

GDP being pledged towards significant reductions (27%; Table 1) represents 9% of the global economy; the upper bound represents 16.7%, which is slightly larger than the GDP of Japan, the world's second largest economy.

Although there is no US federal cooperation with Kyoto, the implementation of climate-change policies by lower levels of government are widespread and governed by pledges that are not dissimilar from the targets adopted in Kyoto. These pooled efforts will ultimately be gauged by the real reductions in emissions that they achieve.

Brendan Fisher, Robert Costanza

Gund Institute for Ecological Economics,
Rubenstein School of Environment and Natural
Resources, University of Vermont, Burlington,
Vermont 05405, USA
e-mail: brendan.fisher@uvm.edu

- Butler, D. & Schiermeier, Q. *Nature* **436**, 156–157 (2005).
- Marland, G., Boden, T. & Andres, R. in *Trends: A Compendium of Data on Global Change* (Oak Ridge Natl Lab., Tennessee, 2003) http://cdiac.esd.ornl.gov/trends/emis/tre_usa.htm.
- Pew Center on Global Climate Change *Analysis of President Bush's Climate Change Plan* www.pewclimate.org/policy_center/analyses/response_bushpolicy.cfm (2002).
- Nature* **431**, 613 (2004).
- Emissions of Greenhouse Gases in the United States 2003* (Dept Energy, Washington DC, 2003).
- Babiker, M., Maskus, M. & Rutherford, K. *Carbon Taxes and the Global Trading System* (working paper 97-7) (Univ. Colorado, Boulder, 1997).
- Babiker, M. H. J. *Int. Econ.* **65**, 421–445 (2005).
- Pew Center on Global Climate Change www.pewclimate.org/policy_center/policy_reports_and_analysis/state/index.cfm (2004).
- Subak, S. E. *Nature* **374**, 300 (1995).
- Victor, D. G. & Salt, J. E. *Nature* **373**, 280–282 (1995).
- Haag, A. *Nature* **432**, 936 (2004).

Supplementary information accompanies this communication on *Nature's* website.

Competing financial interests: declared none.
doi:10.1038/438301a

ANT NAVIGATION

Priming of visual route memories

Ants travelling to and fro between their nest and a foraging area may follow stereotyped foodward and homeward routes that are guided by different visual and directional memory sequences^{1–6}. Honeybees are known to fly a feeder-to-hive or hive-to-feeder vector according to whether or not they have recently fed — their feeding state controls which compass direction they select⁷. We show here that the feeding state of the wood ant *Formica rufa* also determines the choice between an outward or inward journey, but by priming the selective retrieval of visual landmark memories.

We trained the ants along a foraging route in which the appearance of a landmark differed on the ants' foodward and homeward paths. The ants ran 1 m from a start-pot to a drop of sucrose, both of which lay 20 cm from a black wall that was 2 m long and 20 cm high. They

were guided by the remembered appearance of the wall⁸, which was to their left on the way to food and to their right on the way home. (For methods, see supplementary information.)

To investigate the role of feeding state in priming visual memories for the foodward or homeward route, trained ants that had either been fed or left unfed were placed individually in a start-pot midway along the wall (Fig. 1a). Unfed ants walked so that they viewed the wall on their left (59 out of 63 paths from 23 ants); fed ants viewed the wall on their right (56 of 61 paths from 20 ants). The wall was regularly rotated during training and the visual scene was identical for fed and unfed ants. We conclude that the ants' feeding state, rather than the compass orientation or panoramic context, determines whether foodward or homeward memories are primed.

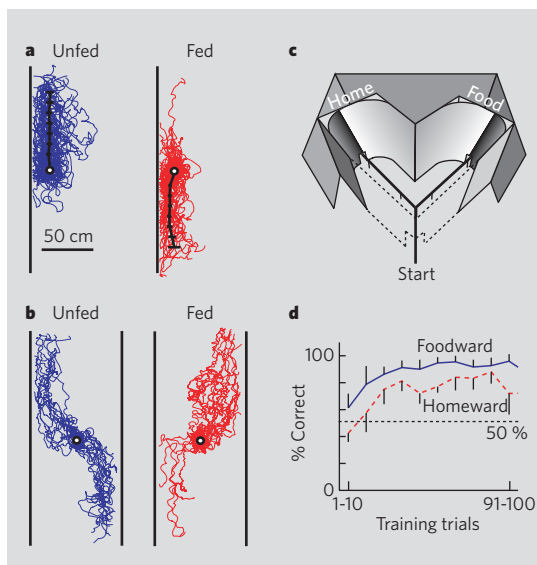


Figure 1 | Wood ants use feeding state to select visual memories for guiding routes towards food or the nest.

a, Individual trajectories of unfed and previously fed ants released from a start-pot (white circle). Thick line indicates the mean path, with 95% confidence interval (CI) plotted every 10 cm. **b**, Trajectories of ants when the start-pot is placed midway between two walls. The exit from the start-pot is at the top of the figure. Fed ants left in the direction of the exit; unfed ants circled the pot before choosing a direction. **c**, Y-shaped maze (dotted lines indicate front wall) with different patterns for homeward and foodward routes (see supplementary information). Distance from Y junction to pattern, 33 cm. **d**, Ants' performance on foodward and homeward journeys in training, showing mean choices of 11 ants (95% CI).

Ants did not just learn fixed motor patterns (for example, to turn left when fed) as the paths were the same, irrespective of whether the exit from the ants' start-pot faced the wall (as in training) or faced away. Ants placed midway between two identical walls 80 cm apart (Fig. 1b) walked closer to the left wall when unfed (20 of 20 paths, 9 ants) and to the right wall when fed (22 of 22 paths, 9 ants), thereby matching the route-specific visual memory that was primed by their feeding state.

In a second experiment, ants learned a foraging route in which they ran twice through the same 'Y' maze, first to reach food and then to be returned to the nest. Each arm of the 'Y' led to a different visual pattern (Fig. 1c). One of the two patterns signalled the way to food, and the other the way home. Training patterns were frequently switched between sides. Ants learned to choose the foodward pattern when unfed and the homeward pattern after feeding (Fig. 1d).

In unrewarded tests, unfed or previously fed ants made two journeys through the maze. On both journeys, ants chose the foodward pattern when unfed (first journey, 41 out of 44 correct; second, 37 of 41 correct) and the homeward pattern when fed (first journey, 38 of 43 correct; second, 25 of 28 correct) (all $P < 0.0001$). We conclude that the ants' visual memories were primed by feeding state and not by the sequence of rewarded patterns.

Although ants are rigid in sticking to familiar routes, they are like honeybees in that they show flexibility in choosing between routes. The selective priming of visual and vector memories specific to a particular route is an important component of this flexibility^{7,9–13}.

Robert A. Harris, Natalie Hempel de Ibarra, Paul Graham, Thomas S. Collett

School of Life Sciences, University of Sussex,
Falmer, Brighton, BN1 9QG, UK
e-mail: t.s.collett@sussex.ac.uk

- Santschi, F. *Rev. Suisse Zool.* **21**, 347–425 (1913).
- Collett, T. S., Dillmann, E., Giger, A. & Wehner, R. *J. Comp. Physiol. A* **170**, 435–442 (1992).
- Wehner, R., Michel, B. & Antonsen, P. *J. Exp. Biol.* **199**, 129–140 (1996).
- Collett, M., Collett, T. S., Bisch, S. & Wehner, R. *Nature* **394**, 269–272 (1998).
- Bisch-Knaden, S. & Wehner, R. *J. Comp. Physiol. A* **189**, 181–187 (2003).
- Kohler, M. & Wehner, R. *Neurobiol. Learn. Mem.* **83**, 1–12 (2005).
- Dyer, F. C., Gill, M. & Sharbowski, J. *Naturwissenschaften* **89**, 262–264 (2002).
- Graham, P. & Collett, T. S. *J. Exp. Biol.* **205**, 2499–2509 (2002).
- Wahl, O. Z. *Vergleich. Physiol.* **16**, 529–589 (1932).
- Koltermann, R. Z. *Vergleich. Physiol.* **75**, 49–68 (1971).
- Menzel, R., Geiger, K., Joerges, J., Müller, U. & Chittka, L. *Anim. Behav.* **55**, 139–152 (1998).
- Reinhard, J., Srinivasan, M. V., Guez, D. & Zhang, S. W. *J. Exp. Biol.* **207**, 4371–4381 (2004).
- Beugnon, G., Lachaud, J.-P. & Chagné, P. *J. Insect Behav.* **18**, 415–432 (2005).

Supplementary information accompanies this communication on *Nature's* website.

Competing financial interests: declared none.
doi:10.1038/438302a

BRIEF COMMUNICATIONS ARISING online
♦ www.nature.com/bca see *Nature* contents.