information are segregated into two sensory channels.

Neuroscience students learn that, in touch, vision and hearing, signals evoked by external events are quickly and reliably channelled to their respective sensory areas in the cortex of the brain through 'relay' neurons in the thalamus (Fig. 1). These channels have been termed 'lemniscal' pathways. But neuroanatomists have long recognized that the lemniscal groups of cells ('nuclei') occupy less than half the volume of the thalamus associated with each type of sensation. The remainder belongs to 'paralemniscal' sensory pathways. The physiological properties of paralemniscal neurons in the thalamus are difficult to classify using typical sensory stimulation protocols. So it has been difficult to assign any specific function to these pathways. But now, Ahissar *et al.*[2] suggest that the paralemniscal pathway associated with touch information picked up by a rat's whiskers can relay to the cortex information about the position of touched objects.

Each full forwards–backwards sweep of a rat's whiskers is called a whisking cycle. For the brain to obtain any useful information about the location of objects touched during this cycle, it needs to reconstruct the trajectory of the whiskers. Conceivably, the sensory cortex could receive data about the cycle directly from the motor systems that generate the whisker movements. But this does not appear to be the case. Motor cortex, although a major source of input to sensory cortex, does not carry a strong signal about whisker position[3]. By default, then, information about the whisking cycle must arise through a signal transmitted from the whiskers.

To identify the signal that reveals whisker position, Ahissar *et al.*[2] induced whisker movement in anaesthetized rats by directing air-puffs along the nose. The whisker deflections, in the range of 2–8 Hz, were taken as experimentally controlled whisking cycles.

The flow of information from whiskers to cortex is shown in Fig. 1. Lemniscal signals are transmitted from receptors at the base of the whiskers, via the brainstem trigeminal complex, to the medial portion of the ventral posterior nucleus of the thalamus (VPM), ending up in the tactile region of cortex. Paralemniscal signals are transmitted along a similar pathway, but through the medial portion of the posterior nucleus (POm) in the thalamus. Ahissar *et al.* looked at the neuronal responses to whisker movement in each of these brain regions. For each frequency of whisker deflection, the authors aligned the neuronal responses across cycles to yield an average response per cycle. They then measured the response latency (the time between the start of whisker movement and the beginning of neuronal activity) and response magnitude (the number of 'spikes' of neuronal activity per whisker movement).

They found that neurons in the trigeminal complex — where the lemniscal and paralemniscal pathways are not yet distinct — fired with an identical response latency and magnitude regardless of whisking frequency. In both VPM and POm, by contrast, the response magnitude decreased as the frequency increased. But in VPM, response latency was constant regardless of frequency, whereas in POm response latency increased as whisking frequency increased. Neurons at the cortical targets of the two pathways (cortical layer IV for VPM, and layer Va for POm) behaved similarly to their thalamic inputs.

Ahissar *et al.* propose that a feedback circuit between sensory cortex and POm is responsible for the latency shifts with increasing whisking frequency. Cortical neurons in layer V have intrinsic oscillatory mechanisms[4] and a powerful influence on POm[5]. Ahissar *et al.* suggest that POm neurons activate cortical inhibitory neurons; these then inhibit the cortical oscillators, which in turn drive cortex-to-thalamus feedback. The properties of this loop could account for the changing response latency seen in POm.

There is no direct proof that such feedback loops can decode whisker position. But Ahissar *et al.* have shown that this varying response to whisking frequency endows the paralemniscal system with the ability to process temporal information — such as object location — that varies on timescales as slow as single whisking cycles. By comparing the timing of feedback descending from the cortex with the timing of information ascending from the whiskers, POm neurons could signal where along the whisking sweep an object is located. The lemniscal pathway, by contrast, responds with a fixed latency, so it is better suited to representing object features — such as surface texture — that do not vary along the whisking cycle.

Can these ideas be generalized to other sensations? What must be represented by the brain is unique to each kind of sensation, so one cannot expect the nature of sensory coding to be identical. The tactile sensory pathways form neural representations of objects that contact receptors in the skin; the visual and auditory systems form representations of objects at a distance.

But the observations made by Ahissar *et al.* raise some interesting ideas about how non-tactile stimuli may be represented. For example, neuroscientists debate whether the transmission of information is based on neuronal firing counts over relatively long time windows ('spike-count' coding) or on variations in neuronal firing within brief time windows ('spike-time' coding). Ahissar *et al.* have shown that it may be efficient for these codes to coexist. POm neurons transmit information about the frequency of whisker movements by shifts in response latency — a clear spike-time code. But the response latency determines the time window available for firing, so these timing shifts lead to spike-count differences, too. So frequency information is present in both the total spike count and the spike timing.

Time will tell whether or not these results can be applied to other sensory systems. But it seems that, at least for touch, the parallel pathways long recognized by neuroanatomists are beginning to acquire functional significance. ■

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Atmospheric physics

Enlightening water vapour

Brian J. Soden

The extent to which the Earth's climate will warm as a result of increasing carbon dioxide in the atmosphere depends largely on the response of water vapour in the upper levels of the troposphere (roughly 5–10 km above the surface). But our ability to monitor changes in water vapour there is limited by the scarcity of observing systems with sufficient accuracy and longevity to document its global variation and to detect trends.

On page 290 of this issue[1], Price demonstrates a remarkably robust relationship between upper tropospheric water vapour and global lightning activity. This observation not only supports the idea that atmospheric convection moistens the upper troposphere, a characteristic of climate models that has been the subject of spirited debate[2], but may also provide a unique tool for monitoring purposes.

The importance of water vapour in regulating climate is without question. It is the dominant greenhouse gas, trapping more of the Earth's heat than any other gaseous constituent of the atmosphere. If water vapour concentrations increase in a warmer world, as is widely believed, the added absorption will act to further amplify the initial warming. Mathematical models of the Earth's climate suggest that this would provide considerable positive feedback, more than doubling the sensitivity of surface temperature to anthropogenic greenhouse gases. Current models predict that water vapour concentrations in the upper troposphere could increase by as much as 40% over the next half-century[3]. This amplified moistening in response to the predicted warming not only highlights the significance of water vapour as a feedback mechanism, but also underscores the need for long-term monitoring of upper-tropospheric water vapour in helping to detect climate change and identify its causes.

Some climate researchers have challenged this view. They argue that the treatment of water vapour in climate models is overly simplified and that concentrations in the upper troposphere might actually decrease in a warmer climate. The mechanisms and effects of atmospheric convection and related cloud processes have been central to this debate.

Lindzen[2] postulated that the increased convective overturning of the atmosphere in response to warmer surface temperatures would bring more dry air down from higher altitudes and decrease the moisture in the upper troposphere. That atmospheric convection locally moistens the environment in which it occurs is indisputable. Observations from weather satellites (Fig. 1) clearly show increased levels of humidity (yellow to red) in regions surrounding the areas of active convection, as can be seen from the upper-level cloud cover (grey). However, on a global scale, the net effect of an increase in convective overturning is less obvious. Rising air in convective towers must be balanced in surrounding regions by sinking air, which, in the absence of other sources of moisture, can lead to extremely dry conditions in the upper troposphere (blue in Fig. 1).

Price[1] uses global lightning activity as a proxy for atmospheric convection. This is reasonable because convection not only determines the vertical transport of moisture, but also influences the electrification processes responsible for generating lightning activity. He shows that variations in lightning are well correlated with the observed fluctuations in global upper-tropospheric moisture on both weekly and seasonal timescales. Some may rightly question the reliability of current systems for observing moisture levels, such as the satellite output that Price has used. But he shows that similar variations in water vapour are obtained using independent measurements from different observing systems, which lends further credibility to the results.

By itself, the strong correlation between lightning activity and upper tropospheric water vapour offers a valuable opportunity for testing model simulations of the response of moisture to changes in atmospheric convection. But Price also points out that global lightning activity can be readily monitored from a single location through so-called Schumann resonances, the low-frequency electromagnetic waves discharged by lightning. Because these waves become trapped in the wave guide formed by the Earth's ionosphere, they can travel around the globe several times before dissipating. This means that global monitoring can be done from a single location. Given the close relationship between lightning and upper-tropospheric water vapour, Price suggests that measurements of Schumann resonances could provide an inexpensive method for monitoring the long-term trends in upper-tropospheric moisture.

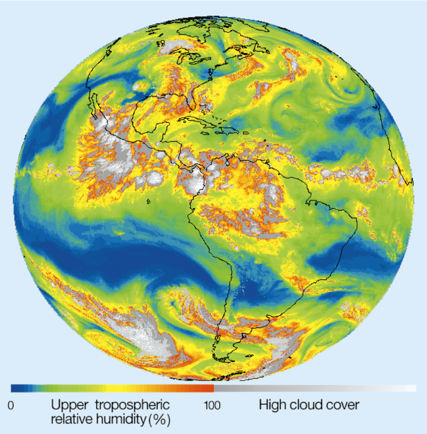

Figure 1 **Water vapour in the upper troposphere. This satellite image shows that higher levels of humidity (yellow to red) are associated with the areas of active atmospheric convection evident from clouds (grey). Price[1] takes global lightning as a proxy for convection, and shows that it might be used to monitor water vapour concentrations in the upper troposphere.**

Water vapour is notoriously difficult to measure and such a capability would be of great value to the climate research community. Water vapour is highly variable in both space and time (Fig. 1), and its concentration in the atmosphere varies by over three orders of magnitude. Although an international network of weather balloons has carried water vapour sensors for nearly half a century, changes in instrumentation and poor calibration make such sensors unsuitable for detecting trends in upper-tropospheric water vapour. Likewise, although weather satellites have provided global measurements of water vapour for over two decades, little effort has gone into making the data appropriate for long-term climate monitoring.

Price has shown that seasonal changes in global lightning activity are well correlated with changes in water vapour in the upper troposphere, but it remains to be seen whether the long-term trends in these quantities exhibit similar consistency. If Price's optimism proves correct, and future trends in lightning activity can indeed be linked to trends in upper-tropospheric water vapour, observations of Schumann resonances could provide a great deal of enlightenment in tracking climate change. ■

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Human behaviour

Fair game

Ruth Mace

Imagine that you are with a group of people from your community, and have been given a sum of money on condition that you share it with an anonymous member of the group. You make them an offer of a proportion of the cash, but neither you nor the other player will get a penny unless they accept your offer. There is only one round of the game, and confidentiality is maintained.

What do you think is a fair offer? The answers to this question, for a range of cultures from around the world, were the subject of a symposium* held last month: economic game theory met human behavioural ecology with fascinating results.

The rational way to play the game, known in economics as the ultimatum game, is for the first player to offer as little as possible and for the second player to accept it — something is always better than nothing. But when groups of university students play, the most common offer is 50% of the money, with a mean of about 40%. Offers below 20% are almost always rejected. Rejection is pure spite, as no one gains, but it is the only way of punishing the proposer for a mean offer. A range of other experiments confirm a general tendency in humans both to be generous to distantly related individuals and to punish cheaters, sometimes at great personal cost (H. Gintis, Univ. Massachusetts, Amherst).

Western university students are the social scientist's equivalent of the laboratory rat, yet evolutionary psychologists and economists are often tempted to assume that results obtained with them represent universal human preferences. But Westerners, not

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