark, half of the environment they are probably looking for objects that glisten in the light from above. In contrast one may speculate that the eye movements of insects, higher crustaceans, cephalopods and vertebrates have evolved to detect motion, either self-generated as in locomotion, or caused by prey or predators, and that the reason for the maintenance of eye stability is the need to avoid confusion between eye movement and image movement.

Scanning, in the present sense of deliberate smooth eye movements, has been reported in only three other contexts. In the copepod *Copilia* (Gregory, Ross and Moray, 1964), where a minute retina of only five receptors scans laterally across the field of view of a single large lens. In jumping spiders (Land, 1969), where the slit-like retinae of the principal eyes are moved through a complex pattern of translatory and rotatory movements that are probably concerned with pattern recognition, specifically with determining whether the target is a potential prey or another jumping spider. And finally one should include the 'peering' movements made by locusts, whose function is to extract parallax information for the purpose of distance estimation (Wallace, 1959; Collett, 1978). In all these cases, as well as that of *Oxygyrus*, scanning is a search procedure concerned with the extraction or analysis of information from a stationary scene.

Although there are no studies of *Oxygyrus* catching prey, it is a reasonable assumption that both horizontal and vertical coordinates of a prey object are available to the animal: the former from actual retinal location, and the latter from the position of the eye in its scanning cycle.

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