the specialized face-processing system in the sheep brain offers advantages for long-term recognition of many individuals that are similar to those for humans. In humans, analogous brain regions and neural circuits are activated equivalently when we see or form mental images of the faces of specific individuals[9]. This suggests that sheep may be capable of using the same system to remember and respond emotionally to individuals in their absence.

Keith M. Kendrick, Ana P. da Costa, Andrea E. Leigh, Michael R. Hinton, Jon W. Peirce
Laboratory of Cognitive and Developmental Neuroscience, Babraham Institute,
Cambridge CB2 4AT, UK
e-mail: keith.kendrick@bbsrc.ac.uk

1. Kendrick, K. M., Atkins, K., Hinton, M. R., Heavens, P. & Keverne, E. B. *Anim. Behav.* **49**, 1665–1676 (1995).
2. Kendrick, K. M., Atkins, K., Hinton, M. R., Heavens, P. & Keverne, E. B. *Behav. Proc.* **38**, 19–35 (1996).
3. Peirce, J. W., Leigh, A. E. & Kendrick, K. M. *Neuropsychologia* **38**, 475–483 (2000).
4. Peirce, J. W., Leigh, A. E., da Costa, A. P. C. & Kendrick, K. M. *Behav. Proc.* **55**, 13–26 (2001).
5. Kendrick, K. M., Hinton, M. R., Atkins, K., Haupt, M. A. & Skinner, J. D. *Nature* **395**, 229–230 (1998).
6. Kendrick, K. M. & Baldwin, B. A. *Science* **236**, 448–450 (1987).
7. Broad, K. D., Mimmack, M. L. & Kendrick, K. M. *Eur. J. Neurosci.* **12**, 731–741 (2000).
8. Perrett, D. I., Hietanen, J. K., Oram, M. W. & Benson, P. J. *Phil. Trans. R. Soc. Lond. B* **335**, 23–30 (1992).
9. Kreiman, G., Koch, C. & Fried, I. *Nature* **408**, 357–361 (2000).

Eutrophication

Nitrate flux in the Mississippi River

Increased delivery of biologically available nitrogen to estuaries and coastal oceans in recent decades has been linked to eutrophication and seasonal hypoxia in the northern Gulf of Mexico[1,2] and elsewhere[3,4]. We have developed a model that accounts for 95% of annual variation in delivery of nitrate to the Gulf of Mexico by the Mississippi River in 1960–98. Retrospective analysis indicates that this nitrate flux could have been reduced by 33% if the use of nitrogen-containing fertilizer in the Mississippi River basin had been cut by 12%.

Across a wide range of temperate river systems, riverine nitrogen flux has been correlated with net anthropogenic nitrogen input (NANI) to the drainage basin. NANI is defined as nitrogen input from fertilizer and by fixation and atmospheric deposition of oxidized nitrogen, minus nitrogen exported in food and feed[5,6]. For each unit

Figure 1 Observed nitrate flux in the lower Mississippi River, including the Old River outflow, in 1955–98 (diamonds) and nitrate flux estimated using our equation (see text; black line). The thick red line shows the estimated average nitrate flux to the Gulf of Mexico if nitrogen input from fertilizer were to be reduced by 12%, assuming no reduction in crop yields. Thin red lines define the 95% confidence interval for the mean of each annual estimate. Flux values before 1960 were not included in the regression analysis because data concerning crop and livestock production data before 1950, which would be needed to calculate NANI6–9, are not readily available.

of NANI to a drainage basin, an average of about 0.25 units are transported to coastal waters, with the other 0.75 units being converted to gaseous compounds or stored in soil or groundwater.

Relatively little attention has been paid to temporal variation in the relationship between NANI and riverine nitrogen flux for particular river basins, which is essential for developing effective protection strategies for estuary and coastal marine ecosystems. We have focused on the temporal variation of nitrate flux in the lower Mississippi River in 1960–98, during which period a 2.5-fold increase in nitrate concentration accounted for almost all of the increase in total nitrogen concentration in the river[7]. A positive trend in precipitation during this period also produced a 30% increase in water yield (or stream flow), which probably enhanced nitrate delivery.

In 1960–98, NANI to the Mississippi River basin increased by roughly 80%. In the 1960s, riverine nitrate flux was 8% of NANI; by the 1990s, this figure had increased to 18%. The trend in the ratio of riverine nitrate flux to NANI is statistically significant and the ratio is significantly correlated with discharge and NANI ($P < 0.001$).

By combining and adapting two earlier models that related terrestrial nitrogen input to riverine nitrogen flux[5,8], we developed the following model, which accounts for 95% ($P < 0.001$) of the variation in annual nitrate flux in the lower Mississippi River, including the Old River ouflow, in 1960–98:

$$N_{LM} = 0.66 \times W^{0.93} \times e^{(0.13 \times \text{NANI2-5} + 0.06 \times \text{NANI6-9})}$$

where N_{LM} is the annual nitrate flux (in kg N ha^{-1} yr^{-1}), NANI2–5 is the average annual net anthropogenic nitrogen input during the previous 2–5 years (in kg N ha^{-1} yr^{-1}), NANI6–9 is the average annual net anthropogenic N input during the previous 6–9 years (in kg N ha^{-1} yr^{-1}) and W is the annual water yield (in m yr^{-1}).

The root-mean-square error was 12% of average riverine nitrate flux and the serial correlation of residuals was not statistically significant ($P < 0.05$) for lags 1–12. The results of Monte Carlo simulations for the 1980–98 period suggested that 95% of the estimation uncertainty was due to fitting the regression coefficients and 5% was due to uncertainty in components of NANI (for details, see supplementary information). The 95% confidence interval for the mean estimated nitrate flux for an individual year was $\pm 15\%$.

Our model suggests that changes in NANI to the Mississippi River basin influence riverine nitrate flux for the succeeding 2–9 years, although the greatest impact tends to be during the first 2–5 years. Furthermore, the observed exponential relationship suggests that small changes in NANI may lead to relatively large changes in riverine nitrate flux. This pattern may be a consequence of NANI exceeding the capacity of terrestrial and/or aquatic systems to assimilate nitrogen input.

Calculations using our equation, and made on the basis of the observed annual water yields in 1960–98, suggest that a 14.2% reduction in NANI would have led to a 33% reduction in annual average riverine nitrate flux at St Francisville in 1980–98 (Fig. 1). This reduction in fertilizer use would have been most effective in years with the greatest water yield (and therefore the greatest nitrate flux). In years with low water yield, however, there was no statistical difference between estimates of mean nitrate flux with or without a 14.2% reduction in NANI.

The 14.2% reduction in NANI could have been accomplished by a 12% reduction in nitrogen input from fertilizer if crop yields remained constant. A small reduction in such nitrogen input is unlikely to have reduced crop yields significantly, if at all. Crop yields tend to approach an economic optimum in an asymptotic manner as rates of fertilizer application increase[9,10]. Moreover, data concerning usage of nitrogen fertilizer suggest that there is a tendency among farmers to apply more than is necessary to achieve economically optimal production[11–13].

Our findings indicate that achieving conservation goals for the Gulf of Mexico may require less reduction in fertilizer use than has been estimated from simulation modelling of edge-of-field nitrogen losses and assumptions of constant in-stream denitrification loss[14]. By using the available data concerning riverine nitrate transport, our analysis incorporates the effects of variation in in-stream denitrification.

The relationship between riverine nitrate flux in the Mississippi basin and NANI may continue to change as a result of
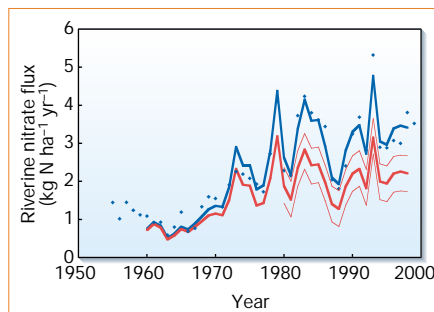
modifications in the river, in climate and in nitrogen-management practice. Continued monitoring of riverine nitrogen and NANI will refine our understanding of nitrogen dynamics in river basins and will facilitate adaptive management of conservation policies and programmes.

Gregory F. McIsaac*, Mark B. David*, George Z. Gertner*, Donald A. Goolsby†

*Department of Natural Resources and Environmental Sciences, University of Illinois, Turner Hall, 1102 South Goodwin Avenue, Urbana, Illinois 61801, USA

e-mail: gmcisaac@uiuc.edu

†US Geological Survey, Denver Federal Center, Denver, Colorado 80225, USA

1. Turner, R. E. & Rabalais, N. N. *Nature* **368**, 619–621 (1994).
2. Rabalais, N. N., Turner, R. E., Justic, D., Dortch, Q. & Wiseman, W. J. *NOAA Coastal Ocean Prog. Decision Anal. Ser.* **15** (Silver Spring, Maryland, 1999).
3. National Research Council` *Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution* (Natl Acad. Press, Washington DC, 2000).
4. Diaz, R. J. *J. Environ. Qual.* **30**, 275–281 (2001).
5. Howarth, R. W. *et al. Biogeochemistry* **35**, 75–139 (1996).
6. Jordan, T. E. & Weller, D. W. *BioScience* **46**, 655–664 (1996).
7. Goolsby, D. A. & Battaglin, W. A. *Hydrol. Proc.* **15**, 1209–1226 (2001).
8. Caraco, N. F. & Cole, J. J. *Ambio* **28**, 167–170 (1999).
9. Cerrato, M. E. & Blackmer, D. G. *Agron. J.* **82**, 138–143 (1990).
10. Bullock, D. G. & Bullock, D. S. *Agron. J.* **86**, 191–195 (1994).
11. Legg, T. D., Fletcher, J. J. & Easter, K. W. *J. Prod. Agric.* **2**, 110–116 (1989).
12. US Department of Agriculture National Agricultural Statistic Service. Agricultural Chemical Usage (PCU-BB) http://usda.mannlib.cornell.edu/reports/nassr/other/pcu-bb
13. Taylor, H. H. *Stat. Bull.* **893** (Econ. Res. Service, US Dept Agric., Washington DC, 1994).
14. Doering, O. C. *et al. NOAA Coastal Ocean Prog. Decision Anal. Ser.* **20** (Silver Spring, Maryland, 1999).

Supplementary information accompanies this communication on *Nature*'s website (www.nature.com).

Neural-network models

Predicting spontaneous recovery of memory

Long after a new language has been learned and forgotten, relearning a few words seems to trigger the recall of other words. Neural-network models[1–3] indicate that this form of spontaneous recovery may result from the storage of distributed representations, which are thought to mediate human memory. Here we use a psychomotor learning task to show that a corresponding effect of spontaneous memory recovery occurs in human subjects.

Spontaneous recovery is a generic characteristic of systems in which associations are distributed over many processing units (neurons, for example)[1–3]. In neural-network models, after learning a set of associations, forgetting can be induced by adding noise to connections between 'neurons'. As every association depends on all connections, relearning a subset of these associations forces all connections towards their original values, resulting in improved performance on non-relearned associations; this form of spontaneous recovery is also known as the transfer effect[1,2].

The task we used to test for a transfer effect in humans involved learning to type on a keyboard on which letters had been rearranged. In each of three sessions, subjects ($n = 12$) were presented with an upper-case letter on each trial, and were required to press the corresponding keyboard letter. Letters were presented in random order, with an inter-trial interval of 1 second. Twenty-four letters were divided into three disjoint subsets (such as A = {ENLHUBWK}, B = {TORCFPYJ}, C = {AISDMGVX}). Subjects learned two intermixed subsets (A and B) for 480 trials (session 1). After 48 hours, subset A was relearned for 80 trials (session 2). Immediately after session 2, subjects were tested for 80 trials on subset B (session 3). The protocol in all three sessions was identical.

We predicted that, after initially learning subsets A and B (session 1), relearning subset A (session 2) would facilitate performance on the non-relearned subset B (session 3). Accordingly, we compared reaction times for subset B (session 3) in this transfer condition with those in a control condition. In the control condition, instead of relearning subset A in session 2, subjects learned a 'new' subset, C.

Each subject participated in the transfer and control conditions (Fig. 1). These two conditions used different keyboard layouts, and different letters in subsets A, B and C. Results for the two conditions were obtained a week apart, with a fully counterbalanced design. The skew of reaction-time (RT) distributions was reduced by taking logarithms (designated as RT_{log}). We binned each subject's RT_{log} values (16 trials per bin in session 1; 8 trials per bin in sessions 2 and 3) and analysed bin means using repeated-measures two-factor MANOVAs (condition and bin number); we then used linear contrasts to test specific hypotheses, denoted F_{LC}. Response accuracy was not significantly less than 100% in any session. After learning subsets A and B, RT_{log} for subset B (session 3) was significantly smaller after relearning subset A than after learning subset C (mean reaction times, 0.990 s and 1.123 s, respectively; Fig. 1c).

It is possible that this difference was caused by increased reaction time in the control condition (for example, through 'interference' from learning new items in subset C), rather than by reduced reaction time in the transfer condition. However, two findings are inconsistent with this interpretation. First, comparison of performance with and without learning of new items (that is, testing subset B in the control condition and relearning subset A in the transfer condition) shows no difference ($F_{LC}(1) = 0.821$, $P = 0.352$). Second, in the
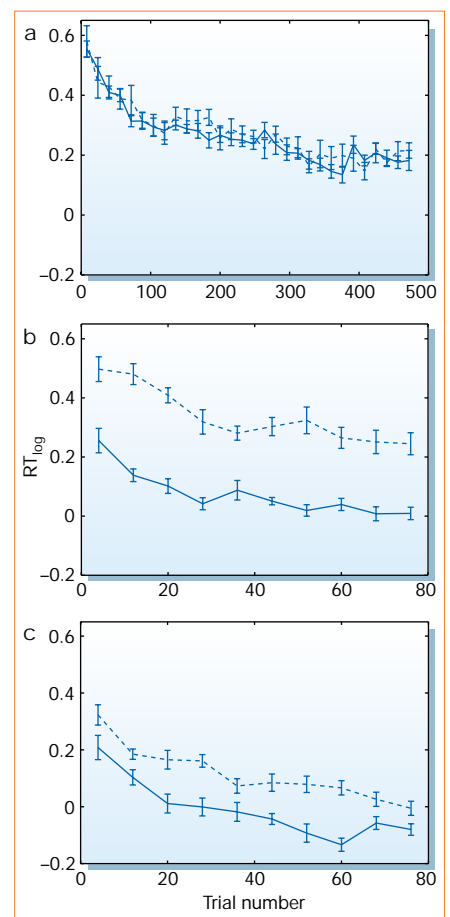

Figure 1 Reaction time (RT_{log}) plotted against trial number for three different experimental sessions (solid lines, transfer condition; dashed lines, control condition; error bars, standard errors of bin means; see text). **a,** Session 1: learning intermixed letter subsets A and B. RT_{log} decreases as letter positions are learned ($F(29,290) = 17.44$, $P < 0.001$), with no effect of condition ($P = 0.560$) and no condition × trial interaction ($P = 0.697$). **b,** Session 2: relearning subset A (transfer condition), and learning new subset C (control condition). RT_{log} during relearning of subset A was less than RT_{log} during learning of subset C ($F_{LC}(1) = 34.298$, $P < 0.001$). **c,** Session 3: testing subset B. RT_{log} for subset B was significantly smaller after relearning subset A (transfer condition) than after learning subset C (control condition) ($F_{LC}(1) = 7.930$, $P = 0.006$).

transfer condition, RT_{log} during session 3 was significantly smaller than during session 2 ($F_{LC}(1) = 3.647$, $P = 0.036$). This suggests that relearning of subset A in session 2 involved implicit relearning of subset B.

This investigation was stimulated by mathematical analyses of neural-network models. Our findings are consistent with a form of spontaneous recovery (the transfer effect) and support a computational account of learning and relearning in human memory. Moreover, the transfer effect may contribute to the savings that are observed when forgotten associations come to be relearned[4].

James V. Stone*, Nicola M. Hunkin†, Angela Hornby*

*Department of Psychology and †Academic Neurology Unit, Sheffield University,