

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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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 $A = \{ENLHUBWK\}$, $B = \{TORCFPY\}$, $C = \{AISDMGVX\}$). 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 counter-balanced 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

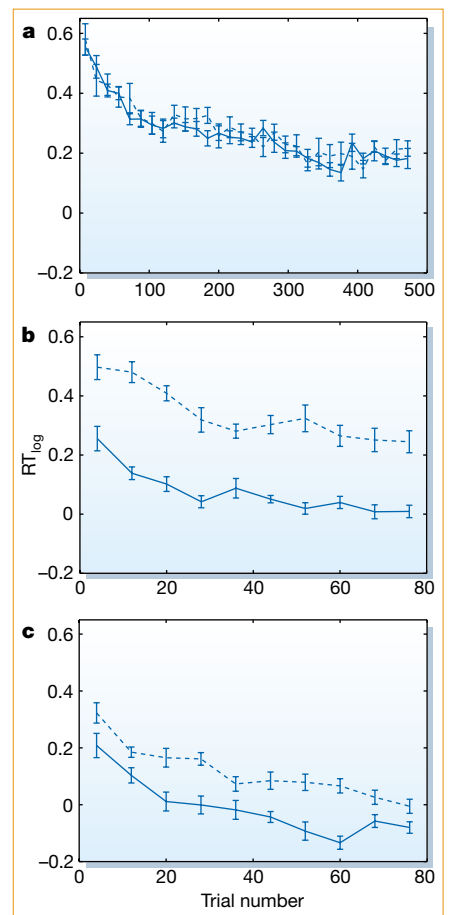


Figure 1 Reaction time (RT_{log}) plotted against trial number for three different experimental sessions (solid lines, transfer condition; dashed lines, control condition; error bars, standard errors of bin means; see text). **a**, Session 1: learning intermixed letter subsets A and B. RT_{log} decreases as letter positions are learned ($F(29,290) = 17.44$, $P < 0.001$), with no effect of condition ($P = 0.560$) and no condition \times 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 relearned⁴.

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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 *Leishmania*^{3,4}. Accordingly, selection for hunger tolerance may also select for pathogen susceptibility in flies. Here we provide evidence of a link between these advantageous and costly^{5,6} 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)⁷. 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 levels^{4,8} 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

plants⁴ 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 infected⁷. 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 of infection in 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 progeny 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 gut^{3,8} — 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* promastigotes⁷. 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

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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 Bermuda^{1,2}, 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. Haas¹, however, has observed *C. clypeatus* digging up and clearing debris from partially buried shells in Bermuda, which was also seen by Kellogg³ in laboratory conditions.

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

Pre-infection diet	Flies dead	No. of flies	Flies infected	Parasites per fly	
	(%)		(%)	Mean	s.e.
<i>Atriplex halimus</i>	56.7	18	61.1*	4,075	434
<i>Malva nicaeensis</i>	57.6	16	75.0*	588	113
Water only	53.6	33	78.8*	920	243
30% sucrose	0	78	12.8	211	136
None	0	177	25.4†	531	248

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 infection⁷; another was 1 day old when infected. Infective meals consisted of 1 × 10⁶ mi⁻¹ promastigotes (MHOM/IL/90/LRC-L585 and IPAP/IL/84/LRC-L465) 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)¹¹.

†Combined results of nine series.