

more drug companies are rushing into bed with one another. Rhône-Poulenc and Hoechst are attempting to merge, and Glaxo Wellcome is still looking for a suitable partner after spurning SmithKline Beecham last year and Bristol Myers Squibb this year. For the moment, only Zeneca and Astra have succeeded in consummating their affair.

Correspondence

A new category of eye movements in a small fish

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One of the main functions of the oculomotor system in vertebrates and most invertebrates is to keep the image of the world relatively still on the retina [1,2]. Eye re-locations are often rapid gaze shifts or 'saccades' which move the eyes with high velocity in order to minimise the period during which the image is destabilised [2]. Here, we describe unusual drifting eye movements in a small teleost fish, the sandlance (*Limnichthys fasciatus*). This animal breaks the universal rule of image stabilisation by showing large postsaccadic drifts as part of its normal oculomotor repertoire.

When observing its environment, the sandlance shows spontaneous monocular saccades to eccentric eye positions in order to locate prey items in the water column above it (Figure 1a); the two eyes are very rarely synchronous. Its oculomotor range is large, covering almost 180 degrees horizontally (rostral to caudal) and 90 degrees vertically (lateral to dorsal) (Figure 1c,d). Between 20% and 40% of the spontaneous saccades are followed

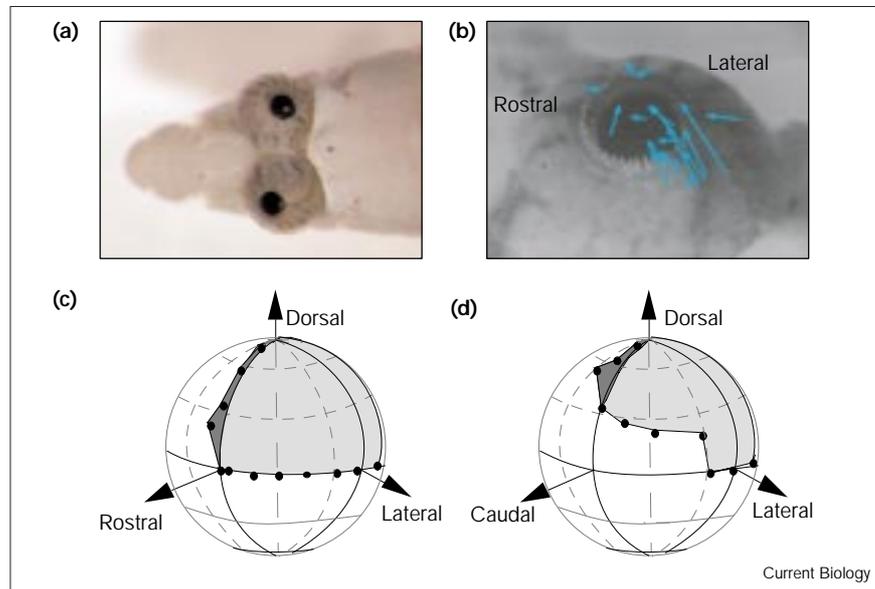
by postsaccadic drifts, especially when the saccades are to very eccentric eye positions (Figure 2a–c). The drifts can cover up to 35 degrees of angular distance and their average speed is between 2 and 3 degrees per second (Figure 2c), slower than that of saccades by two orders of magnitude (Figure 2b,c). Drifting leads the eye from an eccentric position back to a more relaxed 'home position', which is defined by the most relaxed state of the eye muscles. This indicates that the drift is not visually driven but results from a passive relaxation of the eye muscles after a saccade.

Sandlance eye drifts occur after apparently spontaneous as well as visually evoked saccades. During eye movements elicited by rotation of the environment (optokinesis), drifts can be recorded at slow stimulus speeds (our unpublished observations). Sandlances can, however, maintain stable fixation

when confronted with prey items in the water column; this alternate oculomotor strategy could perhaps indicate a higher motivational state. Other fish that also feed on small planktonic prey, such as the pipefish (*Corythoichthys intestinalis*), maintain stable fixation after saccades in all circumstances, and this is so for all other vertebrates whose eye movements have been studied (Figure 1c; [1]). Stabilisation is mediated by a very strong optokinetic mechanism that uses input of the world 'panorama' over a large input visual field in order to stabilise the eye. The eye drift in the sandlance shows that this fish can suppress the onset of this powerful reflex, an ability unique among vertebrates, although it is known to occur, for other reasons, in a few invertebrates [1].

Sandlances have a deep pit fovea with the highest ganglion-cell density that has been reported in a

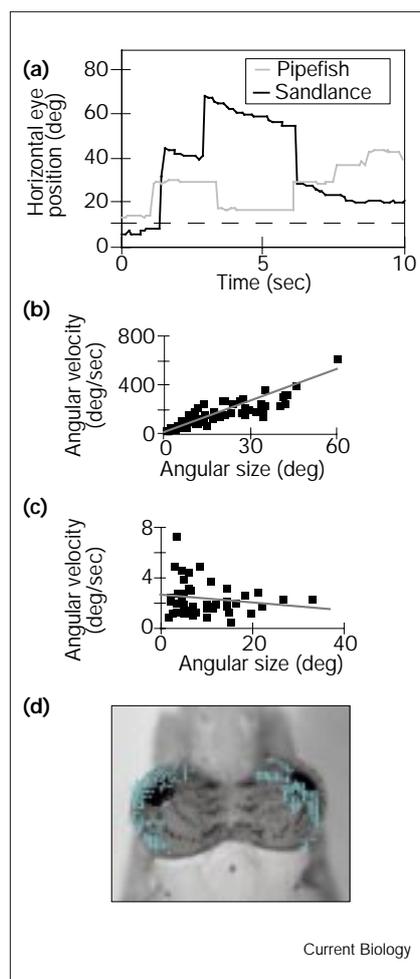
Figure 1



Drifts in the sandlance (*Limnichthys fasciatus*). (a) Head of a sandlance showing its turret-like, very mobile eyes. (b) The onset, direction and termination of a series of drifts (arrows) superimposed on the eye of a sandlance. From all eccentric positions the eye drifts back to a more relaxed position, which points forward and upwards. (c,d) Estimate of

the range of eye movements in the sandlance. The illustration shows possible eye position (grey) as measured from the centre of the pupil mapped onto the visual space (globe): (c) anterior view, (d) posterior view. The dots represent data points of maximal eye position. The darker shaded area indicates movements into the contralateral visual field.

Figure 2



(a) Trace of spontaneous saccades in the sandlance and the pipefish. In the sandlance, the saccades are immediately followed by a drift that is directed towards the relaxed position (indicated with a broken line). The pipefish shows stable fixation after saccades, like all other vertebrates. (b) Saccade velocities plotted as a function of the saccade size ($n = 60$; correlation coefficient = 0.86). The linear relationship of increased velocity with increasing angular size is characteristic for saccades and found in all vertebrates. Peak saccade velocities reach around 700 degrees per second. (c) Graph of drift velocity as a function of drift size ($n = 45$; correlation coefficient = 0.15). The velocity rarely exceeds 4 degrees per second and is independent of the size of the drift. (d) Sequential eye positions superimposed on the eyes of a sandlance while the animal observes its environment with spontaneous saccades over a period of 60 seconds. Drifts lead the eye from eccentric positions back to a more central eye position, which results in a clustered distribution around the home position.

fish [3] and a 'telephoto' lens–cornea arrangement similar to the chameleon [4,5]. It appears that the visual system of this fish is highly evolved, and closely parallels that of the chameleon, in order to manage the difficult task of catching small prey with ballistic strikes [6]. It is likely that the postsaccadic drifts are in some way advantageous to the sandlance and not simply a sign of an inaccurate oculomotor system. The fact that the maximum speed of postsaccadic drifts rarely exceeds 4 degrees per second also suggests that the slipping of the image over the retina does not cause the image quality to deteriorate significantly [7].

Possible advantages and explanations of drifting eye movements are as follows. Firstly, considering the large oculomotor range, drifts back to a more central home position could help to maintain the panoramic view and allow smaller less energetically costly saccades to any new point of interest (Figure 2d). Secondly, drifting eye movements are less conspicuous than saccades, so they might enhance the camouflage of this small fish, which is heavily preyed on and normally lies buried in sand with only its eyes protruding (J.D. Pettigrew, S.P. Collin and K.A.F., unpublished observations). Thirdly, because the drift velocity does not lead to image degradation, the drifts themselves might help the fish to examine the world for minute planktonic prey by slowly moving the fovea over a large area of the visual field. The extremely high resolving power in the fovea and the relatively poor resolving power of surrounding eye regions may make this pseudo-scanning eye movement necessary [1]. Finally, as suggested by Mike Land [8], if the background of sea above the buried sandlance appears relatively featureless to the fish, the poor spatial detail might lead to rather loose optokinetic stabilisation, making drifting inevitable.

The interesting questions of how the unique oculomotor behaviour of the sandlance is possible without causing the equivalent of 'dizziness', and why it is not seen in other animals, remain to be answered. It is possible that the motionless posture of the sandlance, buried in the sand, results in a steady reference frame which would allow accurate integration of the drifts in relation to the visual world and its own position. Alternatively, being buried may simply provide solid enough mechanoreceptive information, rendering visual feedback of the fish's position in the world unnecessary.

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