are able to recognize each other from past interactions. Nor does it require that one agent can observe and recall how the other agents behaved with third parties. Therefore cooperation on the basis of similarity could be widely applicable in situations where repeated interactions are rare, and reputations are not established. Indeed, the basis for similarity can be completely arbitrary, such as for chemical markers or cultural attributes. Cultural artefacts that can serve as tags include accents, practices or artefacts subject to fashion such as wearing hats of particular colours[18]. The basis for similarity also can be 'secret handshakes' or other arbitrary behavioural signals that individuals can detect[19]. As an agent does not have to remember previous interactions with another agent, let alone know anything about that agent's behaviour with others, an agent only needs very limited signal-detection capability. Indeed, kin recognition may use tag-based mechanisms such as the 'green beard'[1,20–23] and 'armpit' effects[24–28]. Using tags may also be interpreted as imposing an abstract topology on the agents in which an agent's 'neighbourhood' is defined by its tag and threshold of similarity tolerance[14]. In summary, our results show that cooperation can become established and be sustained even without memory. Not only do the agents not require continuing interactions, they do not even need to observe the behaviour of others or receive reports from third parties. Strategies of donating to others who have sufficiently similar heritable tags—even though such tags are initially arbitrary—can establish cooperation without reciprocity. ☐

Received 3 August; accepted 17 September 2001.

1. Hamilton, W. D. The genetical evolution of social behaviour, I and II. *J. Theor. Biol.* **7,** 1–52 (1964).
2. Trivers, R. The evolution of reciprocal altruism. *Q. Rev. Biol.* **46,** 35–57 (1971).
3. Axelrod, R. & Hamilton, W. D. The evolution of cooperation. *Science* **211,** 1390–1396 (1981).
4. Axelrod, R. *The Evolution of Cooperation* (Basic Books, New York, 1984).
5. Nowak, M. A. & May, R. M. Evolutionary games and spatial chaos. *Nature* **359,** 826–829 (1992).
6. Lomborg, B. Nucleus and shield: the evolution of social structure in the iterated prisoner's dilemma. *Am. Soc. Rev.* **61,** 278–307 (1996).
7. Cohen, M. D., Riolo, R. L. & Axelrod, R. The role of social structure in the maintenance of cooperative regimes. *Rationality Soc.* **13,** 5–32 (2001).
8. Alexander, R. D. *The Biology of Moral Systems* (Aldine de Gruyter, New York, 1987).
9. Boyd, R. & Richerson, P. J. The evolution of indirect reciprocity. *Social Networks* **11,** 213–236 (1989).
10. Nowak, M. A. & Sigmund, K. Evolution of indirect reciprocity by image scoring. *Nature* **393,** 573–577 (1998).
11. Axelrod, R. *The Evolution of Cooperation* 146–150 (Basic Books, New York, 1984).
12. Holland, J. H. *Hidden Order: How Adaptation Builds Complexity* (Addison Wesley, Reading, Massachusetts, 1995).
13. Riolo, R. L. in *Proc. 7th Int. Conf. Genetic Algorithms (ICGA97)* (ed. Bäck, T.) 378–385 (Morgan Kaufmann, San Francisco, 1997).
14. Cohen, M. D., Riolo, R. L. & Axelrod, R. The emergence of social organization in the prisoner's dilemma: how context preservation and other factors promote cooperation. Working paper 99-01-002 (Santa Fe Institute, New Mexico, 1999).
15. Nowak, M. A. & Sigmund, K. Oscillations in the evolution of reciprocity. *J. Theor. Biol.* **137,** 21–26 (1989).
16. Lindgren, K. in *Artificial Life II* (eds Langton, C. G. *et al.*) 295–312 (Addison-Wesley, Reading, Massachusetts, 1991).
17. Linster, B. Evolutionary stability in the infinitely repeated prisoner's dilemma played by two-state Moore machines. *South. Econ. J.* **58,** 880–903 (1992).
18. Allison, P. D. The cultural evolution of beneficent norms. *Social Forces* **71,** 279–301 (1992).
19. Robson, A. J. Efficiency in evolutionary games: Darwin, Nash and the secret handshake. *J. Theor. Biol.* **144,** 379–396 (1990).
20. Dawkins, R. *The Selfish Gene* 96 (Oxford Univ. Press, Oxford, 1976).
21. Haig, D. Gestational drive and the green-bearded placenta. *Proc. Natl Acad. Sci. USA* **93,** 6547–6551 (1996).
22. Grafen, A. Evolutionary biology—green beard as death warrant. *Nature* **394,** 521–523 (1998).
23. Keller, L. & Ross, K. G. Selfish genes: a green beard in the red fire ant. *Nature* **394,** 573–575 (1998).
24. Dawkins, R. *The Extended Phenotype* 146–151 (Freeman, San Francisco, 1982).
25. Hauber, M. E., Sherman, P. W. & Paprika, D. Self-referent phenotype matching in a brood-parasite: the armpit effect in brown-headed cowbirds (*Molothrus ater*). *Anim. Cogn.* **3,** 113–117 (2000).
26. Hauber, M. E. & Sherman, P. W. The armpit effect in hamster kin recognition. *Trends Ecol. Evol.* **15,** 349–350 (2000).
27. Mateo, J. M. & Johnston, R. E. Kin recognition and the 'armpit effect': evidence of self-referent phenotype matching. *Proc. R. Soc. Lond. B* **267,** 695–700 (2000).
28. Isles, A. R., Baum, M. J., Ma, D., Keverne, E. B. & Allen, N. D. Genetic imprinting—urinary odour preferences in mice. *Nature* **409,** 783–784 (2001).

Acknowledgements

For financial support we thank the Intel Corporation and the University of Michigan College of Literature, Science and the Arts Enrichment Fund. For computing facilities we thank the University of Michigan Center for the Study of Complex Systems.

Correspondence and requests for materials should be addressed to R.L.R. (e-mail: rlriolo@umich.edu).

Effects of experience and social context on prospective caching strategies by scrub jays

N. J. Emery* & N. S. Clayton†

** Sub-department of Animal Behaviour, University of Cambridge, Cambridge CB3 8AA, UK*
† Department of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, UK
The authors contributed equally to this work

Social life has costs associated with competition for resources such as food[1]. Food storing may reduce this competition as the food can be collected quickly and hidden elsewhere[2–4]; however, it is a risky strategy because caches can be pilfered by others[5–9]. Scrub jays (*Aphelocoma coerulescens*) remember 'what', 'where' and 'when' they cached[10–13]. Like other corvids[6–9,14], they remember where conspecifics have cached, pilfering them when given the opportunity, but may also adjust their own caching strategies to minimize potential pilfering. To test this, jays were allowed to cache either in private (when the other bird's view was obscured) or while a conspecific was watching, and then recover their caches in private. Here we show that jays with prior experience of pilfering another bird's caches subsequently re-cached food in new cache sites during recovery trials, but only when they had been observed caching. Jays without pilfering experience did not, even though they had observed other jays caching. Our results suggest that jays relate information about their previous experience as a pilferer to the possibility of future stealing by another bird, and modify their caching strategy accordingly.

In the wild, food-storing corvids return to caches that they had hidden in the presence of conspecifics, and readily re-cache them in new places when the observers are no longer present (for example ravens[8,9], European jays[15], scrub jays; N.S.C., unpublished observations). We proposed that birds re-cache to minimize potential pilfering by observers. We therefore predicted that they would be more likely to re-cache any uneaten food, and specifically in new sites unbeknown to an observer, but only if they had been watched during the caching trial. To test this hypothesis, scrub jays were allowed to cache wax worms in a sand-filled caching tray during two

Table 1 Behaviour of the observer + pilferer birds during observed and in private caching treatments

	Caching treatment		Wilcoxon pairs test		
Behaviour	Observed	In private	*n*	*Z*	*P*
No. cached					
Davis	8.19 ± 1.55	4.71 ± 0.81	7	2.37	<0.05
Cambridge	10.48 ± 3.43	9.10 ± 3.05	7	0.51	>0.5
No. recovered					
Davis	4.61 ± 0.93	3.95 ± 0.84	7	0.85	>0.1
Cambridge	5.38 ± 1.56	4.19 ± 1.10	7	0.08	>0.5
Proportion recovered					
Davis	0.71 ± 0.06	0.57 ± 0.07	7	2.03	<0.05
Cambridge	0.56 ± 0.08	0.70 ± 0.09	7	1.69	>0.05
Recovery accuracy*					
Davis	2.21 ± 0.46	3.21 ± 1.01	7	1.15	>0.1
Cambridge	3.07 ± 0.92	1.52 ± 0.24	7	1.36	>0.1
No. re-cached					
Davis	2.19 ± 0.68	0.57 ± 0.32	7	2.20	<0.05
Cambridge	2.74 ± 1.01	0.36 ± 0.19	7	2.20	<0.05
Proportion re-cached					
Davis	0.44 ± 0.20	0.06 ± 0.03	7	2.20	<0.05
Cambridge	0.28 ± 0.07	0.08 ± 0.04	7	2.20	<0.05

Treatments consisted of three trials/caching treatment at Davis, followed by three trials/caching treatment at Cambridge (data are mean ± s.e.m.). A Wilcoxon matched-pairs test compared the effect of caching treatment for each of the behaviours listed.
* Number of looks to find first cache.

experimental conditions: while being observed by a conspecific (observed), and while the observer's view was blocked (in private). The storers recovered their caches 3 h later. During these recovery trials, which were always conducted out of sight of the observer, the birds could eat any caches that they recovered, but they could also re-cache them. They were given access to a new caching tray as well as the original one, so that they could re-cache in both new and old sites. New trays were used on each caching trial so that the cache sites were unique for each trial.

Scrub jays in the observer + pilferer group had participated in an earlier observational learning experiment in which they observed a conspecific cache, and subsequently pilfered those caches[14]. These birds received a series of caching and recovery trials at the University of California, Davis. The design was replicated at the University of Cambridge, UK, using the same birds.

Table 1 summarizes the main findings and statistics. Although birds cached significantly more items when observed by a conspecific at Davis, this effect was not found in the replicate at Cambridge, nor in subsequent tests (see below). The pattern of results for all other behaviours is very similar for both Davis and Cambridge. There was no effect of caching treatment on the number of items recovered, even when we analysed the number of items recovered as a proportion of the number cached. There was also no difference in the birds' accuracy at cache recovery, as measured by the number of searches birds made to find the first cache.

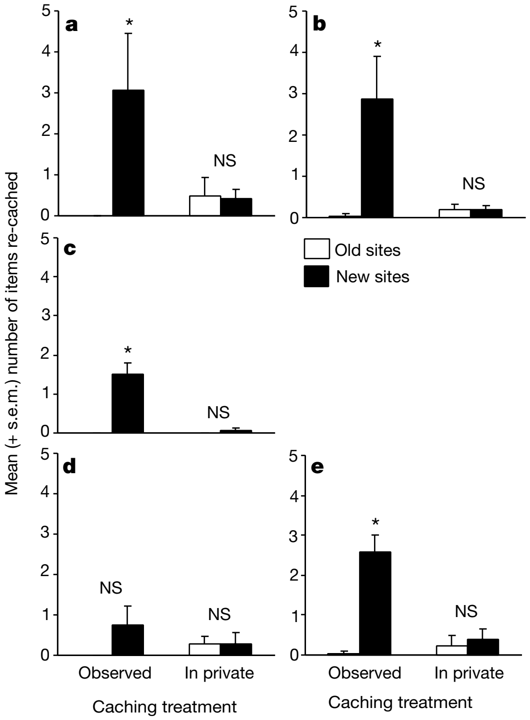

Figure 1 Mean (+ s.e.m.) number of worms re-cached by the three groups. **a**, The observer + pilferer group in Davis re-cached significantly more in the new sites during the observed caching treatment ($n = 7$, $Z = 2.20$, $P < 0.05$), but failed to discriminate between new and old sites during the in private caching treatment ($n = 7$, $Z = 0$, $P = 1.0$). **b**, The observer + pilferer group in Cambridge also re-cached significantly more in new sites when observed during caching ($n = 7$, $Z = 2.20$, $P < 0.05$), but again did not discriminate between re-caching in old or new sites during the in private caching treatment (no statistical comparison possible). **c**, The observer + pilferer group also selectively re-cached food in new sites in the observed tray ($n = 7$, $Z = 2.37$, $P < 0.05$), but did not discriminate between old and new sites in the in private tray during the interleaved caching trials (no statistical comparison possible). **d**, The observer group did not selectively re-cache in either new or old sites during both the observed and the in private caching treatments (old: $n = 7$, $Z = 1.6$, $P > 0.1$; new: no statistical comparison possible). **e**, The pilferer group re-cached significantly more food items in new sites during the observed caching treatment ($n = 7$, $Z = 2.37$, $P < 0.05$), but as with the observer + pilferer group, did not re-cache selectively in either old or new sites during the in private caching treatment (no statistical comparison possible). All analyses were Wilcoxon matched-pairs tests. Asterisk, $P < 0.05$, NS, not significant ($P > 0.05$).

The principal result is that birds re-cached significantly more items during recovery when they had been observed during caching. As the number of items that can be re-cached depends on the number originally cached and subsequently recovered, we calculated the number of worms that were re-cached as a proportion of the number of worms that were recovered per bird. The difference between the observed and in private caching treatments was also found for the proportion of worms re-cached, a measure that controls for differences in the number of items cached and recovered. These results therefore confirmed our prediction that birds would re-cache significantly more if they had been observed caching. We also predicted that caching treatment would influence a bird's choice of re-caching location. Figure 1a, b (Davis and Cambridge, respectively) supports this prediction by showing that re-caching was predominantly in new sites rather than old sites when the bird had been observed during caching. By contrast, birds that had been allowed to cache in private did not discriminate between old and new sites.

Birds in the observer + pilferer group had to remember whether they had been watched during caching to know when to re-cache during recovery, and whether to re-cache in new sites. Being observed recently during caching could lead to a generalized tendency to re-cache when presented with the opportunity to do so at a later time. Alternatively, the bird may remember whether it had been watched while caching in a specific tray. We discriminated between these two possibilities by testing whether the observer + pilferer group could keep track of the social context of previous caching episodes that occurred in close temporal proximity. We used interleaved observed and in private caching trials: the birds cached in one tray while being observed by a conspecific (observed tray), and then cached in another tray in private immediately afterwards (in private tray), and vice versa. After a 3-h retention interval, the birds received a recovery trial in which they were presented simultaneously with both the observed tray and the in private tray in which they had cached, as well as a new tray.

Table 2 shows the mean (± s.e.m.) number of items cached, recovered and re-cached, the number of looks to find the first cache and the proportion of caches recovered and re-cached per tray (observed or in private) during the interleaved trials. Note that the numbers of items cached are much lower than those shown in Table 1, presumably as a consequence of using interleaved trials in which the second caching episode occurred immediately after the first one. In line with the previous results for the observer + pilferer group in Cambridge, however, we found no difference in the number of items cached in the observed tray and in the private tray. The number of items recovered from each tray is also less than that shown in Table 1, probably because the birds had a choice of two trays from which they could recover as opposed to only one, yet the duration of the recovery trial was the same. Birds recovered

Table 2 Behaviour of the observer + pilferer birds in the observed tray and in private tray during the interleaved trials

	Caching treatment		Wilcoxon pairs test		
Behaviour	Observed	In private	*n*	*Z*	*P*
No. cached	3.93 ± 0.77	3.57 ± 0.76	7	0.25	>0.5
No. recovered	3.00 ± 0.53	1.21 ± 0.32	7	1.99	<0.05
Proportion recovered	0.73 ± 0.07	0.39 ± 0.09	7	2.37	<0.05
Recovery accuracy*	4.21 ± 2.03	4.57 ± 0.85	7	0.42	>0.5
No. re-cached	2.00 ± 0.68	0.14 ± 0.14	7	2.20	<0.05
Proportion re-cached	0.45 ± 0.11	0.04 ± 0.04	7	2.37	<0.05

A Wilcoxon matched-pairs test compared the effect of caching treatment for each of the behaviours listed (data are mean ± s.e.m.).
* Number of looks to find first cache.

significantly more items from the observed tray. We found also that the birds recovered proportionally more items from the observed tray. There were no differences in recovery accuracy, however.

Importantly, Table 2 also shows that birds re-cached more of those items that were recovered from the observed tray than from the in private tray, even when the data were analysed as a proportion of the number of items recovered (which adjusts for differences in recovery). Figure 1c shows that re-caching was predominantly made in new sites in the observed tray. By contrast, the birds showed little tendency to discriminate between re-caching in old and new sites in the in private tray. This pattern of results is consistent with those obtained from the previous study. It suggests that jays remember not only whether they were being observed, but can also recall the specific tray in which they cached while being watched, rather than relying on a default mechanism to re-cache if they have been observed recently.

Although some food-storing species avoid caching in those areas from which food has been stolen if the caches are pilfered regularly[16,17], this is not observed after a single pilfering event[18], which suggests that birds may need to learn about the costs and benefits of pilfering. We therefore assessed the role of prior learning by testing the cache recovery behaviour of the observer group that had experience of observing a conspecific cache, but no experience of subsequently pilfering those caches. Birds in the observer group had the same amount of caching and recovery experience as the observer + pilferer birds, and considerable experience of observing the caching behaviour of conspecifics. The observer group had previously observed birds caching during the observational learning study[14] and they served also as observers in the studies described earlier. However, they differed from the observer + pilferer group in that they never had the opportunity to pilfer another bird's caches.

Table 3 displays the mean (± s.e.m.) number of worms cached, recovered and re-cached, the number of looks to find the first cache and the proportion of caches recovered and re-cached during the observed or in private caching treatments for the observer group. It is clear from Table 3 that there is no difference in the number of items cached or recovered between the observed and in private caching treatments, and an analysis of the proportion recovered also failed to find any significant difference. There was also no effect of caching treatment on cache accuracy. Unlike the observer + pilferer group, however, the observer group did not display any significant difference in the number of items re-cached between the observed and in private caching treatments or the proportion of items re-cached.

Figure 1d shows that, in contrast to the observer + pilferer group, birds in the observer group re-cached very little in both the observed and in private caching treatments. They did not selectively re-cache in new sites, and made too few re-caches to permit a valid statistical analysis (Table 3). This pattern of results suggests that birds need pilfering experience to know when to re-cache because the critical difference between the observer and observer + pilferer groups is whether they had the opportunity to pilfer another bird's caches.

Table 3 Behaviour of observer and pilferer birds during observed and in private caching treatments

	Caching treatment		Wilcoxon pairs test		
Behaviour	Observed	In private	*n*	*Z*	*P*
No. cached					
Observer group	6.38 ± 0.80	4.62 ± 0.43	7	1.57	>0.1
Pilferer group	5.53 ± 1.50	7.05 ± 1.95	7	1.01	>0.1
No. recovered					
Observer group	3.36 ± 0.53	2.69 ± 0.30	7	1.10	>0.1
Pilferer group	3.67 ± 0.78	4.00 ± 0.97	7	1.35	>0.1
Proportion recovered					
Observer group	0.59 ± 0.08	0.58 ± 0.07	7	0.17	>0.5
Pilferer group	0.73 ± 0.08	0.62 ± 0.06	7	1.35	>0.1
Recovery accuracy*					
Observer group	2.29 ± 0.53	2.31 ± 0.41	7	0.34	>0.5
Pilferer group	2.62 ± 0.78	2.12 ± 0.53	7	0.73	>0.1
No. re-cached					
Observer group	0.69 ± 0.43	0.29 ± 0.21	7	1.60	>0.1
Pilferer group	2.09 ± 0.50	0.62 ± 0.42	7	2.20	<0.05
Proportion re-cached					
Observer group	0.10 ± 0.04	0.06 ± 0.04	7	1.60	>0.1
Pilferer group	0.44 ± 0.09	0.09 ± 0.06	7	2.37	<0.05

A Wilcoxon matched-pairs test compared the effect of caching treatment for each of the behaviours listed (data are mean ± s.e.m.).
* Number of looks to find first cache.

To verify this hypothesis, and to test whether experience of observing caching behaviour is also critical for prospective caching, a further group of birds was tested. Birds in the pilferer group had the opportunity to listen to, but not observe, another bird caching, and were then allowed to pilfer those caches in the earlier observational learning study[14]. As all the birds had received extensive caching experience, they readily searched for caches even when they had not seen the storer hide food[10–13]. These birds differed therefore from observer and observer + pilferer birds in not having the opportunity to observe conspecifics caching in these experiments. In common with the observer + pilferer group, but in contrast to the observer group, the pilferer group had previous experience of pilfering. If pilfering, but not observation, is the critical experience for knowing when to re-cache, then birds of the pilferer group should show the same pattern of results as the observer + pilferer group.

Table 3 also displays the mean (± s.e.m.) number of worms cached, recovered and re-cached, the number of looks to find the first cache and the proportion of caches recovered and re-cached during either observed or in private caching treatments for the pilferer group. We found no significant difference between the two caching treatments in the number of items cached or recovered. There was also no significant difference between the observed and in private caching treatments in the proportion of items recovered or accuracy to find a cache. However, in line with the observer + pilferer group, and in contrast to the observer group, the number of items re-cached was significantly greater in the observed caching treatment. An analysis of the proportion of items re-cached confirmed this result.

Figure 1e shows that the pilferer group re-cached more items during recovery if they had been observed during caching, and predominantly in new sites. There was no preference for caching in new sites when they had previously cached in private. Taken together, this pattern of results demonstrates that birds need experience of being a pilferer to know when to re-cache, and whether to re-cache in new sites, but they do not need experience of being an observer.

To our knowledge, this is the first experimental demonstration that a non-human animal can remember the social context of specific past events, and adjust their present behaviour to avoid potentially detrimental consequences in the future, in this case pilfering. To do this, scrub jays need experience of pilfering another bird's caches, but do not require experience of observing a conspecific hide food. They can recall specific past events[10–13], but the present results raise the possibility that they can also plan for the future. The jays seem to have transferred their previous experience of being a pilferer to the current situation in which their own caches might be stolen. This may be a good candidate for knowledge attribution in conspecifics[19] (seeing leads to knowing), use of this knowledge to influence subsequent behaviour[20] (re-caching in new locations) or even tactical deception[21]. Mental time travel (episodic memory and future planning) and mental attribution were thought to be unique to humans[22,23]. The cache recovery model presents a new way of addressing these issues in animals. □

Methods

Subjects

A total of 21 adult hand-raised scrub jays were used, all of whom had been tested in previous studies of caching behaviour[24], memory[10–13] and observational learning[14]. All of the birds had the same experience of caching and recovering food. The only difference between the birds was their experience in the earlier observational learning study[14]—observer, pilferer or observer + pilferer. These categories are directly related to the specific experiences in the previous experiment, not the developmental histories of the birds. Although we cannot state that birds in the pilferer group had never observed other birds cache they did not do so in the previous study or in the current one. Importantly, the observer birds have never pilfered another bird's caches.

The observer + pilferer ($n = 7$) group was first tested at the University of California, Davis (19–26 July 2000), with a replicate study performed at the University of Cambridge (15 January to 16 February 2001). Birds in the observer ($n = 7$) and pilferer ($n = 7$) groups were tested at Cambridge (15 January to 16 February 2001). The interleaved trials study (observer + pilferer group only) was performed at Cambridge (27–28 February 2001). All of the birds were housed individually in cages ($45 \times 76 \times 76$ cm). In Davis, birds were housed in an outdoor aviary. In addition to natural lighting, we provided fluorescent strip lighting. In Cambridge, the birds were housed in the same cages as Davis, but these were placed in a quarantined indoor room in which only fluorescent lighting was provided. Birds were fed a mixture of Iams mini-chunk dog food biscuits and peanuts, both of which were provided in powdered form to ensure that the birds could not cache outside of the experiment. Water was provided *ad libitum*.

Apparatus

The fronts of the individual cages were made of aluminium wire and the sides were made of solid aluminium. The storer was placed in a cage located adjacent to a second cage containing the observer, with a 20-cm-wide gap between the two cages. On the back of each cage was a $25\,\text{cm}^2$ perspex panel, which allowed the storer and observer to see one another. Caching trays[10–13] were constructed from sand-filled plastic ice-cube trays, each containing a 2×8 array of moulds that were attached to a wooden board. Each caching tray was made unique by attaching different configurations of Lego (Netfield) bricks onto the board behind the ice-cube tray.

Procedure

Birds were deprived of food overnight. Caching trials started at 10:00 (Davis) or 11:00 (Cambridge) the following day. During every 15-min caching trial ($n = 3$ per caching treatment, observer + pilferer group in Davis and observer, pilferer and observer + pilferer groups in Cambridge; $n = 2$ pairs, observer + pilferer group interleaved trials in Cambridge) each subject received one sand-filled caching tray and a bowl containing 50 wax worms. During the unobserved caching treatment (in private), a towel covered the back of the cage so that the view of the observer bird was completely obscured. During the observed caching treatment, the observer had a clear view of the storer. At the end of each caching trial, the tray and food bowl were removed from each cage. The experimenters recorded the number and location of wax worms cached in the tray. Any extraneous food that the birds did not cache was removed. The number of worms cached therefore refers to the number of worms that remained in the tray at the end of the caching trial. Observers were given 15 min in which they were allowed to eat their maintenance diet at the end of the caching trial, and each bird was given three wax worms. In Davis and Cambridge, two caching trays were placed inside the subject's cage during recovery trials. One of the trays was unfamiliar to the bird. The other tray contained the previously cached worms and was placed in its original location. Three caching trays were placed inside the subject's cage during recovery trials for the interleaved trials study. One tray was unfamiliar to the bird, whereas the other two trays contained the previously cached worms, which were placed in the same locations as they were placed during the observed tray and in private tray caching treatments.

The subjects were allowed to recover the cached food items for 10 min. The number and location of the searches was recorded by direct observation, as well as the number of caches recovered and whether these were eaten or re-cached. We also noted the location of the re-cached food items, and whether they were made in new sites compared to those places the bird had cached in during the previous caching trial (old site). We calculated the number of searches to find the first cache (recovery accuracy), the proportion of worms recovered and the proportion of those recoveries that were re-cached. All 21 birds had previous experience with the presence of towels on their cages for at least three trials each. They were restricted from caching during these trials, but were given powdered food and three wax worms.

Analysis

We used the Wilcoxon matched-pairs test on the mean values summed across trials for each caching treatment. As the number of items recovered depends on the number of items cached, and the number of items re-cached depends on the number of caches that are recovered, we also analysed the proportion of caches that were recovered and the proportion of those re-cached. For all analyses, alpha was set at 0.05.

Received 23 July; accepted 20 September 2001.

---

1. Zentall, T. R. & Galef, B. G. (eds) *Social Learning. Psychological and Biological Perspectives* (Lawrence Erlbaum Associates, London, 1998).
2. Shettleworth, S. J. in *Behavioral Brain Research in Naturalistic and Semi-naturalistic Settings* (eds Alleva, E., Fasolo, A., Lipp, H.-P. & Nadel, L.) 158–179 (Kluwer Academic, The Hague, 1995).
3. Vander Wall, S. B. *Food Hoarding in Animals* (Univ. Chicago Press, Chicago, 1990).
4. Clarkson, K., Eden, S. F., Sutherland, W. J. & Houston, A. I. Density dependence and magpie food hoarding. *J. Anim. Ecol.* **55,** 111–121 (1986).
5. Gibb, J. A. Populations of tits and goldcrests and their food supply in pine populations. *Ibis* **102,** 163–208 (1960).
6. Bednekoff, P. A. & Balda, R. P. Observational spatial memory in Clark's nutcrackers and Mexican jays. *Anim. Behav.* **52,** 833–839 (1996).
7. Heinrich, B. & Pepper, J. W. Influence of competitors on caching behavior in the common raven, *Corvus corax*. *Anim. Behav.* **56,** 1083–1090 (1998).
8. Bugnyar, T. & Kotrschal, K. Do ravens manipulate the others' attention in order to prevent or achieve social learning opportunities? *Adv. Ethol.* **36.** 106 (2001).
9. Heinrich, B. *Mind of the Raven* (Harper Collins, New York, 1999).
10. Clayton, N. S. & Dickinson, A. D. Episodic-like memory during cache recovery by scrub jays. *Nature* **395,** 272–278 (1998).
11. Clayton, N. S. & Dickinson, A. D. Scrub jays *(Aphelocoma coerulescens)* remember the relative time of caching as well as the location and content of their caches. *J. Comp. Psychol.* **113,** 403–416 (1999).
12. Clayton, N. S. & Dickinson, A. D. Memory for the contents of caches by Scrub Jays. *J. Exp. Psychol. Anim. Behav. Proc.* **25,** 82–91 (1999).
13. Clayton, N. S., Yu, K. & Dickinson, A. D. Scrub jays *(Aphelocoma coerulescens)* can form integrated memory for multiple features of caching episodes. *J. Exp. Psychol. Anim. Behav. Proc.* **27,** 17–29 (2001).
14. Clayton, N. S., Griffiths, D. P., Emery, N. J. & Dickinson, A. D. Episodic-like memory in animals. *Phil. Trans. R. Soc. Lond. B* **356,** 1483–1491 (2001).
15. Goodwin, D. Further observations on the behaviour of the jay. *Ibis* **98,** 186–219 (1956).
16. Stevens, T. A. & Krebs, J. R. Retrieval of stored seeds by marsh tits *(Parus palustris)* in the field. *Ibis* **128,** 513–515 (1984).
17. Hampton, R. R. & Sherry, D. F. The effects of cache loss on choice of cache sites in the black-capped chickadee. *Behav. Ecol.* **5,** 44–50 (1994).
18. Baker, M. C. & Anderson, P. Once-pilfered cache sites not avoided by black-capped chickadees. *Anim. Behav.* **49,** 1599–1602 (1995).
19. Hare, B., Call, J., Agnetta, B. & Tomasello, M. Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* **59,** 771–785 (2000).
20. Hare, B., Call, J. & Tomasello, M. Do chimpanzees know what conspecifics know? *Anim. Behav.* **61,** 139–151 (2001).
21. Whiten, A. & Byrne, R. W. Tactical deception in primates. *Behav. Brain Sci.* **11,** 233–244 (1988).
22. Suddendorf, T. & Corbalis, M. C. Mental time travel and the evolution of the human mind. *Genet. Soc. Gen. Psychol. Monogr.* **123,** 133–167 (1997).
23. Heyes, C. M. Theory of mind in nonhuman primates. *Behav. Brain Sci.* **21,** 101–148 (1998).
24. Clayton, N. S. & Dickinson, A. D. Motivational control of caching behaviour in the scrub jay, *Aphelocoma coerulescens*. *Anim. Behav.* **57,** 435–444 (1999).

Acknowledgements

This work was supported by the National Institutes of Health, National Institute on Aging and Whitehall foundation grants to N.S.C. N.J.E was funded by a Medical Research Council programme grant to E. B. Keverne. We thank S. Hettige, D. Jennings and V. R. Metcalf for help in running the experiments. We also thank the University of California, Davis, for allowing us to conduct the first trials there and for providing the necessary facilities. We thank S. Baron-Cohen, E. B. Keverne, K. N. Laland, D. I. Perrett and C. J. Saldanha for comments on the manuscript. We are especially grateful to T. J. Bussey, A. Dickinson and N. J. Mackintosh for discussion and comments on the manuscript.

Correspondence and requests for materials should be addressed to N.S.C.
(e-mail: nsc22@cam.ac.uk).

The central nervous system stabilizes unstable dynamics by learning optimal impedance

**Etienne Burdet[*,†,§,‖], Rieko Osu[†,‖], David W. Franklin[§,¶],
Theodore E. Milner[¶] & Mitsuo Kawato[†,§]**

* *Department of Mechanical Engineering, National University of Singapore,
119260, Singapore*
† *Kawato Dynamic Brain Project, ERATO, JST, Hikaridai, Seika-cho,
Soraku-gun, Kyoto, 619 0288, Japan*
§ *ATR Human Information Science Laboratories, Hikaridai, Seika-cho,
Soraku-gun, Kyoto, 619 0288, Japan*
¶ *School of Kinesiology, Simon Fraser University, Burnaby,
British Columbia V5A 1S6, Canada*
‖ *These authors contributed equally to the work*

To manipulate objects or to use tools we must compensate for any forces arising from interaction with the physical environment. Recent studies indicate that this compensation is achieved by learning an internal model of the dynamics[1–6], that is, a neural representation of the relation between motor command and

6. Chan, F. K., Siegel, M. R. & Lenardo, J. M. Signaling by the TNF receptor superfamily and T cell homeostasis. *Immunity* **13,** 419–422 (2000).
7. Yang, Y., Fang, S., Jensen, J. P., Weissman, A. M. & Ashwell, J. D. Ubiquitin protein ligase activity of IAPs and their degradation in proteasomes in response to apoptotic stimuli. *Science* **288,** 874–877 (2000).
8. Tschopp, J., Martinon, F. & Hofmann, K. Apoptosis: Silencing the death receptors. *Curr. Biol.* **9,** R381–R384 (1999).
9. Van Antwerp, D. J., Martin, S. J., Kafri, T., Green, D. R. & Verma, I. M. Suppression of TNF-α-induced apoptosis by NF-κB. *Science* **274,** 787–789 (1996).
10. Liu, Z. G., Hsu, H., Goeddel, D. V. & Karin, M. Dissection of TNF receptor 1 effector functions: JNK activation is not linked to apoptosis while NF-κB activation prevents cell death. *Cell* **87,** 565–576 (1996).
11. Deveraux, Q. L. *et al.* IAPs block apoptotic events induced by caspase-8 and cytochrome *c* by direct inhibition of distinct caspases. *EMBO J.* **17,** 2215–2223 (1998).
12. Roy, N., Deveraux, Q. L., Takahashi, R., Salvesen, G. S. & Reed, J. C. The c-IAP-1 and c-IAP-2 proteins are direct inhibitors of specific caspases. *EMBO J.* **16,** 6914–6925 (1997).
13. Sarin, A., Conan-Cibotti, M. & Henkart, P. A. Cytotoxic effect of TNF and lymphotoxin on T lymphoblasts. *J. Immunol.* **155,** 3716–3718 (1995).
14. Zheng, L. *et al.* Induction of apoptosis in mature T cells by tumour necrosis factor. *Nature* **377,** 348–351 (1995).
15. Duckett, C. S. *et al.* A conserved family of cellular genes related to the baculovirus iap gene and encoding apoptosis inhibitors. *EMBO J.* **15,** 2685–2694 (1996).
16. Chan, F. K. & Lenardo, M. J. A crucial role for p80 TNF-R2 in amplifying p60 TNF-R1 apoptosis signals in T lymphocytes. *Eur. J. Immunol.* **30,** 652–660 (2000).
17. Arch, R. H., Gedrich, R. W. & Thompson, C. B. Translocation of TRAF proteins regulates apoptotic threshold of cells. *Biochem. Biophys. Res. Commun.* **272,** 936–945 (2000).
18. Huang, H. *et al.* The inhibitor of apoptosis, cIAP2, functions as a ubiquitin-protein ligase and promotes *in vitro* ubiquitination of caspases-3 and -7. *J. Biol. Chem.* **275,** 26661–26664 (2000).
19. Rothe, M., Wong, S. C., Henzel, W. J. & Goeddel, D. V. A novel family of putative signal transducers associated with the cytoplasmic domain of the 75 kDa tumor necrosis factor receptor. *Cell* **78,** 681–692 (1994).
20. Rothe, M., Sarma, V., Dixit, V. M. & Goeddel, D. V. TRAF2-mediated activation of NF-κB by TNF receptor 2 and CD40. *Science* **269,** 1424–1427 (1995).
21. Reinhard, C., Shamoon, B., Shyamala, V. & Williams, L. T. Tumor necrosis factor α-induced activation of c-jun N-terminal kinase is mediated by TRAF2. *EMBO J.* **16,** 1080–1092 (1997).
22. Weiss, T. *et al.* Enhancement of TNF receptor p60-mediated cytotoxicity by TNF receptor p80: requirement of the TNF receptor-associated factor-2 binding site. *J. Immunol.* **158,** 2398–2404 (1997).
23. Weiss, T. *et al.* TNFR80-dependent enhancement of TNFR60-induced cell death is mediated by TNFR-associated factor 2 and is specific for TNFR60. *J. Immunol.* **161,** 3136–3142 (1998).
24. Erickson, S. L. *et al.* Decreased sensitivity to tumour-necrosis factor but normal T-cell development in TNF receptor-2-deficient mice. *Nature* **372,** 560–563 (1994).
25. Clem, R. J. *et al.* c-IAP1 is cleaved by caspases to produce a pro-apoptotic C-terminal fragment. *J. Biol. Chem.* **276,** 7602–7608 (2000).
26. Duckett, C. S. & Thompson, C. B. CD30-dependent degradation of TRAF2: implications for negative regulation of TRAF signaling and the control of cell survival. *Genes Dev.* **11,** 2810–2821 (1997).
27. Brown, K. D., Hostager, B. S. & Bishop, G. A. Differential signaling and tumor necrosis factor receptor-associated factor (traf) degradation mediated by CD40 and the epstein-barr virus oncoprotein latent membrane protein 1 (Imp1). *J. Exp. Med.* **193,** 943–954 (2001).
28. Peschon, J. J. *et al.* TNF receptor-deficient mice reveal divergent roles for p55 and p75 in several models of inflammation. *J. Immunol.* **160,** 943–952 (1998).
29. Lorick, K. L. *et al.* RING fingers mediate ubiquitin conjugating enzyme (E2)-dependent ubiquitination. *Proc. Natl Acad. Sci. USA* **96,** 11364–11369 (1999).
30. Memon, S. A., Petrak, D., Moreno, M. B. & Zacharchuk, C. M. A simply assay for examining the effect of transiently expressed genes on programmed cell death. *J. Immunol. Methods* **180,** 15–24 (1995).

Supplementary Information accompanies the paper on *Nature's* website (http://www.nature.com).

Acknowledgements

We are grateful to A. Weissman, C. Duckett, and Z. Liu for provision of reagents and reviews of this manuscript. X.L. is a visiting fellow from Bethune International Hospital, China.

Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to J.D.A. (e-mail: jda@pop.nci.nih.gov).

---

correction

Effects of experience and social context on prospective caching strategies by scrub jays

N. J. Emery & N. S. Clayton

Nature **414,** 443–446 (2001).

The exact number of species of American jays is a matter of debate[1]. This is particularly evident within the scrub-jay lineage of *Aphelocoma*[2]. Traditionally, *A. coerulescens* included the Florida scrub-jay and the western scrub-jay, among others. It has recently been brought to our attention that the Committee on Classification and Nomenclature of the American Ornithologists' Union now use *A. coerulescens* to refer exclusively to the Florida scrub-jay and *A. californica* to refer to the western scrub-jay[2]. The birds used in the Emery & Clayton[3] and Clayton & Dickinson[4] studies were western scrub-jays: *A. californica*, not *A. coerulescens*. We therefore wish to correct the oversight in this paper and our other papers using these birds, and apologize for any confusion that has arisen. We thank R. Curry, T. Langen and G. Woolfenden for alerting us to the change in nomenclature. ☐

1. Madge, S. & Burn, H. *Crows and Jays. A Guide to the Crows, Jays and Magpies of the World* (Houghton Mifflin, New York, 1999).
2. American Ornithologists' Union *Check-list of North American Birds* 7th edn (American Ornithologists' Union, Washington DC, 1998).
3. Emery, N. J. & Clayton, N. S. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* **414,** 443–446 (2001).
4. Clayton, N. S. & Dickinson, A. Episodic-like memory during cache recovery by scrub jays. *Nature* **395,** 272–278 (1998).

---

erratum

Tyrannosaurus was not a fast runner

John R. Hutchinson & Mariano Garcia

Nature **415,** 1018–1021 (2002).

In this Letter, the row in Table 1 corresponding to '*Gallus*, m_{i} (%m_{body})' should read: 1.1, 0.08, 2.0 and 1.5 for the hip, knee, ankle and toe respectively. ☐

6. Chan, F. K., Siegel, M. R. & Lenardo, J. M. Signaling by the TNF receptor superfamily and T cell homeostasis. *Immunity* **13,** 419–422 (2000).
7. Yang, Y., Fang, S., Jensen, J. P., Weissman, A. M. & Ashwell, J. D. Ubiquitin protein ligase activity of IAPs and their degradation in proteasomes in response to apoptotic stimuli. *Science* **288,** 874–877 (2000).
8. Tschopp, J., Martinon, F. & Hofmann, K. Apoptosis: Silencing the death receptors. *Curr. Biol.* **9,** R381–R384 (1999).
9. Van Antwerp, D. J., Martin, S. J., Kafri, T., Green, D. R. & Verma, I. M. Suppression of TNF-α-induced apoptosis by NF-κB. *Science* **274,** 787–789 (1996).
10. Liu, Z. G., Hsu, H., Goeddel, D. V. & Karin, M. Dissection of TNF receptor 1 effector functions: JNK activation is not linked to apoptosis while NF-κB activation prevents cell death. *Cell* **87,** 565–576 (1996).
11. Deveraux, Q. L. *et al.* IAPs block apoptotic events induced by caspase-8 and cytochrome *c* by direct inhibition of distinct caspases. *EMBO J.* **17,** 2215–2223 (1998).
12. Roy, N., Deveraux, Q. L., Takahashi, R., Salvesen, G. S. & Reed, J. C. The c-IAP-1 and c-IAP-2 proteins are direct inhibitors of specific caspases. *EMBO J.* **16,** 6914–6925 (1997).
13. Sarin, A., Conan-Cibotti, M. & Henkart, P. A. Cytotoxic effect of TNF and lymphotoxin on T lymphoblasts. *J. Immunol.* **155,** 3716–3718 (1995).
14. Zheng, L. *et al.* Induction of apoptosis in mature T cells by tumour necrosis factor. *Nature* **377,** 348–351 (1995).
15. Duckett, C. S. *et al.* A conserved family of cellular genes related to the baculovirus iap gene and encoding apoptosis inhibitors. *EMBO J.* **15,** 2685–2694 (1996).
16. Chan, F. K. & Lenardo, M. J. A crucial role for p80 TNF-R2 in amplifying p60 TNF-R1 apoptosis signals in T lymphocytes. *Eur. J. Immunol.* **30,** 652–660 (2000).
17. Arch, R. H., Gedrich, R. W. & Thompson, C. B. Translocation of TRAF proteins regulates apoptotic threshold of cells. *Biochem. Biophys. Res. Commun.* **272,** 936–945 (2000).
18. Huang, H. *et al.* The inhibitor of apoptosis, cIAP2, functions as a ubiquitin-protein ligase and promotes *in vitro* ubiquitination of caspases-3 and -7. *J. Biol. Chem.* **275,** 26661–26664 (2000).
19. Rothe, M., Wong, S. C., Henzel, W. J. & Goeddel, D. V. A novel family of putative signal transducers associated with the cytoplasmic domain of the 75 kDa tumor necrosis factor receptor. *Cell* **78,** 681–692 (1994).
20. Rothe, M., Sarma, V., Dixit, V. M. & Goeddel, D. V. TRAF2-mediated activation of NF-κB by TNF receptor 2 and CD40. *Science* **269,** 1424–1427 (1995).
21. Reinhard, C., Shamoon, B., Shyamala, V. & Williams, L. T. Tumor necrosis factor α-induced activation of c-jun N-terminal kinase is mediated by TRAF2. *EMBO J.* **16,** 1080–1092 (1997).
22. Weiss, T. *et al.* Enhancement of TNF receptor p60-mediated cytotoxicity by TNF receptor p80: requirement of the TNF receptor-associated factor-2 binding site. *J. Immunol.* **158,** 2398–2404 (1997).
23. Weiss, T. *et al.* TNFR80-dependent enhancement of TNFR60-induced cell death is mediated by TNFR-associated factor 2 and is specific for TNFR60. *J. Immunol.* **161,** 3136–3142 (1998).
24. Erickson, S. L. *et al.* Decreased sensitivity to tumour-necrosis factor but normal T-cell development in TNF receptor-2-deficient mice. *Nature* **372,** 560–563 (1994).
25. Clem, R. J. *et al.* c-IAP1 is cleaved by caspases to produce a pro-apoptotic C-terminal fragment. *J. Biol. Chem.* **276,** 7602–7608 (2000).
26. Duckett, C. S. & Thompson, C. B. CD30-dependent degradation of TRAF2: implications for negative regulation of TRAF signaling and the control of cell survival. *Genes Dev.* **11,** 2810–2821 (1997).
27. Brown, K. D., Hostager, B. S. & Bishop, G. A. Differential signaling and tumor necrosis factor receptor-associated factor (traf) degradation mediated by CD40 and the epstein-barr virus oncoprotein latent membrane protein 1 (Imp1). *J. Exp. Med.* **193,** 943–954 (2001).
28. Peschon, J. J. *et al.* TNF receptor-deficient mice reveal divergent roles for p55 and p75 in several models of inflammation. *J. Immunol.* **160,** 943–952 (1998).
29. Lorick, K. L. *et al.* RING fingers mediate ubiquitin conjugating enzyme (E2)-dependent ubiquitination. *Proc. Natl Acad. Sci. USA* **96,** 11364–11369 (1999).
30. Memon, S. A., Petrak, D., Moreno, M. B. & Zacharchuk, C. M. A simply assay for examining the effect of transiently expressed genes on programmed cell death. *J. Immunol. Methods* **180,** 15–24 (1995).

Supplementary Information accompanies the paper on *Nature's* website (http://www.nature.com).

Acknowledgements

We are grateful to A. Weissman, C. Duckett, and Z. Liu for provision of reagents and reviews of this manuscript. X.L. is a visiting fellow from Bethune International Hospital, China.

Competing interests statement

The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to J.D.A. (e-mail: jda@pop.nci.nih.gov).

---

correction

Effects of experience and social context on prospective caching strategies by scrub jays

N. J. Emery & N. S. Clayton

Nature **414,** 443–446 (2001).

The exact number of species of American jays is a matter of debate[1]. This is particularly evident within the scrub-jay lineage of *Aphelocoma*[2]. Traditionally, *A. coerulescens* included the Florida scrub-jay and the western scrub-jay, among others. It has recently been brought to our attention that the Committee on Classification and Nomenclature of the American Ornithologists' Union now use *A. coerulescens* to refer exclusively to the Florida scrub-jay and *A. californica* to refer to the western scrub-jay[2]. The birds used in the Emery & Clayton[3] and Clayton & Dickinson[4] studies were western scrub-jays: *A. californica*, not *A. coerulescens*. We therefore wish to correct the oversight in this paper and our other papers using these birds, and apologize for any confusion that has arisen. We thank R. Curry, T. Langen and G. Woolfenden for alerting us to the change in nomenclature. □

1. Madge, S. & Burn, H. *Crows and Jays. A Guide to the Crows, Jays and Magpies of the World* (Houghton Mifflin, New York, 1999).
2. American Ornithologists' Union *Check-list of North American Birds* 7th edn (American Ornithologists' Union, Washington DC, 1998).
3. Emery, N. J. & Clayton, N. S. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* **414,** 443–446 (2001).
4. Clayton, N. S. & Dickinson, A. Episodic-like memory during cache recovery by scrub jays. *Nature* **395,** 272–278 (1998).

---

erratum

Tyrannosaurus was not a fast runner

John R. Hutchinson & Mariano Garcia

Nature **415,** 1018–1021 (2002).

In this Letter, the row in Table 1 corresponding to '*Gallus*, m_{i} ($\%m_{\mathrm{body}}$)' should read: 1.1, 0.08, 2.0 and 1.5 for the hip, knee, ankle and toe respectively. □