Report

Western Scrub-Jays Anticipate Future Needs Independently of Their Current Motivational State

Sérgio P.C. Correia,[1,2] Anthony Dickinson,[1] and Nicola S. Clayton[1,*]
[1] Department of Experimental Psychology
University of Cambridge
Downing Street
Cambridge CB2 3EB
United Kingdom
[2] Programa Gulbenkian de Doutoramento em Biomedicina
Instituto Gulbenkian de Ciência
P-2781-901 Oeiras
Portugal

Summary

Planning for the future has been considered to be a uniquely human trait [1–3]. However, recent studies challenge this hypothesis by showing that food-caching Western scrub-jays (*Aphelocoma californica*) can relate their previous experience as thieves to the possibility of future cache theft by another bird [4], are sensitive to the state of their caches at recovery ([5] and S. De Kort, S.P.C.C., D. Alexis, A.D., and N.S.C., unpublished data), and can plan for tomorrow's breakfast [6]. Although these results suggest that scrub-jays are capable of future planning, the degree to which these birds act independently of their current motivational state is a matter of contention. The Bischof-Köhler hypothesis [1] holds that nonhuman animals cannot anticipate and act toward the satisfaction of a future need not currently experienced or cued by their present motivational state. Using specific satiety to control for the jays' current and future motivational states, here we specifically test this hypothesis by dissociating current and future motivational states. We report that Western scrub-jays anticipate the recovery of their caches, as well as their own future needs, by acting independently of their current motivational state and immediate needs. The fact that the birds act in favor of a future need as opposed to the current one challenges the hypothesis that this ability is unique to humans.

Results and Discussion

The mental time travel (MTT) hypothesis holds that only humans can cognitively displace themselves in time [1]. Many people have assumed that nonhuman animals were cognitively stuck in time (e.g., [1–3]), incapable of acting on the basis of either the recollection of specific past episodes (retrospective cognition) or the contemplation of possible states of affair beyond the immediate future (prospective cognition). Over the past nine years, an increasing number of studies have challenged the

MTT hypothesis by presenting evidence for retrospective cognition in Western scrub-jays and, more recently, in rodents [7–11]. Although evidence in humans supports common mechanisms underlying both episodic memory and future planning [12–15], only recently have researchers addressed the question of whether nonhuman animals can plan for the future.

According to the Bishof-Köhler hypothesis, nonhumans are bound to their present motivational state and cannot anticipate or take appropriate action toward the satisfaction of a need or motivational state that is not currently experienced [1]. In order to fulfill this future planning criterion, the behavior should be independent of the current motivational state. Although some primates and corvids take actions on the basis of their future consequences ([2, 5, 16–18] and S. De Kort, S.P.C.C., D. Alexis, A.D., and N.S.C., unpublished data), these have not been shown to be selected with reference to future motivational states ([2, 5, 16, 17] and S. De Kort, S.P.C.C., D. Alexis, A.D., and N.S.C., unpublished data) or without extensive reinforcement of the anticipatory act [18]. Recent research on the food-caching behavior of Western scrub-jays, however, does provide some evidence for future planning by showing that these birds can provision for a future motivational state, both by preferentially caching food in a place in which they have learned that they will be hungry the following morning, and by differentially storing a particular food in a place in which that type of food will not be available the next morning [6]. These findings suggest that the jays spontaneously plan for tomorrow without reference to their current motivational state, thereby challenging the idea that this is a uniquely human ability. However, this study did not explicitly dissociate current and future motivational states [6]. Here we tested the Bishof-Köhler hypothesis directly by using specific satiety to contrast the impact of the jays' current and future motivational states.

Our experiment investigates whether Western scrub-jays can make appropriate caching decisions that would maximize the satisfaction of their future motivational state, even in opposition to their current motivational state. To control for and dissociate the jays' current and future motivational states, we capitalized on the fact that that when jays and other animals are prefed on a particular type of food, they become specifically sated on that particular food [19–21]. When given the choice of two foods that they can eat and/or cache, the birds preferentially eat and cache the type of food that is different from that which they have just been prefed [19]. This specific-satiety effect acts on the animals' motivational state, which modulates the incentive value assigned to the food, thereby controlling behavior [20, 21].

In this experiment, we used the specific-satiety procedure to control for the birds' motivational state on subsequent feeding and caching preference tests. When the birds are prefed on the same food type prior to

*Correspondence: nsc22@cam.ac.uk

caching and recovery, then they should preferentially eat, cache, and recover the food type that is different from that which they have been prefed. By prefeeding the birds on two different food types, one just prior to caching and the other immediately prior to recovery, we can distinguish between the effects of the birds' current and future motivational states. If the birds' caching decisions are controlled only by their current motivational state, then they should cache the food type that is different from that they were prefed on immediately prior to caching, whereas if the birds can dissociate their current and future motivational states, they should cache the same food type as that they were prefed on because that will be the food type they will be motivated to eat at the time of recovery.

Specific-Satiety Feeding Test

In experiment 1, we presented 11 jays with specific-satiety feeding tests (Figure 1). In stage 1, the birds were given the opportunity to eat one of two possible food types (pine seeds or kibbles) for 3 hr until they were sated. Immediately afterward, in stage 2 the birds were given a 10 min preference test in which we recorded the amount of each food type they consumed. The specific-satiety effect predicts that exposure to a specific food during stage 1 should, during the test trial, reduce the consumption of that same food, and that therefore the birds should eat more of the different food, the one that was not prefed. The birds were also given two control conditions, one in which they were prefed both food types during stage 1, and one in which they did not receive either food during stage 1. For both of these conditions, the birds were expected to show an equal preference for both foods during stage 2, but they were expected to eat more in the non-prefed condition than in the case in which they were prefed both food types. In total, the birds received four specific-satiety tests, one in each condition—i.e., prefed pine seeds, prefed kibbles, prefed both pine seeds and kibbles, or non-prefed. The reliability of differences in food consumption during the test trial was assessed with a repeated-measures analysis of variance with prefeeding condition and food type consumed as within-subjects variables. The reliability of effects in this and all subsequent analyses was assessed against a type I error rate of 0.05.

As seen in Figure 1, a specific control over eating can be induced by prefeeding a particular food to satiety. Pre-exposure to a particular type of food reduces the incentive value of that food, and consequently the birds ate more of the non-prefed food type in both the prefed-pine and the prefed-kibble conditions, yet consumed approximately equal amounts of the two foods in the two control conditions. The analysis confirmed the significant prefeeding condition × food type interaction [$F(3,30) = 8.49$, $p < 0.001$]. When the birds were prefed pine seeds, they consumed more kibbles than pine seeds [$F(1,10) = 6.96$, $p < 0.05$], and when they were prefed kibbles they consumed more pine seeds than kibbles [$F(1,10) = 5.12$, $p < 0.05$]. However, when the birds were either prefed both food types or deprived before the feeding test, there were no differences in the relative consumption of the two food types (for both, $F < 1$).
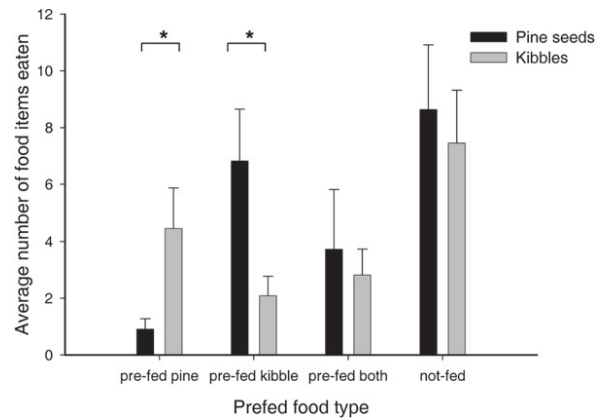

Figure 1. Specific-Satiety Feeding Test

The mean number (±SEM) of pine seeds (black bars) and dog kibbles (gray bars) eaten during stage 2 is shown for each of the four conditions: prefed pine seeds in stage 1; prefed dog kibbles in stage 1; prefed both pine seeds and dog kibbles in stage 1; and the not-fed condition, in which the birds did not receive any food during stage 1. For each condition, * indicates significant difference (p < 0.05) in the amounts of food eaten on the top of the respective bars.

Specific-Satiety Caching Test

In experiment 2, each bird received three trials in which it was given the opportunity to cache and recover pine seeds and kibbles, having been prefed one of the two foods immediately prior to caching and immediately prior to recovery. Each trial consisted of four stages. In stage 1, the birds were given either pine seeds or kibbles to eat for 3 hr, and immediately afterward in stage 2 the jays received a 10 min preference test in which both food types were available for eating and caching. Approximately 30 min later, the jays received a second period of prefeeding on one of the two food types for 3 hr (stage 3), followed immediately by the opportunity to recover the caches they had made for 10 min (stage 4).

The birds were divided into two groups in order to control for and dissociate the jays' current and future motivational states. Birds in the Same group were prefed the same food type as that which they had received during stage 1, whereas birds in the Different group were prefed the food type that they had not received during the first prefeeding period, as illustrated in Figure 2.

We first aimed to replicate the effect of specific satiety on caching, namely that prefeeding with a particular type of food selectively depresses the jays' subsequent caching of the same type of food [19]. If prefeeding exerts a food-specific modulation of caching as well as food consumption, then on the initial trial both groups should preferentially eat and cache in stage 2 the food type they had not been prefed on during stage 1, and similarly they should also preferentially eat and recover during stage 4 the food they had not been prefed on during stage 3.

Both groups should, on subsequent trials, continue to show a preference for eating the non-prefed food in stage 2 and recovering and eating the non-prefed food in stage 4. However, if the jays can dissociate their future motivation from their current motivational state, then groups Same and Different should differ in their caching preferences on subsequent trials. Whereas the birds in
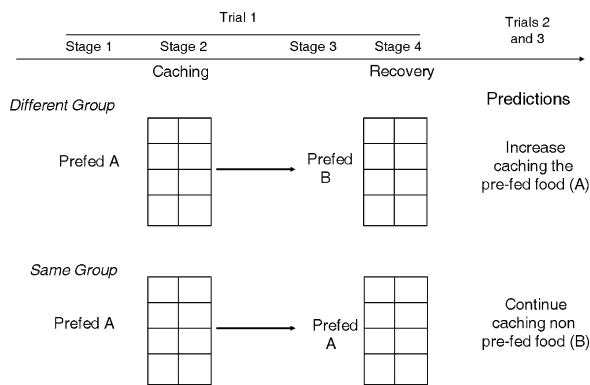
Figure 2. Design and Predictions Scheme

If prefeeding exerts a food-specific modulation of caching, on the initial trial both groups should preferentially eat and cache in stage 2 the food type they had not been prefed on during stage 1. On subsequent trials, the Bischof-Köhler hypothesis predicts that both groups should continue to cache the non-prefed food because that is the food type with the higher current incentive value. By contrast, if the birds can dissociate their current and future motivational states, then on subsequent trials the Different group should switch to caching the same food type because that is the food type that has a higher incentive value for their future motivational state at recovery.

the Same group should continue to preferentially cache the non-prefed food in stage 2, birds in the Different group should switch to caching the prefed food (i.e., the same food type as that which they received during prefeeding in stage 1) because that is the food type that has a higher incentive value for their future motivational state at recovery. By contrast, if the birds cannot dissociate their future motivational need from their present one, then both groups should continue to cache the non-prefed food in stage 2 because that is the food type with the higher current-incentive value (see Figure 2).

Figure 3 shows that in stage 2 both groups cached a smaller proportion of the food that they had been prefed in stage 1 on the first trial. This result replicates the previous finding [19] that a specific control over caching can be induced by prefeeding a particular food to satiety. In terms of the absolute number of items cached, the Different group cached a total of 6.5 ± 2.9 non-prefed items and 0.70 ± 0.7 prefed items (mean ± standard error of the mean [SEM]) on trial 1, and the Same group a total of 3.2 ± 1.2 non-prefed items and 1.2 ± 1.0 prefed items (mean ± SEM) on trial 1. On trials 2 and 3, however, the two groups differed in the proportion of prefed and non-prefed caches that they made. Whereas the Same group continued to preferentially cache the non-prefed food type (with 4.6 ± 2.3 non-prefed items and 0 ± 0 prefed items cached in trial 2 and 2.0 ± 1.1 non-prefed items and 0 ± 0 prefed items on trial 3), the Different group switched their caching preference toward caching the prefed food type (with 0.30 ± 0.2 non-prefed items and 1.2 ± 0.5 items cached on trial 2, and 0 ± 0 non-prefed items and 0.8 ± 0.3 prefed items cached on trial 3). The absolute amount cached is not dependent on the amount eaten and vice versa; the total number of items in the food bowl greatly exceeded the amount eaten and cached.

An initial analysis of the number of food items cached in stage 2 revealed neither a main effect of the food type
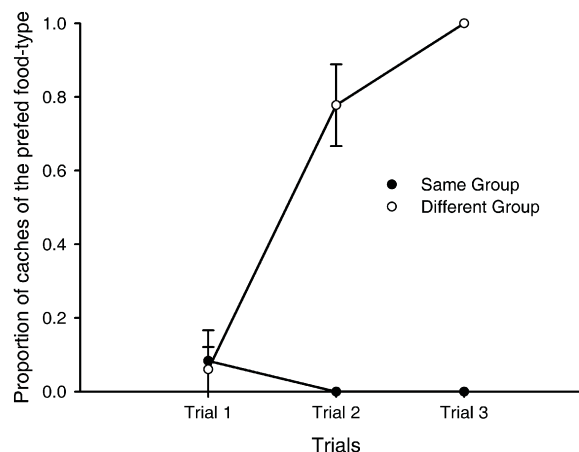

Figure 3. Specific-Satiety Caching Tests

The proportion (±SEM) of the prefed type of food (i.e., the same type of food that the birds were prefed) cached during stage 2 for trials 1–3 is shown for the Same (full dots, n = 5) and Different (open dots, n = 6) groups.

prefed in stage 1 nor an interaction between this factor and that of groups ($Fs < 1$). Therefore, the data were collapsed across the type of prefed food for subsequent analysis, in which we contrasted the groups with the number of caches of the prefed food type as a proportion of the total number of caches made. Although the groups did not differ in the proportion cached in trial 1 (U = 12, n = 10, p > 0.05), a statistically reliable difference was detected between the two groups on trial 2 (U = 0, n = 8, p < 0.05), which arose because the Different group cached a higher proportion of the prefed food than the Same group on the second trial. This effect was accentuated on trial 3, when the Different group only cached the prefed food and the Same group only cached the non-prefed food.

Figure 4 shows that the effect of specific satiety on food consumption was maintained across trials; both
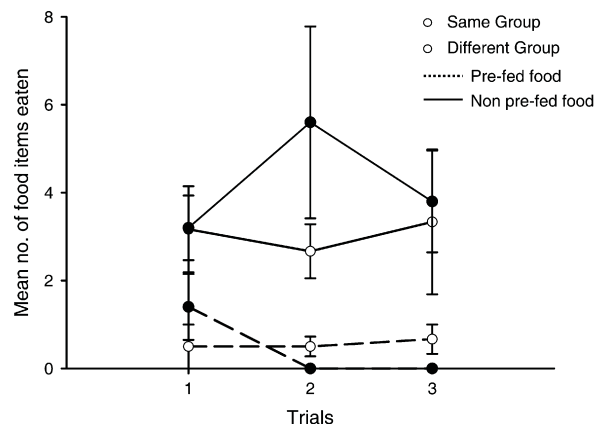

Figure 4. Food Eaten during the Specific-Satiety Caching Tests

The mean number (±SEM) of the prefed (broken lines) and non-prefed (full lines) food types eaten during stage 2 is shown for trials 1–3 for the Same group (filled circles, n = 5), which was prefed the same food at caching and recovery, and for the Different group (open circles, n = 6), which was prefed different foods at caching and recovery.

groups continued to eat more of the non-prefed food than of the prefed food at caching (stage 2) [$F(1,9) = 17.93$, $p < 0.01$]. Neither the main effects of groups and trial on the type of food eaten at caching nor any of the interactions was significant [$Fs < 1$ and $F(2,8) = 1.94$, $p = 0.17$].

The specific-satiety effect was also observed at the time of recovery (stage 4), with the birds eating preferentially the food type that was not prefed in stage 3. On trial 1, in which both groups still cached both food types, the Same group recovered and ate all the items (16) of the food type that was never prefed, but only 17% (1 in 6) of the food type that was prefed at both caching and recovery. By contrast, the Different group recovered all the items (4) of the food type that was prefed at caching (which is different from the food type prefed at recovery), but only 11% (4 in 37) of the food type that was not prefed at caching (which is the one prefed at recovery). For both the Same and Different groups, the food items of the same food type prefed in stage 3 were disregarded or recached at recovery. All the birds that cached more than one food type recovered first the food type that was not prefed in stage 3.

In summary, we report two key results. First, we replicated the specific control over eating and over caching that can be induced by prefeeding a particular food to satiety. Pre-exposure to a particular type of food reduces the incentive value of that food and selectively depresses the jays' subsequent consumption and caching of the same type of food. These results are consistent with previous work that demonstrates that the feeding system can exert both a general- and a specific-satiety effect over feeding and a food-specific modulation of caching ([19] and S. De Kort, S.P.C.C., D. Alexis, A.D., and N.S.C., unpublished data). Second, use of the specific-satiety effect to juxtapose the birds' current and future motivational state demonstrates that the jays can make appropriate caching decisions that maximize the satisfaction of their future motivational state over the current one. They act in favor of a future need that is not currently experienced by their motivational state.

Importantly, the results of this experiment also show that whereas eating is mediated by the current incentive value of the food and therefore modulated by the birds' current motivational state, the birds' caching preferences are also mediated by the incentive value assigned to the food at recovery, a value that is modulated by the birds' future motivational state independently of the current one.

It has been suggested that human decisions are often based on predictions of the hedonic consequences of future events via atemporal representations of those events and their imagined consequences [22]. These predictions may be subject to temporal corrections if one is to consider how these reactions may change if the event is displaced in time. However, the temporal corrections of preliminary inferences requires time, motivation, and cognitive resources, and humans can only dissociate future from current motivational states when they have the opportunity to think and to project themselves mentally in time. When they are required to do another task at the same time and thus their processing becomes automatic, then their decisions are based on current motivational states.

These results show that, contrary to the Bishof-Köhler hypothesis, scrub-jays are not bound to their present motivational state. The birds can anticipate and take appropriate action toward the satisfaction of a future need, one that is not currently experienced. After learning the incentive value of a food at recovery, the jays act independently of their current motivational state by caching the food that they are currently sated on, if that food is the one they will prefer when they come to recover the caches.

Experimental Procedures

Subjects and Apparatus

We conducted two experiments between July 19 and August 25, 2006. The subjects were seven male and four female sexually mature hand-raised Western scrub-jays (*Aphelocoma californica*). All the jays had been hand raised in the laboratory, and had received a variety of caching and recovery experiences prior to these experiments (S. De Kort, S.P.C.C., D. Alexis, A.D., and N.S.C., unpublished data). The birds were housed in groups of four birds in custom-made cages that measured 2 m wide × 2 m high × 1 m deep and could be divided into four test areas by the insertion of opaque dividers. The housing conditions were maintained at a temperature of $21 \pm 1^\circ$C under artificial light on a 12:12 hr light-dark cycle, with a 45 min period of dawn:dusk ramp. The jays received a maintenance diet that consisted of mixed nuts, grains and seeds, and dog biscuits. Fruits, vegetables, and invertebrates were provided at least twice per week. Cuttlefish bone was also provided for the birds to sharpen their beaks and as a source of calcium; they were also given free access to water.

The birds cached in ice-cube trays, each of which consisted of a 2 × 8 array of 2.5 cm ice-cube molds filled with corn kibble (a corn-processing residual). Each tray was attached to a wooden board (15 × 35 cm) and surrounded by children's construction blocks (Lego Duplo; Netfield, Connecticut) so that each tray was visuospatially unique. Each tray was placed in the same location on the floor of the testing area to provide readily available storage sites. All birds were simultaneously and unobtrusively monitored with a multicamera surveillance system (GeoVision GV-900, London).

Procedure for Experiment 1: The Specific-Satiety Feeding Test

In experiment 1, each bird received a two-stage specific-satiety test. During stage 1 of each trial, either the birds were given the opportunity to feed to satiety on pine seeds, dog kibble pieces, or both for 3 hr, or they were deprived of food for the same amount of time. Immediately afterward, the birds received a feeding preference test for 10 min (stage 2), in which they were given the opportunity to eat both foods. The foods were provided in separate bowls, one containing 30 pine seeds and the other containing 30 pieces of dog-food kibble. Each bird received one trial in each of the following four conditions that differed in the type of food items available to the bird during prefeeding (stage 1): pine seeds, dog kibbles, both pine seeds and dog kibbles, or neither (not prefed). The order in which the birds received the four conditions was counterbalanced across birds. To enhance the palatability of the dog kibbles, they were soaked in water for 25 min and then dried on kitchen paper for at least 30 min in order to optimize the consistency for both eating and caching. This procedure also controls for the jays' equivalent preference of kibbles and pine seeds. Each individual dog kibble was then cut into four pieces.

At the start of every pre-feeding condition (stage 1), the maintenance diet was removed and replaced by four bowls containing the prefed food type (except for the deprived condition), which the birds could eat or cache in the cage. When the birds were prefed dog kibbles, fresh items were added every hour. At the start of every preference test (stage 2), the four bowls containing the prefed food type were removed (except for the deprived condition), and the four birds in a cage were separated so that one bird was in each of the four tests areas. The bowls containing the food items were inserted in the middle of each bird test area, perpendicular to the door, and their relative position along the longitudinal axis was varied

randomly across birds and across trials. The experimenter left the experimental room. After the 10 min test period, the experimenter re-entered the room and removed the bowls, as well as any detectable caches the birds made in their test area. The maintenance diet was restored and the dividers between the birds removed. In an adjacent room, the experimenter recorded the number of items removed from each bowl.

Procedure for Experiment 2: Specific-Satiety Caching Test
In experiment 2, each bird received three consecutive trials of a four-stage procedure. At the start of the experiment, the eleven birds were randomly assigned to the Different (n = 6) and Same groups (n = 5), which would differ in the type of food prefed in stage 3.

For stages 1 and 2 of the first trial, the procedure was very similar to that used in experiment 1, except for the inclusion of a caching tray during the preference tests (stage 2) to examine the effects of prefeeding (stage 1) on subsequent caching behavior (stage 2). In stage 1, we allowed the birds the opportunity to feed and cache to satiety during 3 hr on one of two possible food types (pine seeds or dog kibbles). At the outset of the experiment, we randomly allocated the birds such that six birds were prefed pine seeds and five birds were prefed dog kibble in stage 1. In stage 2, which occurred immediately after stage 1, each bird was given a 10 min caching preference test between the two food types, the same food type as that they had received during prefeeding in stage 1 (prefed), and the other food type (non-prefed). The caching tray was always placed on the right-hand side of each bird's test area, centered half-way along the longitudinal axis.

To control for and dissociate the jays' current and future motivational states, we included two subsequent stages: a 3 hr period of prefeeding (stage 3) that was analogous to stage 1 and occurred approximately 30 min after stage 2, and a subsequent 10 min stage 4 in which the birds were given the opportunity to recover the caches they had made in stage 2. At the outset of the experiment, birds were randomly assigned to both the Same and Different groups so that in the Different group there were three birds that during stage 1 were prefed pine seeds, and three birds that were prefed dog kibbles, whereas in the Same group there were three birds that during stage 1 were prefed pine seeds and two birds that were prefed dog kibbles. These groups differed only in whether the type of food they were prefed at stage 3 was the same as or different from that they were prefed in stage 1. Birds in the Same group were prefed the same food type they were prefed in stage 1, whereas those in the Different group were prefed the food type that they had not received during the first prefeeding stage. In stage 4, the birds were given the tray containing the caches they made during stage 2. The tray was refilled with fresh corn kibble, and fresh food items were inserted in the same caching sites within the tray in which the birds had cached them. At the start of the recovery episode, the birds were again separated from their cage mates, and the tray was placed back in the test area. Then, the experimenter left the room for a 10 min recovery period, allowing the birds to inspect the tray and recover the items they found, after which the tray was removed from the cage. The cage dividers were removed, and the maintenance diet was restored 1 hr after the recovery phase. The birds received one trial per day across 3 consecutive days.

The number of items cached and the location of these caches in the trays were recorded in an adjacent room by naive experimenters, as were the food items remaining on the bowls. All trials were videotaped, and the food items remaining at the end of caching were confirmed by watching of the videotapes.

Data Analysis
The reliability of all contrasts was assessed against a type I error rate of 0.05. In experiment 1, differences in food consumption during the test trial were assessed with a repeated-measures analysis of variance with prefeeding condition and food type consumed as within-subjects variables.

For experiment 2 (the caching test), the reliability of differences in food consumption during the test trial was assessed with a mixed analysis of variance with trials and food type as within-subjects variables and group as the between-subjects factor. The reliability of differences in the absolute number of items cached during the test trial were also assessed with a mixed analysis of variance with groups

and the food type prefed in stage 1 (pine seeds and kibbles) as between-subjects factors, and trials and the food type cached in stage 2 as the within-subjects variables. The amount of prefed food cached was assessed as a proportion of the total number of prefed and non-prefed items cached. Because these proportions could not be calculated for birds that failed to cache either food type, one bird in the Different group on trial 1, three birds on the Different group in trial 2, and two birds in each group on trial 3 were excluded for both the analysis and the presentation of the proportions in Figure 3. Because on some trials there was no variance in the proportion of prefed food items cached, the proportions cached by each group were compared by a nonparametric Mann-Whitney U test separately for each trial.

References

1. Suddendorf, T., and Corballis, M.C. (1997). Mental time travel and the evolution of the human mind. Genet. Soc. Gen. Psychol. Monogr. *123*, 133–167.
2. Roberts, W.A. (2002). Are animals stuck in time? Psychol. Bull. *128*, 473–489.
3. Tulving, E. (2005). Episodic memory and autonoesis: Uniquely human? In The Missing Link in Cognition: Evolution of Self-Knowing Consciousness, H. Terrace and J. Metcalfe, eds. (Oxford: Oxford University Press), pp. 3–56.
4. Emery, N.J., and Clayton, N.S. (2001). Effects of experience and social context on prospective caching strategies by scrub jays. Nature *414*, 443–446.
5. Clayton, N.S., Dally, J., Gilbert, J., and Dickinson, T. (2005). Food caching by western scrub-jays (*Aphelocoma californica*) is sensitive to the conditions at recovery. J. Exp. Psychol. Anim. Behav. Process. *31*, 115–124.
6. Raby, C.R., Alexis, D.M., Dickinson, A., and Clayton, N.S. (2007). Planning for the future by Western Scrub-Jays. Nature *445*, 919–921.
7. Clayton, N.S., and Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. Nature *395*, 272–274.
8. Clayton, N.S., Bussey, T.J., and Dickinson, A. (2003). Can animals recall the past and plan for the future? Nat. Rev. Neurosci. *4*, 685–691.
9. Dally, J.M., Emery, N.J., and Clayton, N.S. (2006). Food-caching Western Scrub-Jays keep track of who was watching when. Science *312*, 1662–1665.
10. Babb, S.J., and Crystal, J.D. (2006). Episodic-like memory in the rat. Curr. Biol. *16*, 1317–1321.
11. Roberts, W.A. (2006). Animal Memory: Episodic-like memory in rats. Curr. Biol. *16*, R601–R603.
12. Atance, C.M., and O'Neill, D.K. (2001). Episodic future thinking. Trends Cogn. Sci. *5*, 533–539.
13. Rosenbaum, R.S., Kohler, S., Schacter, D.L., Moscovitch, M., Westmacott, R., Black, S.E., Gao, F.Q., and Tulving, E. (2005). The case of KC: Contributions of a memory-impaired person to memory theory. Neuropsychologia *43*, 989–1021.
14. Klein, S.B., Loftus, J., and Kihlstrom, J.F. (2002). Memory and temporal experience: The effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. Soc. Cogn. *20*, 353–379.

15. Okuda, J., Fujii, T., Ohtake, H., Tsukiura, T., Tanji, K., Suzuki, K., Kawashima, R., Fukuda, H., Itoh, M., and Yamadori, A. (2003). Thinking of the future and past: The roles of the frontal pole and the medial temporal lobes. Neuroimage *19*, 1369–1380.

16. Mulcahy, N.J., and Call, J. (2006). Apes save tools for future use. Science *312*, 1038–1040.

17. Suddendorf, T. (2006). Foresight and evolution of the human mind. Science *312*, 1006–1007.

18. Naqshbandi, M., and Roberts, W.A. (2006). Anticipation of future events in squirrel monkeys (*Saimiri sciureus*) and rats (*Rattus norvegicus*): Tests of the Bischof-Kohler hypothesis. J. Comp. Psychol. *120*, 345–357.

19. Clayton, N.S., and Dickinson, A. (1999). Motivational control of food-caching behaviour in the scrub jay, *Aphelocoma coerulescens*. Anim. Behav. *57*, 435–444.

20. Dickinson, A., and Balleine, B.W. (1994). Motivational control of goal-directed action. Anim. Learn. Behav. *22*, 1–18.

21. Dickinson, A., and Balleine, B.W. (1995). Motivational control of instrumental action. Curr. Dir. Psychol. Sci. *4*, 162–167.

22. Gilbert, D.T., Gil, M.J., and Wilson, T.D. (2002). The future is now: Temporal correction in affective forecasting. Organizational Behavior and Human Decision Processes *88*, 430–444.

Note Added in Proof

While this manuscript was in press, a relevant paper was accepted for publication. In the five places where we have cited "S. De Kort, S.P.C.C., D. Alexis, A.D., and N.S.C., unpublished data," this citation can be supported by the following reference:

de Kort, S., Correia, S.P.C., Alexis, D., Dickinson, A., and Clayton, N.S. (2007). The control of food-caching in the Western scrub-jay (*Aphelocoma californica*). J. Exp. Psychol. Anim. Behav. Process., in press.