

effects of CO<sub>2</sub> on soil moisture can lead to increased plant growth, especially in dry years<sup>8</sup>. But this does not necessarily imply increased carbon storage, which is controlled by the balance between plant growth and decomposition — under many circumstances, decomposition tends to increase in parallel with plant growth.

Oechel and colleagues found no evidence for long-term stimulation of net ecosystem carbon balance by increased CO<sub>2</sub> alone. Yet theirs was not really a long-term study from the perspective of the lifespan of the tundra plants or the dynamics of global change. Even the complete homeostatic adjustment of net ecosystem carbon balance at higher CO<sub>2</sub> might be an artefact of the study's limited duration or of the climate during those particular years. Clearly, though, increased carbon storage is not an automatic consequence of ecosystem-level exposure to increased CO<sub>2</sub>. Arctic tundra is unique in many respects. Increasingly, it is possible to predict ecosystem responses to

global change, accounting for unique features of different ecosystem types. Long-term, ecosystem-scale experiments provide unparalleled opportunities for testing these predictions and for improving the understanding necessary to make better predictions in the future. □

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## VISION

# When it pays not to see

*Michael J. Morgan*

DURING rapid eye movements, for example those made while scanning this article, we are not normally conscious of the smear caused by movement of the image over the retina. On page 511 of this issue<sup>1</sup>, a group of workers at Pisa and Perth clear up some confusion by showing that this 'central anaesthesia'<sup>2</sup> of vision during eye movement is selective for motion signals.

Eye movements are important in compensating for the poor spatial resolution of our vision outside of the central area (the fovea), but they bring with them a potential inconvenience. During each saccade the retinal image is displaced at several hundred degrees per second, and it is easy to show by psychophysical experiments that such displacements of the image are perceived as movement if they occur when the eyes are stationary. Therefore our vision should be continuously interrupted during eye movements by annoying motion signals, which would interfere with our perception of a stable, external world.

The suggestion that vision is suppressed during saccades was made by Dodge as early as 1900<sup>3</sup>. The experimentally inclined reader can observe this suppression by looking in a mirror and changing fixation from the image of the pupil to the edge of the eye. The eye movement is invisible in the mirror, but this is not because the movements are too small or too fast to be seen: they are easily observed when looking at another person's eyes.

It appears that perception is interrupted

during a saccade. But measurements of the extent of suppression have given contradictory results, and there are many cases where vision is manifestly clear during saccades. For example, when looking at the track from a fast moving train, the sleepers become visible only when we make a saccade against the direction of the train, and thus briefly stabilize the image of the track on our retina. A light-emitting diode viewed in a dark room will appear as a series of dots during a saccade, each dot corresponding to one flash of the diode. Why has suppression failed in these cases?

Burr, Morrone and Ross<sup>1</sup> cleverly show that the suppression is confined to one class of perceptual mechanism, involved mainly in the signalling of motion. The neural substrate of this mechanism is probably the magnocellular pathway leading from a class of ganglion cells in the retina having relatively large receptive fields, and high contrast sensitivity (variously and confusingly called the 'parasol', 'M-cell' and 'P-alpha' group). This pathway is anatomically distinct from the parvocellular pathway, which has smaller cells ('P-beta') of lower contrast sensitivity, at least up to the main input layer (IVc) in the primary cortical visual area V1. A key difference between the M- and P-pathways is that only in the latter are neurons selective for the wavelength of light. The P-pathway thus provides the substrate for our perception of colour. In the M-pathway, on the other hand, the signals from the different cone classes

appear to be randomly combined, so there is no systematic colour signal.

It is possible to devise stimuli that are (at least in theory) visible to the P-pathway because they contain differences in hue, but not to the M-pathway because they have no differences in white–black contrast (luminance). Burr *et al.* show that such 'equiluminant' stimuli are essentially unaffected by saccades. They are as visible when flashed during a saccade as when flashed before or after. The P-pathway is also thought to be responsible for detecting high-spatial-frequency stimuli; in other words, those that can be seen only when the image is in sharp focus. These too are little affected by saccades. On the other hand, coarse gratings containing no hue are suppressed during saccades. These are exactly the kinds of stimuli that would be detected by the M-pathway.

The idea that the M-pathway is selectively suppressed during saccades is supported by a study in which the variation in contrast detection thresholds with wavelength was measured for stimuli presented briefly either during or before a saccade<sup>4</sup>. Thresholds during a saccade showed the sensitivity to wavelength expected of the P-system; those presented outside the saccade were more characteristic of the M-system.

The only puzzling feature of the Burr *et al.* study is the hint of an enhancement of sensitivity to colour during saccades. In interpreting this finding it may be relevant that the P-pathway probably carries both an achromatic and a chromatic signal<sup>5</sup>. Perhaps a saccade destroys the notional equiluminance of the chromatic grating, either for mechanical or neural reasons, thereby making the target more visible.

Why should the M-pathway be selectively suppressed during saccades? The image during a saccade is moving at high velocity, and probably provides an input mainly into the coarse and relatively rapidly acting M-pathway. The P-system may hardly be active during a saccade and so nature, ever economical, has not bothered to suppress it. Bishop Paley would have seen this as another wonderful example of the cleverness of The Designer, and Darwinists will see it as a triumph for the blind watchmaker. In this case, however, it is not only the watchmaker who is blind, but the M-system during saccades. □

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