LETTERS

Planning for the future by western scrub-jays

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Knowledge of and planning for the future is a complex skill that is considered by many to be uniquely human. We are not born with it; children develop a sense of the future at around the age of two and some planning ability by only the age of four to five[1–3]. According to the Bischof-Köhler hypothesis[4], only humans can dissociate themselves from their current motivation and take action for future needs: other animals are incapable of anticipating future needs, and any future-oriented behaviours they exhibit are either fixed action patterns or cued by their current motivational state. The experiments described here test whether a member of the corvid family, the western scrub-jay (*Aphelocoma californica*), plans for the future. We show that the jays make provision for a future need, 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. Previous studies have shown that, in accord with the Bischof-Köhler hypothesis, rats[5] and pigeons[6] may solve tasks by encoding the future but only over very short time scales. Although some primates and corvids[7–9] take actions now that are based on their future consequences, these have not been shown to be selected with reference to future motivational states[10], or without extensive reinforcement of the anticipatory act[11]. The results described here suggest that the jays can spontaneously plan for tomorrow without reference to their current motivational state, thereby challenging the idea that this is a uniquely human ability.

Evidence from both brain-damaged and healthy humans suggests that two forms of mental time travel, retrospective in the case of episodic memory and prospective in the case of future planning, depend on common neuropsychological processes[1,12–14]. On the basis of the observation that western scrub-jays store and recover food caches in the wild, experimental studies have shown that their ability to recover their caches depends on an episodic-like memory for the caching episode. Specifically, jays remember what food they have cached, where and when it was cached[15], and which other birds observed their caching[16]. These memories are then used flexibly, both to guide their recovery of the food caches and to protect their food caches against being stolen by other birds[17]. To the extent that episodic memory and future planning depend on common processes, the caching behaviour of these birds should reflect an ability to anticipate future need states. To assess this prediction, we investigated whether scrub-jays can plan for a future motivational need, as opposed to a current one. To do so, we gave eight birds experience of two different compartments on alternate mornings for six days. In one compartment they were always given breakfast and in the other they were not. After this training, the jays were unexpectedly given food to eat and cache in the evening. If they were capable of forward thinking, they should have cached more food in the compartment in which they had not been given breakfast and therefore would expect to be hungry the next morning, relative to the compartment in which they had been given breakfast.

Each bird was housed in three adjoining compartments, A, B and C (Fig. 1). These compartments could be divided from each other or left open so that a bird had access to all three spaces. In the 'planning for breakfast' experiment, on training days, having not eaten during the night, each bird was shut in compartment A or C on alternate mornings for two hours with identical substrate-filled caching trays. In one compartment (the 'breakfast' compartment) they received a breakfast of powdered pine nuts, which they could eat but not cache, and in the other they were not given breakfast (the 'no-breakfast' compartment). Throughout the rest of the day they had access to all compartments with food freely available. Two hours before darkness, the caching trays were again placed in compartments A and C and the birds were deprived of food for 90 min. In compartment B, they were then given powdered, non-cacheable pine nuts, which they could eat freely for the 30 min before darkness. During this period the birds continued to have access to all three compartments. After each bird had experienced three 'no-breakfast' training trials and three 'breakfast' training trials, they were tested one evening for their ability to anticipate the future by replacing the powdered food with whole, cacheable pine nuts, thereby giving them for the first time the opportunity to cache in the trays in compartments A and C for the morning, as well as eating the food immediately.

The birds anticipated their hunger the next morning by storing significantly more pine nuts in the caching tray in the 'no-breakfast' compartment (16.3 ± 1.8; mean $\pm$ s.e.m.) than in the 'breakfast' compartment (5.4 ± 1.8; mean $\pm$ s.e.m.) (paired *t*-test with 7 degrees of freedom, $t_7 = 3.01$, $P = 0.02$) .

We considered the possibility that the differential caching was due to a propensity to cache in places associated with hunger. Rats have been shown to eat more in a room previously associated with hunger[18], suggesting that hunger can be conditioned to a particular context. Consequently, a second experiment was devised to contrast a conditioned hunger account with an explanation in terms of future planning. In the 'breakfast choice' experiment, the birds were always given breakfast in the morning but the food that they received differed depending on their location; for example, the jays were always given dog kibble on mornings when they were confined to compartment A (the 'kibble-for-breakfast' compartment) and peanuts on
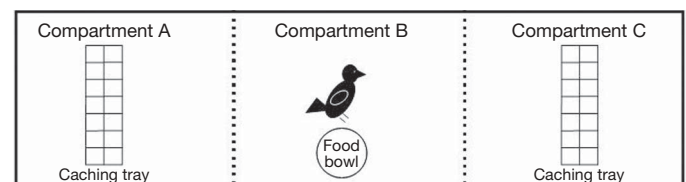
Figure 1 | Compartmental layout used for the 'planning for breakfast' experiment . The position of caching trays is shown in compartments A and C, and of the food bowl in compartment B. Dotted lines represent the compartmental divisions, although during caching no dividers were in place. In the second experiment, the compartmental layout was the same except that two food bowls, equidistant from compartments A and C, were used.

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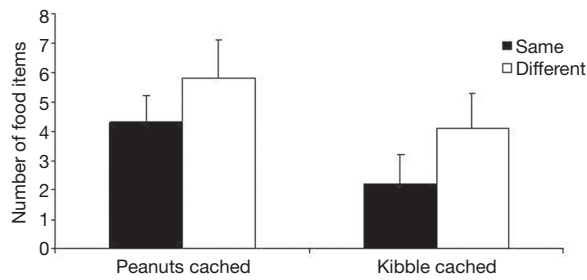
Figure 2 | Mean number of peanuts and kibble cached in the 'breakfast choice' experiment. The scenario in which peanuts were cached in the 'peanuts-for-breakfast' compartment and kibble was cached in the 'kibble-for-breakfast' compartment is denoted as 'same'. The scenario in which peanuts were cached in the 'kibble-for-breakfast' compartment and kibble was cached in the 'peanuts-for-breakfast' compartment is denoted as 'different'. The jays cached significantly more items of the food type that was different to the food that they had previously received for breakfast in that compartment relative to the number of items they cached of the food that was the same as they received for breakfast in that compartment ($F_{(1,8)} = 5.48$; $P = 0.047$). There was no overall difference between the amount of food cached in each compartment ($F < 1$), nor did the jays cache either food type more than the other overall ($F_{(1,8)} = 2.29$, non-significant), ($n = 9$). Error bars, $\pm$ s.e.m.

mornings that they were confined to compartment C (the 'peanuts-for-breakfast' compartment), or vice versa. Apart from this difference, the experimental procedure was identical to the first experiment except that in the evening both foods were offered in powdered form in compartment B. It has been shown that associating a place with a particular food potentiates consumption of that specific food in that location[19] and that caching and eating by scrub-jays are controlled by a common motivational system[20]. Therefore a conditioning account would predict that the jays would cache a particular food in the compartment previously associated with that food. If, however, jays prefer a choice of food at breakfast and are capable of forward planning, they should have preferentially cached the 'different' food rather than the 'same' food in each compartment when offered both foods in cacheable form.

In accord with the future planning account, and contrary to the conditioning account, at test the birds stored significantly more of the 'different' food than the 'same' food in each compartment relative to the amount of that food that they stored in the other compartment. The results and statistics are summarized in Fig. 2.

These results challenge the Bischof-Köhler hypothesis[4] by demonstrating that caching on one day was controlled by the next day's motivational state and available resources. The birds were mildly hungry when given food to cache as this promotes caching, but they ate food at the same time as caching. If they were caching for current hunger, they would have no reason to cache preferentially in one compartment rather than the other, or to cache one food rather than the other in a particular compartment. In the absence of language, there is no knowing whether this reflects episodic future thinking, in which the bird is projecting itself into tomorrow morning's situation, or semantic future thinking, in which the jay takes prospective action, but without personal mental time travel into the future. However, in either case it shows that these birds must have the capability to plan for a future motivational state over a timescale stretching at least into tomorrow. These results, therefore, challenge the assumption that the ability to anticipate and take action for future needs evolved only in the hominid lineage.

METHODS

Subjects and apparatus in the 'planning for breakfast' experiment. Five female and three male adult western scrub-jays were used, all of whom had participated in a suite of experiments on episodic-like memory[17] and prospective cognition[9]. They were housed in pairs in a row of four linked compartments, each measuring 2 m $\times$ 1 m $\times$ 1 m. One of each pair of birds was tested each week, and training

and testing were conducted in three of the compartments (A, B and C in Fig. 1). During an experiment the test subject was periodically confined to one of the compartments, which was divided from the other two by clear plastic dividers so the other two compartments of the housing remained visible. The bird that was not participating was located in the fourth adjoining compartment, separated from the other bird by opaque dividers.

The jays were maintained under artificial light on a 12:12 h light-dark cycle and fed a maintenance diet of shelled peanuts, sunflower seeds, grains, and dog biscuits. During experimental training and tests they were given pine nuts presented in 14.5-cm-diameter plastic bowls. During training the pine nuts were in a non-cacheable powdered form (mixed with some powdered maintenance diet to avoid 'clumping') to ensure that the birds only cached during the experimental test. Birds cached in plastic ice-cube trays (11 cm wide $\times$ 26 cm long), which consisted of an array of 16 cube moulds (4.5 cm $\times$ 3 cm $\times$ 3 cm) filled with corn cob, each of which was a potential cache site. Each tray was attached to a wooden board (15 cm wide $\times$ 30 cm long).

Procedure for the 'planning for breakfast' experiment. Each bird received six training trials followed by one test trial. From 09:00–17:00 each day the birds' maintenance diet was freely available. At 17:00 the test subject was separated from its companion into compartments A, B and C. Maintenance diet was removed for 90 min at 17:00 and caching trays were put in compartments A and C. At 18:30 a bowl containing 10 g of powdered pine nuts, which could be eaten but not cached, was put in the centre of compartment B for 30 min. At 19:00 the bowl of pine nuts and the caching trays were removed. The birds were deprived of food overnight so that they were mildly hungry in the morning. Each morning at 07:00 the experimental bird was confined in either compartment A or C for two hours. The caching trays were returned to both compartments A and C for this period. In one compartment the bird was given no food ('no-breakfast' compartment) and in the other the bird was given powdered pine nuts ('breakfast' compartment). Each bird experienced the two compartments on alternate days, with the compartment that was the 'breakfast' compartment (A or C) counterbalanced across birds. The order in which each bird experienced the two compartments was also counterbalanced. The test day followed exactly the same evening routine as training days with the exception that 30 (cacheable) whole pine nuts were given at 18:30 instead of powdered food. The jays did not get the opportunity to recover their caches on the morning after the test trial.

Subjects and apparatus in the 'breakfast choice' experiment. Two adult jays, one male and one female, were added to those tested in the first experiment. However, one was excluded for failing to approach either caching tray on test, leaving a total of nine birds. The birds' maintenance diet was changed to exclude peanuts and dog kibble, and to include Harrison's high potency fine organic bird food. The experimental set-up was identical to that described for the first experiment in all but one respect. The jays were fed peanuts and dog kibble in two separate bowls during the training and testing, instead of pine nuts.

Procedure for the 'breakfast choice' experiment. The experimental protocol was exactly the same as for the first experiment in all but four respects. On training days at 18:30 two bowls, one containing 10 g of powdered peanuts and one containing 10 g of powdered dog kibble were put in the centre of compartment B, equidistant from compartments A and C for 30 min. In the mornings in one of compartments A or C the birds were given powdered peanuts ('peanut' compartment) and in the other they were given powdered dog kibble ('kibble' compartment). Birds were counterbalanced both with respect to the order in which they experienced each food and with respect to each compartment. Tests followed exactly the same evening routine as on training days with the exception that 15 whole dog kibble and 15 whole peanuts were given at 18:30 instead of powdered food.

Analysis. The caching data in the first experiment were analysed using a paired t-test and in the second experiment using a repeated measures ANOVA. Alpha was set at 0.05. Parametric tests were used because our data conform to the standard assumptions of homogeneity of variance and normality. In the 'planning for breakfast' experiment, $n = 8$, in the 'breakfast choice' experiment, $n = 9$.

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