

3. Smith, M. W. *et al.* *Science* **277**, 959–965 (1997).
4. Berger, E. A., Murphy, P. M. & Farber, J. M. *Annu. Rev. Immunol.* **17**, 657–700 (1999).
5. Cairns, J. S. & D'Souza, M. P. *Nature Med.* **4**, 563–568 (1998).
6. Rucker, J. *et al.* *Cell* **87**, 437–446 (1996).
7. White, J. H. *et al.* *Nature* **396**, 679–682 (1998).
8. Vila-Coro, A. J. *et al.* *FASEB J.* (in the press).
9. Rodríguez-Frade, J. M. *et al.* *J. Cell Biol.* **144**, 755–765 (1999).
10. Rodríguez-Frade, J. M. *et al.* *J. Clin. Invest.* **100**, 497 (1997).

## Climate variability and crop yields in Europe

Hulme *et al.*<sup>1</sup> make a valid distinction between the relative importance for European water runoff and wheat yields of human-induced climate change and naturally occurring climate variability, when considered over timescales of several decades. They use the HadCM2 climate model to show that, in many European cases, the human-induced climate change 'signal' could be swamped by naturally occurring climatic 'noise'.

However, the effect of any climate variability signal also depends on the temporal scale (for example, annual versus decadal) of such variability. For wheat crop yields, the relevant timescale for climatic variability is over years or even days, rather than decades, simply because wheat is an annual crop. Hulme *et al.* decided not to alter either inter-annual or inter-daily climatic variability.

By using an earlier global climate model (UKTR; ref. 2) than Hulme *et al.*, we have analysed the response of a wheat simulation model<sup>3</sup> to scenarios of climate change with and without changes in the inter-annual variability of precipitation (intensity and occurrence) and temperature. We introduced changes in climate variability derived from UKTR using a stochastic weather generator<sup>4</sup>. To measure the effect of inter-annual climate variability, we studied mean grain yield and its coefficient of variation (CV) from 30 individual years of simulation (the same total period as used by Hulme *et al.*).

We looked at two of the same sites as Hulme *et al.* For Spain, the simulated mean for the baseline climate wheat yield was 5.6 tonnes per hectare, with a CV of 0.24 (Table 1). In the climate scenario without a change in inter-annual variability, mean yield fell slightly to 5.2 t ha<sup>-1</sup>, with a CV of 0.23. With changes in climate variability, simulated mean yield dropped to 3.9 t ha<sup>-1</sup> but its CV more than doubled to 0.48, largely

	Mean grain yield (t ha <sup>-1</sup> ) (CV)	
	Spain	UK
Baseline climate	5.6 (0.24)	9.8 (0.06)
UKTR without changes in inter-annual variability	5.2 (0.23)	11.5 (0.08)
UKTR with changes in inter-annual variability	3.9 (0.48)	11.4 (0.09)

Simulated over a period of 30 years.

because there were more prolonged dry spells over the vegetation period. The probability of producing yields of less than 3.5 t ha<sup>-1</sup> in the 'with variability' scenario was nearly 0.50, compared with about 0.10 for the baseline and 'without variability' scenarios. Such changes in annual yield variability would make wheat a risky crop to grow in Spain and have important economic and social consequences.

For the United Kingdom, changes in climate variability had little effect on either mean grain yield or its CV (Table 1). In contrast, Hulme *et al.* found no change in the range (and hence the variability) of simulated yields for these sites as a result of either multi-decadal natural or anthropogenic variability. The timescale of the imposed variability can therefore alter qualitatively whether or not variability has an effect.

We conclude that it is important when assessing the impact of climate change to differentiate between natural climate variability and anthropogenic climate change, as highlighted by Hulme *et al.*, but also to apply changes in climate variability at appropriate timescales.

**John R. Porter\***, **Mikhail A. Semenov†**

\*Department of Agricultural Sciences,  
The Royal Veterinary and Agricultural University,  
2630 Taastrup, Denmark  
e-mail: jrp@kvl.dk

†ACR Long Ashton Research Station,  
University of Bristol, Bristol BS41 9AF, UK

1. Hulme, M. *et al.* *Nature* **397**, 688–691 (1999).
2. Murphy, J. M. & Mitchell, J. F. B. *J. Clim.* **8**, 57–80 (1995).
3. Jamieson, P. D. *et al.* *Eur. J. Agron.* **8**, 161–180 (1998).
4. Semenov, M. A. & Barrow, E. M. *Clim. Change* **35**, 397–414 (1997).

Hulme *et al.* reply — Porter and Semenov point out the importance of changes in climate variability on different timescales when assessing the significance of climate-change impacts. They are correct to assert that changes in inter-daily, inter-annual and multi-decadal climate variability are important, but our study<sup>1</sup> was intended to draw attention to natural multi-decadal climate variability and to indicate how it might obscure the identification of significant effects of anthropogenic climate change. It was therefore primarily a study of signal-to-noise ratios in impacts indicators, something that has not previously been attempted using low-frequency climate variability. The effects on crop yields of changes in inter-annual and inter-daily climate variability have been considered previously<sup>2–4</sup>.

We do not agree with Porter and Semenov that the primary climate-variability timescale of relevance for wheat yields is the inter-annual. Changes in the daily variability of climate and in the frequency of extreme events can be very important for crop performance<sup>5</sup>, and daily climate variability can change independently of annual or decadal timescales. Porter and Semenov did not

perturb daily climate variability in their study<sup>2</sup>. We think that decadal climate variability is also important for wheat yields: such low-frequency changes in climate (whether or not they are accompanied by changes in higher climate frequencies) can profoundly affect crop suitability and economic viability<sup>6</sup> and alter the competitiveness of different agricultural products on these timescales.

The effect of anthropogenic changes in inter-annual and/or inter-daily climate variability on an impact indicator will depend on their magnitude with respect to natural changes (for example, for Europe, in relation to the North Atlantic Oscillation). This is also a signal-to-noise problem that can be explored using our methodology, but was not addressed by Porter and Semenov.

The challenge for those studying the impacts on climate is to examine the effects of changes in the full spectrum of climate variability, clearly distinguishing between anthropogenic and natural changes, and interpreting these effects in the light of other forces of environmental change. If these can be quantified more comprehensively than in the past, then we can provide decision-makers and resource managers with information that can better assist them to manage future risks arising from climatic change.

**Mike Hulme\***, **Paula Harrison†**,  
**Nigel Arnell‡**

\*Climatic Research Unit,  
School of Environmental Sciences,  
University of East Anglia, Norwich NR4 7TJ, UK  
†Environmental Change Unit,  
University of Oxford, Oxford OX1 3TB, UK

‡Department of Geography,  
University of Southampton,  
Southampton SO17 1BJ, UK

1. Hulme, M. *et al.* *Nature* **397**, 688–691 (1999).
2. Semenov, M. A. & Porter, J. R. *Agric. Forest. Meteorol.* **73**, 265–283 (1995).
3. Riha, S. J., Wilks, D. S. & Simeons, P. *Clim. Change* **32**, 293–311 (1996).
4. Mearns, L. O., Rosenzweig, C. & Goldberg, R. *Clim. Change* **35**, 367–396 (1997).
5. Harrison, P. A., Butterfield, R. E. & Downing, T. E. *ECU Res. Rep.* 9 (ECU, Oxford, 1995).
6. Parry, M. L. & Carter, T. R. *Clim. Change* **7**, 95–110 (1985).

## A movement-sensitive area in auditory cortex

It is important to recognize sound patterns, regardless of their position and motion. The ability to locate sound sources and track their motion involves various levels of the auditory pathways<sup>1,2</sup>. Motion and pattern analysis may first be spatially separated in the auditory cortex. We have examined this by using functional magnetic resonance imaging (fMRI) and find a higher-order field in the right auditory cortex that is

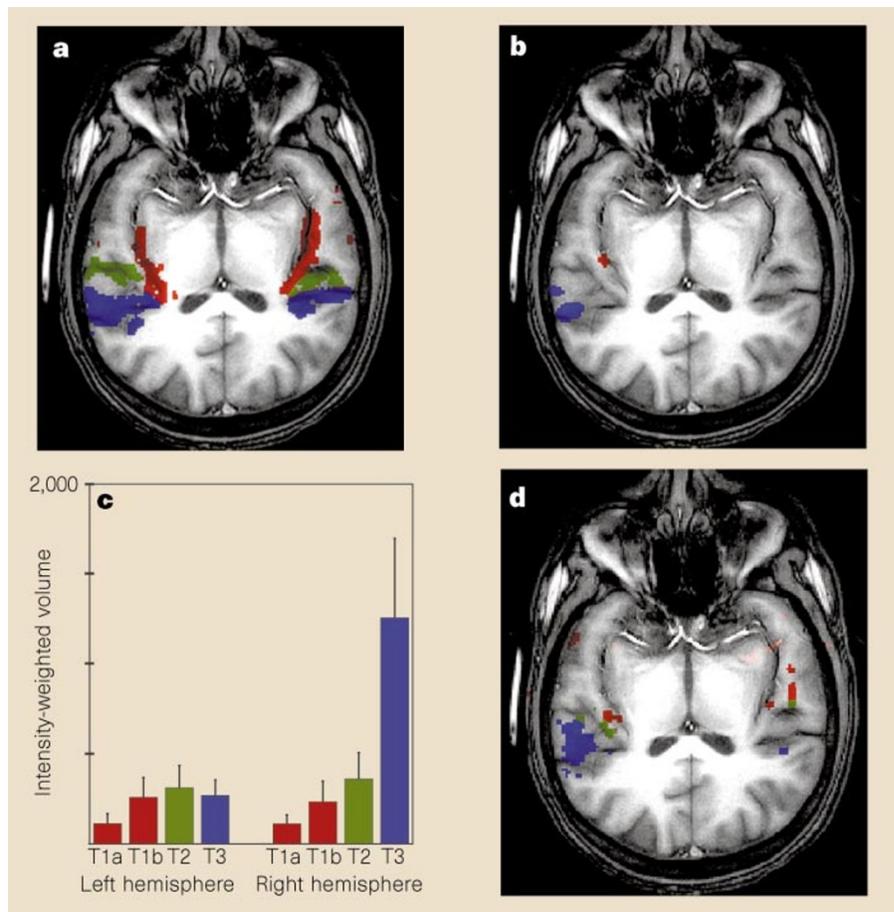
activated by sound motion significantly more than other fields of the auditory cortex. This area distinguishes whether a sound pattern is moving or stationary.

We compared activation of the auditory cortex by two acoustic stimuli with identical spectral-temporal patterns but with different binaural timing. The pattern consisted of a tonal carrier that was amplitude modulated (AM, 80% modulation depth, sine<sup>2</sup> waveform) at slow rates (0.08 to 0.2 Hz). In the 'movement' version, the envelope was 90° out of phase at the two ears, generating perception of a sound moving at varying speed in azimuth. In the 'stationary' version, the envelope was in phase at the two ears, generating perception of varying loudness of the same, but stationary, sound. The AM carrier, a frequency-modulated (FM) tone (1 to 6 kHz, 4 Hz sawtooth modulation), was designed to activate a broad range of frequency channels and was previously found to delineate various fields in human auditory cortex. Four such fields — T1a, T1b (AI), T2 and T3 — were distinguished by a combination of structural landmark delineation and differential functional activation<sup>3</sup>.

In ten right-handed subjects, three contiguous fMRI slices (4 mm thick) were obtained encompassing and parallel to the superior plane of the temporal lobe in both hemispheres. Electrodynamical headphones<sup>3</sup> were used for stimulus presentation (root-mean-square 72 dB sound pressure level, SPL). For each slice, 108 functional images were collected by using a low-noise imaging sequence (48 dB SPL)<sup>3</sup> at 3 tesla. The experiment consisted of six cycles comprising stationary FM, moving FM and silent phases. Attention was controlled by target detection (pauses of the AM lasting 2–4 seconds, right key press). Functional activation in individual subjects was assessed by correlations to the stimulus input functions. Activation differences across subjects were analysed by using intensity-weighted volumes of significantly activated volumes<sup>4</sup>.

We found activation by both the moving and stationary patterns with respect to silence in all four fields of auditory cortex in both hemispheres (Fig. 1a). Across-subject analysis contrasting the activation from the moving and stationary patterns revealed a large residual activity in only T3 on the right planum temporale (Fig. 1b,d). This residual activity was significantly different from that of the left T3 (Wilcoxon,  $P=0.037$ ) and all other fields bilaterally (Fig. 1c).

Our results indicate that there is an area in the auditory cortex whose activity distinguishes whether a sound pattern is moving or stationary. Both the moving and stationary stimuli strongly activated various fields of the auditory cortex bilaterally in which this motion dependence



**Figure 1** Nonspecific and specific activation by motion stimulus. **a**, Motion-induced activation compared with silence in a single subject mapped on the dorsal surface of the temporal lobe ( $P<0.05$ ). Voxels in different fields are colour-coded (T1b(AI) and some T1a voxels more rostrally, red; T2, green; T3, blue). **b**, Correlation contrast activity difference from moving compared with stationary sound in the same subject ( $P<0.05$ ). **c**, Residual intensity-weighted volume (volume in microlitres  $\times$  percentage intensity) across subjects for moving compared with stationary stimuli in all fields. **d**, As **b**, but showing the average from all ten subjects mapped onto an individual brain.

was not seen. These data do not imply that T3 in the right hemisphere contains neurons that are movement selective (in the sense of responding only to movement or preferring a particular movement direction). But even if T3 were only a space map of position-sensitive neurons, its overall activation by motion is clearly higher than that of the other auditory cortical areas studied.

It is interesting that the significant effect was found only on the right planum temporale, because an area sensitive to sound movement has been described in the right parietal cortex<sup>5</sup>, which is dorsal to our scanned area. Furthermore, results from the visual domain indicate that the right hemisphere tends to be dominant for processing spatial information<sup>6</sup>, whereas the left human planum temporale may be specialized for speech processing<sup>7</sup>. Thus, in a motion context, certain types of sound pattern, as found in speech<sup>8</sup>, may introduce a left planum temporale bias into the described right dominance.

Previous studies have found evidence of

motion-sensitive auditory space maps in the midbrain<sup>9</sup>, patchy distributions of primary auditory-cortex neurons that are motion sensitive or motion selective<sup>10</sup>, and an area in the right human parietal cortex that is sensitive to sound movement<sup>5</sup>, which is presumably association cortex. Our results indicate that a missing neural link for this critical brain function may be a specialized area predominantly in the right posterior auditory cortex.

**Frank Baumgart\***,  
**Birgit Gaschler-Markefski\***,  
**Marty G. Woldorff\*†**, **Hans-Jochen Heinze‡**,  
**Henning Scheich\***

\*Leibniz-Institute for Neurobiology,  
 Brenneckestrasse 6, 39118 Magdeburg, Germany

†Research Imaging Center,  
 University of Texas Health Science Center,  
 San Antonio, Texas 78284-6240, USA

‡Department for Neurology II,  
 Otto-von-Guericke-University,  
 Leipzigerstrasse 44, 39120 Magdeburg, Germany

1. Wagner, H., Kautz, D. & Poganiatz, I. *Trends Neurosci.* **20**, 583–588 (1997).
2. Knudsen, E. I. & Konishi, M. *Science* **200**, 795–797 (1978).

3. Scheich, H. et al. *Eur. J. Neurosci.* **10**, 803–809 (1998).
4. Woldorff, M. G. et al. *Hum. Brain Map.* **7**, 49–66 (1999).
5. Griffiths, T. D. et al. *Nature Neurosci.* **1**, 74–79 (1998).
6. Awh, E. & Jonides, J. in *The Attentive Brain* (ed. Parasuraman, R.) 353–381 (MIT Press, Cambridge, MA, 1998).
7. Galaburda, A. M., Le May, M., Kemper, T. L. & Geschwind, N. *Science* **199**, 852–856 (1978).
8. Belin, P. et al. *J. Cogn. Neurosci.* **10**, 536–540 (1998).
9. King, A. J. & Hutchings, M. E. *J. Neurophysiol.* **57**, 596–624 (1987).
10. Ahissar, M., Ahissar, E., Bergman, H. & Vaadia, E. *J. Neurophysiol.* **67**, 203–215 (1992).

## Striped rabbits in Southeast Asia

The Annamite mountains of Laos and Vietnam have yielded several important mammalian discoveries<sup>1</sup>. We have found a striped rabbit of the previously monospecific genus *Nesolagus*, extending its known range more than 1,500 km north from the island of Sumatra into mainland Southeast Asia. The Sumatran and mainland Annamite populations are morphologically similar, but genetic data indicate that they have been isolated for millions of years.

The first evidence of *Nesolagus* in the Annamite mountains came from freshly captured animals offered for sale in a food market in the rural town of Ban Lak, Laos (18°11' N, 104°58' E) between December 1995 and February 1996 (Fig. 1). The rabbits have since been found at other sites in the Annamite mountains of Vietnam.

The only previously known striped lagomorph was the critically endangered *Nesolagus netscheri*, a monotypic rabbit genus endemic to forest habitat within the Barisan



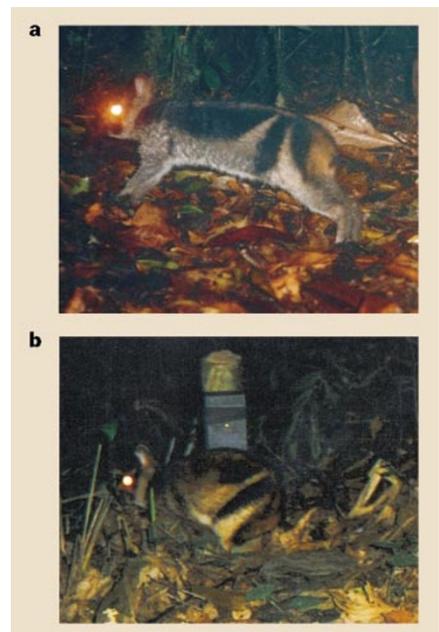
**Figure 1** Map of Southeast Asia showing the Sunda islands of Sumatra, Borneo and Java. The site of the first discovery of a striped rabbit in the Annamites of central Laos is marked, as is the Kerinci Seblat National Park in Sumatra, where *Nesolagus netscheri* was photographed in the wild.

mountains and further north to Mount Leuser in Sumatra. There had been just one confirmed sighting of *N. netscheri* since 1916 and only around 15 museum specimens of the species exist, all of which were collected between 1880 and 1929 (ref. 2). In early 1998, *N. netscheri* was photographed by an automatic camera trap in the Kerinci Seblat National Park in Sumatra by Fauna and Flora International<sup>3</sup>. Externally, the Annamite rabbits closely resemble *N. netscheri*, having black or dark brown dorsal stripes, ferruginous rumps and short tails and ears (Fig. 2).

Morphological analysis of 30 characters (including pelage elements, external proportions, postcranial characters, tooth morphology and cranial morphometrics) in both Annamite and Sumatran rabbits reveals that there is a significant difference in the minimum interorbital distance as a percentage of condylobasal length (Annamite, range 19.0–23.6, mean(±s.d.) 20.5(±1.6),  $n=10$ ; Sumatran, 16.9–18.7, 17.5(±0.7),  $n=6$ ;  $P<0.001$ , Wilcoxon–Mann–Whitney test).

Genetic analysis was undertaken of 653 continuous base pairs of the mitochondrial gene encoding 12S ribosomal RNA prepared from three museum specimens of *N. netscheri* and three rabbits from Laos. The results indicate that *N. netscheri* and the Annamite specimens (Genbank accession numbers AF176583 to AF176589) are sister taxa within a phylogenetic framework of lagomorph genera<sup>4</sup>. There is considerable divergence between them: the genetic distance (Kimura two-parameter) is 0.0552, which falls outside the range observed between other congeneric leporid species (0.0226–0.0427, mean 0.0324, from six species in two genera), but within that between different leporid genera (0.0469–0.1199, mean 0.0748, from seven genera). Assuming a steady rate of divergence over time at this gene<sup>5</sup>, the Sumatran and Annamite rabbits would have been diverging genetically for approximately 8 million years.

Despite an apparently high degree of conserved morphology, the large genetic divergence between these two taxa of striped rabbit indicates that they separated in the Pliocene epoch. In this region, glacial periods were cool and dry, characterized by expanding grassland, whereas forest cover increased during interglacial periods<sup>6</sup>. During glacial maxima, sea levels over the Sunda shelf were almost 150 metres lower than today, connecting Sumatra, Java and Borneo to the Asian mainland<sup>7</sup>. The ancestral *Nesolagus* may have been distributed over areas of this region at a time of lower sea level in the Pliocene, and its range would have been repeatedly dissected by periodic changes in both sea level and forest habitat.



**Figure 2** Automatic camera-trap photographs of the striped rabbits. **a**, *Nesolagus netscheri* in Kerinci Seblat National Park in Sumatra (photograph from FFI). **b**, The striped rabbit from the Annamite mountains, photographed in the Pu Mat Nature Reserve, Vietnam (photograph from SFNC EC).

The existence of refugia for forest species during dry glacial periods has been postulated for both the Annamite mountains and Sumatra<sup>8</sup>. The contraction and expansion of ranges in and out of such allopatric refugia can generate divergence, with the sister genomes being protected by hybrid zones if they make contact, leading to speciation<sup>9</sup>. Our discovery of the rabbit in the Annamite mountains may provide insight into the factors governing current patterns of biodiversity in Southeast Asia, leading to its protection into the future.

**Alison K. Surridge\***, **Robert J. Timmins†‡**, **Godfrey M. Hewitt\***, **Diana J. Bell\***

\*Population and Conservation Biology Sector, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK

e-mail: a.surridge@uea.ac.uk

†Wildlife Conservation Society, PO Box 6712, Vientiane, Laos

‡Present address: 25 Cradley Road, Cradley Heath, West Midlands B64 6AG, UK

1. Gao, P. M. et al. *Anim. Conserv.* **1**, 61–68 (1998).
2. Flux, J. E. C. in *Rabbits, Hares and Pikas* (eds Chapman, J. A. & Flux, J. E. C.) 137–139 (IUCN, Gland, Switzerland, 1990).
3. Fauna and Flora International *Fauna Flora News* **9**, 3 (1998).
4. Halanych, K. & Robinson, T. J. *J. Mol. Evol.* **48**, 369–379 (1999).
5. Allard, M. W. & Honeycutt R. L. *Mol. Biol. Evol.* **9**, 27–40 (1992).
6. van der Kaars, W. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **85**, 239–302 (1991).
7. Verstappen, H. T. in *Modern Quaternary Research in Southeast Asia* (eds Bartsra, G.-J. & Casparie, W. A.) 3–35 (Balkema, Rotterdam, 1975).
8. Brandon-Jones, D. *Biol. J. Linn. Soc.* **59**, 327–350 (1996).
9. Hewitt, G. M. *Biol. J. Linn. Soc.* **58**, 247–278 (1996).