Rodwell and colleagues' study. Advances in ocean modelling may overcome the difficulty, but only in the long term.

Meantime, we need to be able to reproduce Rodwell and co-workers' result with other atmospheric models, and to understand the mechanisms by which the atmosphere 'feels' the SST anomalies. The authors suggest a thermodynamic mechanism in which SST anomalies induce changes in the heat flux from ocean to atmosphere. With this mechanism, a positive SST anomaly would warm the overlying atmosphere through turbulent heat transfer and convection, followed by a change in the circulation. This however implies that, contrary to observations, the atmosphere damps the SST anomalies. As Rodwell et al. suggest, such a discrepancy is best addressed with coupled

ocean–atmosphere models where both ocean and atmosphere are allowed to interact. □

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Neurobiology

The eyes have it!

Karl Gegenfurtner

The transmission of visual signals from eye to brain involves considerable delays in conduction and processing[1]. Because stimuli of varying intensity or colour can cause different delays, it could be difficult to synchronize events from different parts of a visual scene — in particular, our perception of moving stimuli would consistently trail behind their real locations. But the visual system can circumvent such delays by anticipating the path of moving stimuli. Such motion anticipation was assumed to be controlled by high-level motion areas of the visual cortex. Now, very much to our surprise, Berry et al.[2] (page 334 of this issue) report that motion anticipation is already accomplished to a large extent in the retina, by neural circuits that were discovered long ago.

Judging the location of moving objects is important for evading obstacles or predators and for catching prey. These tasks would be almost impossible if the relevant information was delayed. If, for example, we assume a processing delay[1] of about 100 ms, an animal (or a car nowadays) moving at a speed of 40 km per hour would be seen more than one metre behind its actual position. To overcome this potentially lethal problem, evolution has selected mechanisms that anticipate the path of motion.

The existence of mechanisms that compensate for visual delays was uncovered by clever psychophysical experiments, which compared the perceived locations of flashed and moving objects[3–6] (Fig. 1). If presented at the same position, flashed objects are seen to trail moving objects by as much as 80 ms. The common interpretation of this phenomenon was that both types of stimuli — flashed and moving — go through the same delays in the eye, and that the position of the

predictable, moving stimulus is then corrected by movement-selective mechanisms in areas of the brain concerned with analysing visual motion.

In a stunning surprise, Berry et al.[2] now show that motion anticipation not only starts at the retina, the first stage of processing in the visual system, but that it also follows from current models of retinal processing[7]. The basic ingredients are all studied and common to many stages of processing in the visual system[8]. So how do these ingredients work to produce motion anticipation? The most important part of the process is actually the simplest — namely that retinal ganglion cells pool their inputs over large regions of the visual scene (their receptive fields). In the case of a moving bar, a neuron will start firing as soon as the bar enters its receptive field (Fig. 2). This leads to activity before the bar reaches the centre of
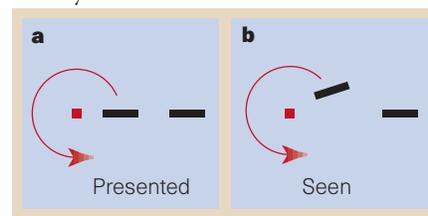

Figure 1 **Illustration of motion anticipation. Because of processing delays, our perception of moving stimuli would trail behind their real positions were it not for the development of mechanisms to anticipate the path of moving stimuli. This phenomenon has been demonstrated by psychophysical experiments in which a stationary bar is flashed at the same time as a rotating bar is aligned with it** (a). **Rather than both bars being perceived at the same position, the moving bar is seen ahead of the stationary bar** (b).

the field, yet, because of the transduction processes in the photoreceptors and retinal network, the peak firing rate would still occur some time after the bar has passed the centre.

Of course, it is physically impossible to shift the firing of neurons forward in time. But this is not necessary. The important feature for later processing seems to be the time when the firing rate reaches its peak, and this peak can be shifted forward simply by decreasing the firing rate after a while. That is what the two other ingredients of Berry and colleagues' model do. First, the temporal response of the cell is biphasic and leads to inhibition after a certain time delay. Second, contrast gain control sets the cell's overall sensitivity to stimulation in inverse proportion to retinal contrast[9]. Contrast gain control is a mechanism similar to light adaptation, only it acts on differences in intensity (contrast). So, both of these mechanisms actively inhibit the cell, causing the peak of firing to occur when the leading edge of the bar crosses the centre of the receptive field.

Berry et al.[2] used rabbits and salamanders in their experiments. They show that these 'lower' species clearly do have motion anticipation, meaning that this is an important property that was implemented very early during evolution of the visual system. But are their results valid for primates as well? The retina of lower species contains cells that are selective to the direction of motion, whereas in primates motion processing is done in the cortex. Although Berry and colleagues show that directionally selective cells were not
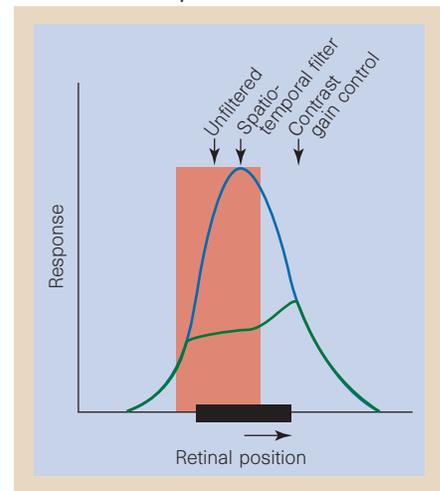

Figure 2 **Components of motion anticipation in the retina. The graph represents the 'neural image' of a moving bar at one point in time. The physical position of the bar is shown in black, and its (hypothetical) delayed image in red. Spatio-temporal filtering (blue curve) widens the neural image and shifts the peak firing activity of neurons towards the centre of the bar. Contrast gain control (green curve) shifts the response peak even further ahead towards the leading edge of the bar, as observed by Berry et al.[2].**

directly involved in motion anticipation, these cells could, nevertheless, contribute indirectly. I don't think that we need to worry overly about this. The basic mechanisms described by Berry *et al.* are common in many species and at many stages of the primate visual system[7–9]. This has the advantage that further delays in transmission from the retina to the cortex can be corrected using the same mechanisms.

More importantly, looking back at the human psychophysical literature, there are many indications that motion anticipation occurs in the retina. For example, during sudden, abrupt reversals of motion, the perceived location of the reversal is not overshot[5] — a finding that argues against cortical extrapolation. Furthermore, whereas most aspects of human visual motion processing are independent of contrast[10], the magnitude of motion anticipation strongly depends on it[6]. And, most significantly, a study by Nijhawan[4] on colour vision indicates that motion extrapolation occurs in the retina.

Nijhawan flashed a red line on a moving green bar, which should lead a viewer to perceive yellow if inputs from retinal red and green cones are combined. Instead, the red and green were de-coupled, and viewers observed that the flashed red bar trailed the moving green bar. Guided by the firm assumption that motion perception (and, therefore, motion anticipation) occurs in the

cortex, Nijhawan concluded that the synthesis of red and green cone outputs into 'yellow' occurs in the cortex, a conclusion that was regarded with great suspicion by colour scientists[11]. But the alternative idea — that motion anticipation was done in the retina — seemed even more far-fetched.

Now, Berry *et al.* show that motion anticipation is achieved very well in the retina. Their model calculations show that motion anticipation has nothing to do with motion perception. Instead, it follows in a straightforward way from visual processing mechanisms that were known all along. One wonders what other 'high-level' phenomena could be solved by the low-level retinal circuitry. □

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Seismology

Free oscillations illuminate the mantle

R. Widmer-Schnidrig

Large earthquakes radiate seismic waves that pass through the entire volume of the Earth. Because they are trapped inside the Earth, these waves experience multiple reflections, and interference between waves travelling in opposite directions eventually leads to a standing wave pattern: the 'normal modes' of the Earth (Fig. 1). These 'body' waves are also affected by the medium through which they pass, so they have encoded in them valuable information regarding the distribution of elastic properties and the location of discontinuities.

In two articles published in the *Journal of Geophysical Research*[1,2], Resovsky and Ritzwoller analyse frequency spectra of ground motion, from globally distributed seismic observatories, to model the heterogeneous distribution of elastic properties of the Earth's mantle. Free oscillations are most sensitive to the elastic parameters controlling the shear-wave velocity (the velocity of transversely polarized body waves), which is itself

a function of the chemical composition, pressure and temperature of the mantle.

Whether viewed as thermal or chemical anomalies, images of the lateral variation of the speed of high-frequency seismic waves provide some of the most direct evidence for a vigorously convecting, dynamic Earth. However, the style of convection that the mantle is undergoing, and whether it involves a single layer, double layer or something more complex, remains disputed.

In spectra from typically 1–3-day-long seismograms the normal modes show up as discrete peaks, and whereas the locations of the peaks constrain the mantle structure averaged over spherical surfaces, split peaks are evidence of large-scale asphericities and a heterogeneous Earth. Resovsky and Ritzwoller analyse the splitting of 90 normal modes, each yielding independent linear constraints regarding the distribution and size of anomalies in the mantle. Many of the analysed modes are sensitive to structure in the mid-mantle, a region notoriously ill-

sampled by both body and surface waves. Furthermore, the authors fully account for coupling between neighbouring modes, which enables them to obtain constraints for Earth structure of odd spherical harmonic degree. (Simple shapes represented by spherical functions of even and odd harmonic degree are the pumpkin and pear, respectively.) This is the first time that mantle structure of both odd and even spherical harmonic degree have been constrained from normal-mode spectra, providing a more complete picture of the Earth's mantle.

This work has several advantages over previous seismic tomography studies[3,4], despite a much lower resolution. By their very nature, normal modes involve the whole volume of the Earth (down to some characteristic depth), and uneven sampling is not an issue. In this respect, normal-mode studies differ markedly from tomographic studies where the structure is only sampled along narrow ray tubes and large volumes remain unprobed by the rays. Another difference is that tomographic studies are good at imaging patterns of heterogeneity, whereas normal-mode studies place tight constraints on the absolute amplitude of these heterogeneities.

The main drawbacks of normal-mode studies are the limited resolution ($\sim$2,500 km) and dominant sensitivity to even harmonic-degree structure. Global tomographic studies, by comparison, can resolve structures $\sim$500 km in diameter. Two notable examples[3,4] feature high-resolution images of individual tectonic slabs subducted into the lower mantle in central America. Now, for the first time, a smoothed-out image of such anomalies seems to be a robust feature of Resovsky and Ritzwoller's models[1] based on normal modes. The fact that these subducted slabs appear as connected features across the transition zone and the mid-mantle is taken by the authors as evidence that the mantle is convecting as a whole. As such, this model is at odds with geochemical data consisting of isotope concentrations in basalt rock samples from mid-ocean ridges and oceanic islands. These data seem to suggest reservoirs of isotopically distinct material in the upper and lower mantle, which in turn favours a layered model of mantle convection without significant mixing across the layers[5].

How can we make progress on this contradictory view of the mantle? Currently, the seismic models of mid-mantle structure (900–1,800-km depth) put forth by different research groups differ by amounts comparable to the size of the anomalies in the models[1]. One promising way to improve this situation is by extending normal-mode analyses to higher frequency modes. The introduction of new methods for the analysis of normal-mode spectra, such as the fully linear,