

create their own conduits in the form of vertical, chimney-like columns. Only the formation of sea-ice during the winter would prevent further upwards growth of the columns.

To our knowledge, the Ikka columns represent a phenomenon unique in the world. The now inactive tufa towers found at the shores of Mono Lake<sup>8</sup> and Pyramid Lake<sup>9,10</sup>, in the western United States, may represent structures formed in a similar way to the Ikka columns, but in non-marine environments. The high scientific and aesthetic value of the Ikka columns make them appropriate for international protection.

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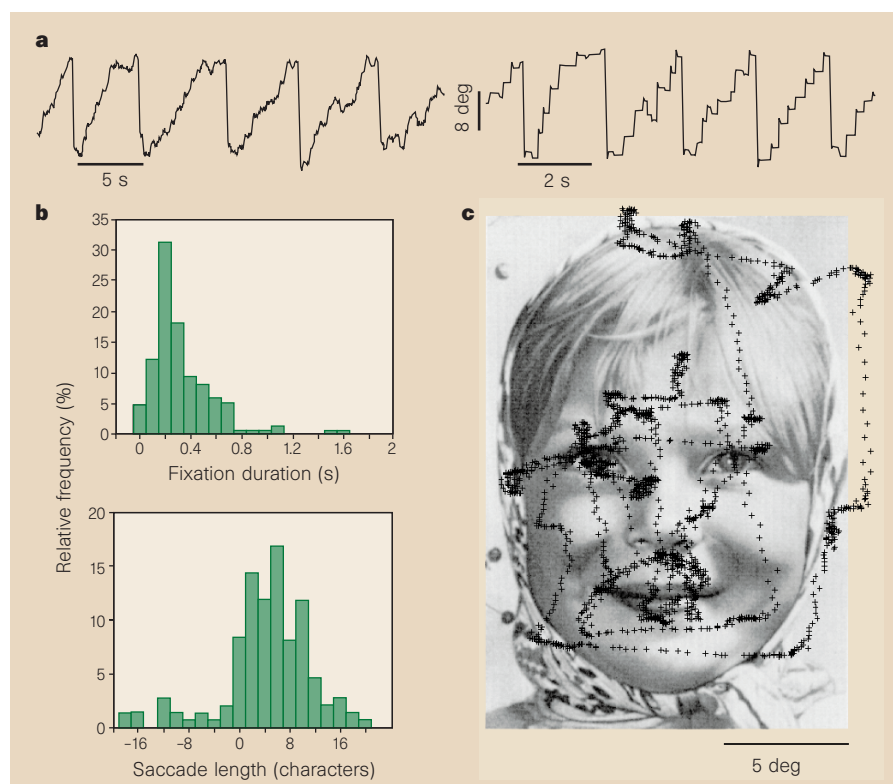
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## Saccades without eye movements

When reading text, human subjects use a pattern of eye movements consisting of fast saccadic movements and fixations<sup>1</sup>. We have found a subject who cannot make eye movements. Her visual perception is surprisingly normal and she is able to read at high speeds. She uses movements of the head to compensate for the absence of eye movements. Her head movements during



**Figure 1** Recordings of head and eye movements. **a**, Head movements from AI (left) and eye movements from a control subject (right) during text reading recorded using a head-mounted search coil. Gaze position was sampled at 40 Hz. The horizontal eye or head displacement (left is down) is plotted against time. The slight overshoot in the eye-movement records is due to lens distortion<sup>7</sup>. AI is considerably slower overall and her head stability is not as good as that of the control subject. There seems to be a small, high-frequency tremor, probably reflecting the inherent instability of the head over the eye. **b**, The distribution of fixation durations and head movement sizes during single-sentence reading. Records were divided into fixation and movement periods on the basis of a velocity exceeding 10 deg s<sup>-1</sup> over a 125-ms period. This eliminates the small-tremor head movements during fixation but allows for the detection of the onset of larger movements. AI's head movements are characteristic of normal eye-movement during reading. **c**, AI's head movements while viewing pictures, taken from the study of picture scanning by Yarbus<sup>4</sup>. The pictures were viewed for 20 s and head position was sampled at 100 Hz.

reading have a saccadic character and show many of the features that characterize eye movements.

Our subject, AI, is a 21-year-old female university undergraduate. As a result of an, apparently congenital, extraocular muscular fibrosis resulting in ophthalmoplegia, AI has had no eye movements since birth. However, she reports no major visual problem associated with her deficit and receives no extra assistance, either with reading or writing, in her studies.

The presence of an optokinetic nystagmus (OKN) response is often taken as an indication of the presence of any residual eye-movement function<sup>2</sup>. We used a sensitive eye-movement recorder<sup>3</sup> to track her eyes during fixation and when presented with a large-field sinusoidal grating. The only eye movements that we recorded were very restricted drift movements ( $\pm 0.5$  deg at most) which were not linked to the stimulus motion. Normal subjects showed a standard OKN response to this stimulus which could not be suppressed.

Reading provides one of the clearest, and

best characterized<sup>1</sup> examples of how visual processes and eye movements are coordinated to acquire information. Eye movements during reading have a number of defining features. The text is scanned in a saccadic manner, the eyes alternating between short fast movements and fixations, where the eye is stable. Most saccades are to the right, although a small proportion are regressive. Rightwards saccades are typically between seven and nine characters long, although the length can vary considerably depending on the text and the individual reader. Steady fixation is maintained between saccades, typically lasting between 200 and 250 ms. It is during fixation that information is gathered from the text. At the end of each line, subjects make a large leftwards return saccade that orients the eyes to the beginning of the next line.

AI's overall reading speed for standard passages of text with a wide range of difficulty was 257 words min<sup>-1</sup> (range 183 to 435), which is consistent with slow but not abnormal reading<sup>1</sup>. This impressive reading speed is supported by movements of her head (Fig.

1a). AI's head movements have a saccadic pattern; most are rightwards with a few regressive movements. The forward fast movements have a modal size of six characters, and fixations have a normal average duration of 200 ms (Fig. 1b). In addition, AI makes the characteristic large return movement at the end of each line.

The saccade/fixate characteristic of eye movements is not restricted to reading, but is used in a range of visual scanning situations<sup>4</sup> such as viewing a picture (Fig. 1c). Like Yarbus's original subjects, AI orients to locations of interest in the picture in a saccade-like manner, showing that her saccadic head movements are not restricted to reading and seem to be her general orienting mechanism.

Although AI's deficit is a peripheral one, her case suggests that saccadic movements, of the head or the eye, form the optimal sampling method for the brain. Given the additional mass of the head, and the non-specialization of the head in humans to make small saccadic movements (although such movements are common among other species<sup>5</sup>), the fact that such saccadic movements are adopted as an adaptive strategy by this subject indicates that the costs of adopting a new sampling strategy, such as smoothly scanning the display, outweigh the costs of moving the whole head in a saccade-like fashion many thousands of times a day.

When making large orienting movements, unimpaired subjects make combined head and eye movements. Recent physiological studies of these combined head and eye movements have focused on the role of the superior colliculus<sup>6</sup>, a midbrain region known to be important in visually guided motor action. Stimulation of neurons in the intermediate and deep layers of the superior colliculus of the rhesus macaque can lead to combined head and eye movements, demonstrating a projection from the superior colliculus to the head control centre in the brainstem. Such results suggest that an adaptation of neural function in the superior colliculus could be responsible for the total transfer of saccadic movements from the eyes to the head shown by this subject.

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## Site of particle selection in a bivalve mollusc

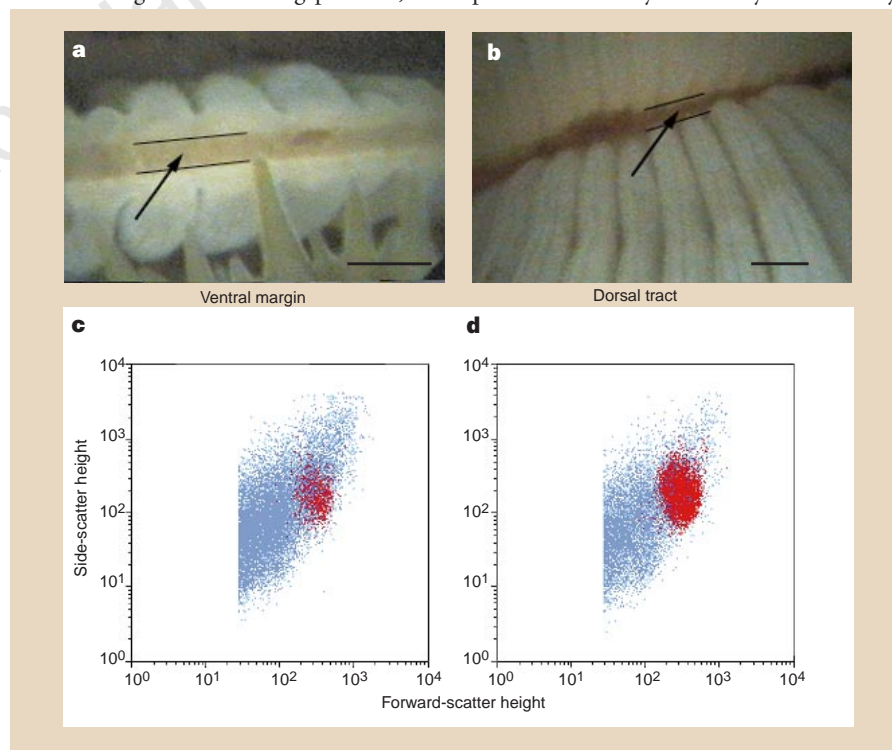
Bivalve molluscs form dense populations that exert profound effects on the particle loads and phytoplankton composition of coastal waters<sup>1</sup>. It has long been known that bivalves can select among different particle types, including selecting against those of poor nutritional value<sup>2–5</sup>, but because of difficulties in observing particle transport processes in the pallial cavity *in vivo*, the mechanism of selection was not known. We now use a combination of video endoscopy<sup>6</sup> and flow cytometry<sup>7</sup> to show that oysters can select living particles from non-living detritus on the gills. Our methods could aid the study of suspension feeding in many animal groups.

Oysters dominate estuarine bivalve assemblages throughout the world and form dense reefs that may strongly affect the seston of estuaries<sup>8</sup>. To determine whether oysters can select among the mixture of living and non-living particles, we

studied the western North Atlantic (*Crasostrea virginica*) and the Pacific (*C. gigas*) oysters. We observed particle transport directly using a surgical endoscope, and with the aid of a micromanipulator we positioned a sampling pipette to sample particles from ciliated transport tracts. We distinguished and counted particle types using flow cytometry.

We fed the oysters a mixture of two equally sized but qualitatively different particle types, the red-coloured microalga *Rhodomonas lens*, and ground dead leaves and stems of the cord grass *Spartina alterniflora*. The *S. alterniflora* had been lying above the highest extent of the tide for at least four months and presumably was less nutritious than the living microalgal cells. *Spartina* spp. salt marshes line the fringes of most eastern North American estuaries and *Spartina* spp. detritus is an important component of the seston<sup>9</sup>.

Oysters have a plicated, heterorhabdic gill with principal and ordinary filaments that allow transport of particles dorsally or ventrally on the gill. Particles may be moved dorsally on the gill to a ciliated tract that drives particles anteriorly in a slurry. Alternatively,



**Figure 1** Feeding selectivity by oysters. **a**, Frame from video of the ventral ciliated tract of *C. gigas*, showing concentration of beige *S. alterniflora* detrital particles. **b**, Dorsal ciliated tract, showing concentration of red *R. lens* algal particles. **c**, Flow cytometric plot for *C. virginica* showing relative abundances of *R. lens* (red) and *S. alterniflora* detrital particles (blue) in the ventral margin, and **d**, from the dorsal tract. *C. virginica* (Friday Harbor Laboratories) and *C. gigas* (Southampton College Marine Laboratory) were exposed in a static chamber to  $10^4$ – $10^6$  cells per litre, roughly equally distributed between live *R. lens* and detrital *S. alterniflora* particles. Particles were sampled after equilibration (30 min). Pseudofaeces were sampled and disaggregated for analysis. Particles were analysed by flow cytometry (Becton Dickinson FACScan bench-top flow cytometer) using detectors for forward scatter, side scatter, chlorophyll (fluorescence >650 nm), and phycoerythrin (fluorescence 560–590 nm). Heterogeneity among sorting efficiencies was significant (Kruskal-Wallis test,  $P < 0.05$ ), showing positive selection for *R. lens* in the dorsal tract and enrichment of detrital particles in the ventral tract and pseudofaeces.