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.

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

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**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 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). 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.

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 uppercase 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 = [AIMDGVX]). 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 in a week apart, with a fully counterbalanced design. The skew of reaction-time (RT) distributions was reduced by taking logarithms (designated as RTlog). We binned each subject’s RTlog values (16 trials per bin in session 1; 8 trials per bin in sessions 2 and 3) and analysed bin means using linear contrasts to test specific hypotheses, designated F1. Response accuracy was not significantly less than 100% in any session.

After learning subsets A and B, RTlog for subset B (session 3) was significantly smaller than after learning 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, these 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 (F1(1) = 0.821, P = 0.352). Second, in the transfer condition, RTlog during session 3 was significantly smaller than during session 2 (F1(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.

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**Parasitic infection**

**Hunger tolerance and Leishmania in sandflies**

The sandfly Phlebotomus papatasi transmits Leishmania major, the agent of cutaneous leishmaniasis, in desert and savannah regions of the Old World1, where seasonal stress of dehydration and heat reduces the quantity of sugar in plant leaves2. Without essential sugar, only a few flies that feed on leaves can survive for long enough to deposit eggs and transmit Leishmania3–5. Accordingly, selection for hunger tolerance may also select for pathogen susceptibility in flies. Here we provide evidence of a link between these advantageous and costly1,4 properties by testing the susceptibility of flies selected by sugar deprivation and of flies from irrigated and arid habitats.

The experimental flies were obtained from a colony maintained on sucrose solution that was established in 1983 using flies from a desert habitat in the Jordan Valley. Susceptibility to infection with L. major promastigotes, the flagellated, parasitic form that inhabits sandflies, was evaluated sporadically using a standard procedure (Table 1). The previously high infection rate (338 of 394 flies, 85.7%) has declined in recent years to only 27.0% (48 of 178).

Experimental native plants Atriplex halimus (Chenopodiaceae) and Malva nicaeensis (Malvaceae), and the domestic Bougainvillea glabra (Nyctaginaceae), were chosen in a dry area. Sugar levels1,4 in the leaves of these plants were 3.6–13.8 times lower than in those of irrigated conspecifics. Groups of female P. papatasi were each fed exclusively on branches of one of the plants1 and other groups were starved until about half of the flies died (4–6 days). The survivors and control groups, one previously maintained for 6 days on 30% sucrose solution and another of day-old flies, were then infected1. Significantly more infections, including greater numbers of parasites, were found in flies selected for hunger tolerance compared with control flies (Table 1).

As the increased susceptibility to parasitic infection could have resulted from pre-infection hunger rather than from being selected, we tested day-old progeny of hunger-selected females. The frequency in infection of the progeny series was 64.3% (9 of 14), 79.7% (59 of 74) and 65.6% (21 of 32) (parents fed on B. glabra or M. nicaeensis or starved, respectively), whereas only 25.4% (45 of 177) of control flies were infected. This difference is statistically as significant as that of the parent generation (Table 1). Similar differences in susceptibility were also seen after pre-infection of hunger-selected and unselected flies were infected with amastigotes, the mammalian parasite form of L. major (results not shown). Assuming that hunger resistance and host competence for L. major improve with size, we measured and found no difference between the experimental and control fly groups (results not shown).

We also tested the correlation between the abundance of plant sugar in an oasis (Neot-Hakikar, Israel) and its scarcity at an arid site (in the Jordan Valley), and the susceptibility of the local P. papatasi populations to L. major. We first tested trapped flies for the presence of sugar in the gut4 — most of the oasis flies (69 of 72, 95.8%), but only one-third of the arid-site flies (60 of 186, 32.3%), were positive. We then infected first-generation progeny of these populations with L. major promastigotes1. Only 24.8% (25 of 101) of the oasis progeny retained parasites (mean ± s.e. per fly, 243 ± 71 promastigotes) compared with 82.5% (156 of 189) of the progeny of arid-site flies (mean ± s.e. per fly, 3,412 ± 686 promastigotes). We conclude that the oasis-adapted population is less susceptible to L. major than are similar flies from an arid area.

The cost of parasitic infection seems to be sufficient to elicit natural selection against competent hosts9. As far as we know, our findings represent the first evidence that this may be compensated for by linkage to endurance against environmental stress. Seasonal and incidental stress are prevalent in the life of insects10, including those that are vectors of disease, and selection may often favour lines of parasites that are adapted to stress-resistant vectors.  

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**correction**

**Ancient homes for hard-up hermit crabs**

David K. A. Barnes  

It has been drawn to my attention that I inadvertently omitted to cite previous work relevant to my results — hermit crabs have also been found to use fossils in Bermuda12, although in a different context. For some Coenobita clypeatus, namely those in Bermuda, the only shells available of appropriate size are fossils, and therefore little choice or active selection is being made by the resource users. The hermit crab Coenobita rugosus (in Madagascar), like most others elsewhere, is not able to excavate buried shells. Haas3, however, has observed C. clypeatus digging up and clearing debris from partially buried shells in Bermuda, which was also seen by Kellogg7 in laboratory conditions.


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**Table 1**  
Suscetibility of starvation-tolerant sandflies to Leishmania major

<table>
<thead>
<tr>
<th>Pre-infection diet</th>
<th>Flies dead</th>
<th>No. of flies</th>
<th>Flies infected</th>
<th>Parasites per fly</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(%)</td>
<td></td>
<td>(%)</td>
<td>Mean ± s.e.</td>
</tr>
<tr>
<td>Atriplex halimus</td>
<td>56.7</td>
<td>18</td>
<td>61.1</td>
<td>4,075 ± 434</td>
</tr>
<tr>
<td>Malva nicaeensis</td>
<td>57.6</td>
<td>16</td>
<td>75.0*</td>
<td>586 ± 113</td>
</tr>
<tr>
<td>Water only</td>
<td>53.6</td>
<td>33</td>
<td>78.8</td>
<td>900 ± 243</td>
</tr>
<tr>
<td>30% sucrose</td>
<td>0</td>
<td>78</td>
<td>97.4</td>
<td>2,111 ± 130</td>
</tr>
<tr>
<td>None</td>
<td>0</td>
<td>177</td>
<td>25.41</td>
<td>531 ± 248</td>
</tr>
</tbody>
</table>

Experimental flies survived for 4–6 days when fed on low-sugar plant branches or starved (water alone). One control group received 30% sucrose for 6 days before artificial infection, another was 1 day old when infected. Insecticidal means consisted of 10 × 10−6 promastigotes (MHOM/MA/89/1RC-1LS05) and (RAPL/84/URC-1465) in rabbit blood. Blood-fed flies were dissected and their parasites counted after 6 days of maintenance on 30% sucrose solution and water.

*Proportional data: arcsine transformed and significantly different from a standard control (P < 0.001, Fisher’s exact test).  
1Combined results of nine series.