and Wunsch[4] suggested, and later work confirmed[5], that internal waves are also generated by tidal forcing at a rate greater than 1 TW. More recently, it was shown that another roughly 0.5 TW is supplied by large-scale currents impinging on the bottom topography[6]. But just as global estimates of internal-wave generation finally seemed to be coming close to the approximately 2 TW required, *in situ* observations showed that internal waves tend to break close to ocean-bottom topography (the equivalent of beaches for surface waves), thus confining mixing to within a few hundred metres of the ocean bottom. So although the energy to support mixing was no longer lacking, the mixing was not delivered uniformly throughout the water column, as was needed to lift waters back to the surface.

The final piece of the puzzle was anticipated in 1998, when another seminal paper[7] pointed out that most of the ocean waters above depths of 2,000 m come to the surface in the Southern Ocean, where winds known as the Roaring Forties, blowing around Antarctica, pull them to the surface along surfaces of constant density. The uplift process therefore requires no mixing. Only in the past few years have oceanographers been able to integrate Munk's hypothesis with the discovery of uplift in the Southern Ocean. The emerging view is that mixing brings bottom waters in all oceans up to about 2,000 m, the characteristic depth of the most prominent oceanic topographic features. The waters then flow at approximately the same depth all the way to the Southern Ocean, where the Roaring Forties lift them to the surface (Fig. 1).

In this new scenario, the potential energy required from mixing is about half that estimated by Munk and Wunsch (the ocean is on average about 4,000 m deep, and mixing lifts the waters up to only half that depth), and it needs to be supplied in the bottom 2,000 m, the characteristic height of the major ocean ridges and sea mountains. Thus, there is no shortage of energy to support mixing, and the mixing is delivered close to the bottom topography, where it is needed. Problem solved? Not quite. *In situ* observations show that the intensity of bottom mixing is highly variable, being strong where topography is rough and bottom flows are fast, and weak elsewhere. Mapping this heterogeneity on a global scale is the next challenge in the quest to track the return journey of abyssal waters to the surface.

Enter Waterhouse *et al.*[1], who have gathered the largest compilation of *in situ* measurements of mixing so far, using them to test whether the new scenario is consistent with all available observations. They confirm that internal waves are indeed generated along the major ridges and sea mountains in the Atlantic, Pacific and Indian oceans. Most importantly, they show that about 70% of the waves break close to the ocean bottom, whereas the remaining 30% propagate away from their generation sites and end up breaking against the continental slopes. They conclude that abyssal waters make their way to the surface along the steep slopes of mid-oceanic ridges and continents, where mixing is strong.

The authors did not address the question of whether mixing is confined to depths below approximately 2,000 m — instead, they lumped together all measurements below 1,000 m. Future work must address this, because the answer is crucial for understanding and modelling the partitioning of carbon between the atmosphere and oceans. It was recently suggested[8] that the drop in atmospheric carbon dioxide concentrations recorded in ice cores from glacial periods is connected to the vertical profiles of ocean mixing. In the present climate, abyssal waters release carbon to the atmosphere when they return to the surface in the Southern Ocean. But in glacial climates, a large fraction of the Southern Ocean was covered by ice, thus trapping carbon in the ocean. This trapping was possible because strong mixing was confined to the ocean bottom, and waters could not be lifted to the surface at ice-free latitudes. Similarly, the present vertical profile of mixing will control the long-term rate (on millennial timescales) at which the ocean takes up the anthropogenic carbon we are releasing into the atmosphere. ■

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SENSORY SYSTEMS

Sound processing takes motor control

Neurons linking the brain region that controls movement to the region involved in auditory control have been found to suppress auditory responses when mice move, but the reason for this inhibition is unclear. See Article p.189

URI LIVNEH & ANTHONY ZADOR

The key to human cognition lies in the neocortex, a modular brain structure that is unique to mammals. Within each neocortical module, small ensembles of neurons are wired together in stereotyped patterns. Subsets of these neurons send long-range axonal projections to other modules to create systems of circuits that transform the activity of single neurons into complex behaviours such as perception, cognition and motor control. Understanding how different neocortical regions — including the motor, visual and auditory cortices — coordinate their activity is a central challenge in systems neuroscience. In this issue, Schneider *et al.*[1] (page 189) describe a technically sophisticated set of experiments that unravels the mechanisms by which the motor cortex exerts control over the auditory cortex during locomotion.

Locomotion facilitates visual responses in the visual cortex[2] but, conversely, Schneider and colleagues observed that it suppresses sound-evoked responses in the auditory cortex. This observation is intriguing because these responses are also suppressed when an animal vocalizes[3] or engages in an auditory task[4], behavioural states that require careful auditory processing. What is the mechanism by which locomotion suppresses neuronal responses in the auditory cortex?

Neuronal firing rates are determined by the balance between signals that promote and inhibit firing, so, in principle, firing can be suppressed by either a decrease in excitatory signals or increased inhibition. To distinguish between these possibilities, Schneider and co-workers performed the challenging feat of making intracellular-activity recordings from neurons in the auditory cortex of mice running on a treadmill. These experiments revealed that decreased auditory responses during locomotion are the result of an increase in inhibition. Cortical inhibition arises almost entirely from local inhibitory interneurons that make only short-range connections with nearby neurons, so the interneurons are probably driven by long-range excitatory inputs that transmit signals into the auditory

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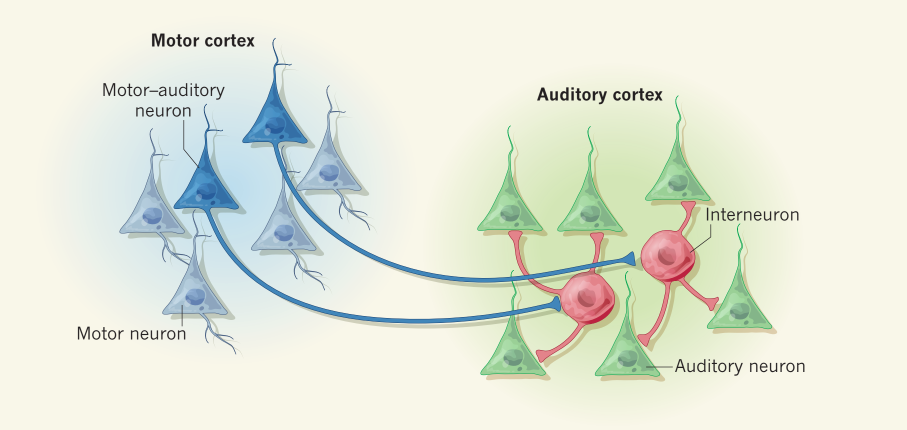

Figure 1 | Quiet in the auditory cortex. Schneider *et al.*[1] report that responses in the auditory cortex of the brain are suppressed during locomotion. When mice move, a subset of neurons in the motor cortex (motor–auditory neurons) sends excitatory signals to the interneurons of the auditory cortex, which in turn inhibit auditory neurons.

cortex. But which long-range inputs are responsible?

The authors hypothesized that long-range inputs arrive from the motor cortex. To test this, they labelled the subset of motor-cortex neurons that sends axonal projections to the auditory cortex (motor–auditory neurons) with a protein that fluoresces when activated, and monitored the neurons during locomotion. They found that the activity of motor–auditory neurons is increased before and throughout movement, indicating that they could be responsible for auditory-cortex suppression (Fig. 1). The researchers therefore set out to demonstrate that activation of motor–auditory neurons was not just correlated with suppression, but was also causally involved.

To establish causality, Schneider *et al.* infected motor–auditory neurons with a virus that enabled them to express channelrhodopsin-2 protein. Expression of channelrhodopsin-2 (which is originally derived from algae[5]) allows neurons to be activated in response to light. Selective stimulation of the axon terminals of motor–auditory neurons with light resulted in a suppression of the auditory cortex that was indistinguishable from that elicited by locomotion, supporting a causal role for this direct projection. However, this experiment alone was inconclusive, because excitation of motor–auditory axons may travel backwards along the motor projection, exciting other targets of the motor neurons and so indirectly affecting auditory responses. To rule out the possibility that suppression was indirect, the authors repeated the experiments while pharmacologically blocking activity in the motor cortex, and achieved the same result.

Finally, Schneider and colleagues inhibited motor-cortex neurons during locomotion, which disabled motor inputs to the auditory cortex. The authors found that in the absence of motor-cortex activity, locomotion was not accompanied by auditory suppression. Thus, the motor-to-auditory cortex projection is both necessary and sufficient for locomotion to suppress auditory responses.

Why should the auditory cortex be suppressed during locomotion? One might imagine that decreased activity in the auditory cortex implies reduced auditory sensitivity. However, behavioural conditions that require enhanced auditory processing typically suppress responses in the auditory cortex[3,4], raising the possibility that suppressed responsiveness serves to increase sensitivity. Such a seemingly paradoxical increase in sensitivity in the face of a general decrease in auditory cortical activity would occur if a privileged subset of cortical outputs were spared the effect of feedback suppression. In much the same way that shushing a noisy audience makes it possible to hear the seminar speaker, so feedback suppression may act to 'shush' all but the most important outputs from the auditory cortex.

The current results might be best considered in the framework of active sensation — that is, how animals separate self-induced sensory inputs from externally induced ones[6]. Movement and locomotion generate various types of self-induced sensation (for example, the movement of an object on your retina as you move your head), and so sensory inputs consist of both externally derived and self-induced sensations. Our perception separates these two sources of sensation to provide us with a movement-independent representation of the environment. To achieve this separation, a copy of the motor command might be used to indicate to the sensory cortices that movement is occurring. This copy could then be used to subtract the self-induced motor signal from the externally generated signal. The present results provide a detailed description of a circuit that may be involved in just such a computation. ■

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This article was published online on 27 August 2014.

ASTROPHYSICS

Quasar complexity simplified

An analysis of a sample comprising some 20,000 mass-accreting supermassive black holes, known as quasars, shows that most of the diverse properties of these cosmic beacons are explained by only two quantities. SEE LETTER P.210

MICHAEL S. BROTHERTON

If a picture is worth a thousand words, then a spectrum can be worth a thousand pictures. That is perhaps an underestimate when dealing with star-like blobs of light that look fuzzy even through the world's largest telescopes, as is the case with quasars. First recognized more than five decades ago as counterparts to radio sources[1], these extremely energetic entities are supermassive black holes in the nuclei of distant galaxies[2]. The black holes themselves do not emit light, but their gravity accelerates gas into swirling accretion disks that can outshine the galaxies they dwell in. Determining the physical properties of these systems from spectroscopic observations is challenging. But a study by

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