biology letters

Animal behaviour

Eurasian jays (*Garrulus glandarius*) overcome their current desires to anticipate two distinct future needs and plan for them appropriately

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Western scrub-jays (*Aphelocoma californica*) have been shown to overcome present satiety to cache food they will desire in the future. Here, we show that another corvid, the Eurasian jay (*Garrulus glandarius*), can distinguish between two distinct future desires and plan for each appropriately, despite experiencing a conflicting current motivation. We argue that these data address the criticisms of previous work, and suggest a way in which associative learning processes and future-oriented cognition may combine to allow prospective behaviour.

1. INTRODUCTION

Animals regularly act in the present to secure future benefits; however, much of this future-oriented behaviour is driven by genetic predisposition [1] rather than conscious *awareness* of the future. The 'mental time travel' (MTT) hypothesis [2] states that the ability to 're-experience' the personal past (episodic memory) and 'pre-experience' the personal future (episodic future thinking) is uniquely human. The phenomenology of re- or pre-experiencing an event is usually assessed in humans using verbal description and may be impossible to test for without language. The MTT hypothesis thus risks being unfalsifiable. A further hypothesis, the Bischof-Köhler hypothesis (BKH), states that animals' apparently future-oriented actions are driven only by current needs [2]. The advantage of the BKH is that it yields behavioural predictions for non-verbal subjects: that animals cannot act for a future need that is different from their current one.

A number of studies have claimed to challenge the BKH [3–6]. Arguably, the best-controlled study showed that western scrub-jays cache food that they would want when retrieving their caches, rather than food currently desired [7]. This study made use of a phenomenon known as 'specific satiety', in which an individual sated on one food subsequently has reduced motivation for that food relative to other foods. The

birds were fed to satiety on one food before being given the opportunity to cache that and another food. Later, birds were either fed the same food or a different food before cache-retrieval. By the third trial, those that were fed the same food in both phases (same group) continued caching mostly the non-pre-fed food (the food they wanted at caching), but those that were fed a different food at retrieval (different group) cached a higher proportion of the pre-fed food (the food they wanted at cache-retrieval). One critique [8] argued that, as the different group only showed a decrease in caching the non-pre-fed food rather than an increase in the pre-fed food, they were not responding to their future desires, just learning what not to cache. However, as satiation does not increase desire for a non-pre-fed food, but decreases desire for a pre-fed food, one would not expect an increase in pre-fed food. For example, if I buy a sandwich and a cake for tomorrow's lunch, only to discover that sandwiches are provided, then this will not mean that I will subsequently buy two cakes, merely that I will cease buying sandwiches.

Here, we present an extension of the scrub-jay work [7] with a new species, the Eurasian jay (*Garrulus glandarius*), and a within-subjects design. Jays cached in two locations, one which they could later retrieve from after being pre-fed the same food as at caching, and one which they could later retrieve from after being pre-fed a different food (figure 1a).

2. MATERIAL AND METHODS

(a) Subjects

Four Eurasian jays: Hoy and Ainsley (males), Hunter and Wiggins (females), all aged 2 years, pair-housed in $4 \times 1 \times 1$ m cages which could be divided into two test areas by inserting opaque dividers. Birds were maintained at $21 \pm 1°C$ on a 12 L : 12 D cycle. Birds received a maintenance diet (MD) of kibble, vegetables, fruit and seeds. Water was always available. Subjects cached in Tupperware boxes (17×24 cm) filled with wood chips and individuated by coloured blocks.

(b) Experimental procedure

Two experiments were conducted: 'specific satiety' and 'planning'.

(i) Specific satiety

To use the specific satiety procedure in the planning experiment, it was necessary to first establish specific satiety in Eurasian jays. Subjects were food-deprived and isolated in half of their home cage for 2 h before testing. They were then given 15 min access to a powdered/liquidized version of one of the test foods (food A: peanuts, food B: either suet pellets or raisins depending on birds' preference). This processed food was not cacheable. Subjects were then given a caching tray, 40 items of food A and 40 items of food B and allowed to eat and cache for 15 min, the trays were then removed and the cages cleaned. Trays were inspected for caches out of sight. The number of food items eaten was calculated as the items missing when the bowls, cage and trays had been searched. Trays were then returned allowing cache-retrieval. Finally, birds were reunited with their cage-mate and MD was returned. This procedure was then repeated on a different day such that each bird was pre-fed both foods once.

(ii) Planning experiment

Each bird received three trials of a three-stage procedure (figure 1a). Subjects were food-deprived and isolated for 1 h before each stage. On the first trial ('baseline'), subjects were pre-fed MD before the caching phase such that they would cache according to their general preference. On the two subsequent trials, they were pre-fed on one of the test foods (powdered/liquidized), such that a preference for the non-pre-fed food was established before the caching period. Pre-feeding order across all stages was counterbalanced between birds (figure 1b).

Stage 1: caching. Subjects were pre-fed for 15 min before being given access to two caching trays (trays 1 and 2) placed equidistantly from two bowls each containing 40 food items (foods A and B) and

(a)

(b)

	trial 1 (baseline)			trial 2			trial 3		
	stage 1	stage 2	stage 3	stage 1	stage 2	stage 3	stage 1	stage 2	stage 3
	caching	retrieval 1 (tray 1 available)	retrieval 2 (tray 2 available)	caching	retrieval 1 (tray 1 available)	retrieval 2 (tray 2 available)	caching	retrieval 1 (tray 1 available)	retrieval 2 (tray 2 available)
Hoy	pre-fed MD	pre-fed suet	pre-fed peanuts	pre-fed peanuts	pre-fed suet	pre-fed peanuts	pre-fed peanuts	pre-fed suet	pre-fed peanuts
Hunter	pre-fed MD	pre-fed peanuts	pre-fed suet	pre-fed peanuts	pre-fed peanuts	pre-fed suet	pre-fed peanuts	pre-fed peanuts	pre-fed suet
Wiggins	pre-fed MD	pre-fed peanuts	pre-fed raisins	pre-fed raisins	pre-fed peanuts	pre-fed raisins	pre-fed raisins	pre-fed peanuts	pre-fed raisins
Ainsley	pre-fed MD	pre-fed peanuts	pre-fed raisins	pre-fed peanuts	pre-fed peanuts	pre-fed raisins	pre-fed peanuts	pre-fed peanuts	pre-fed raisins

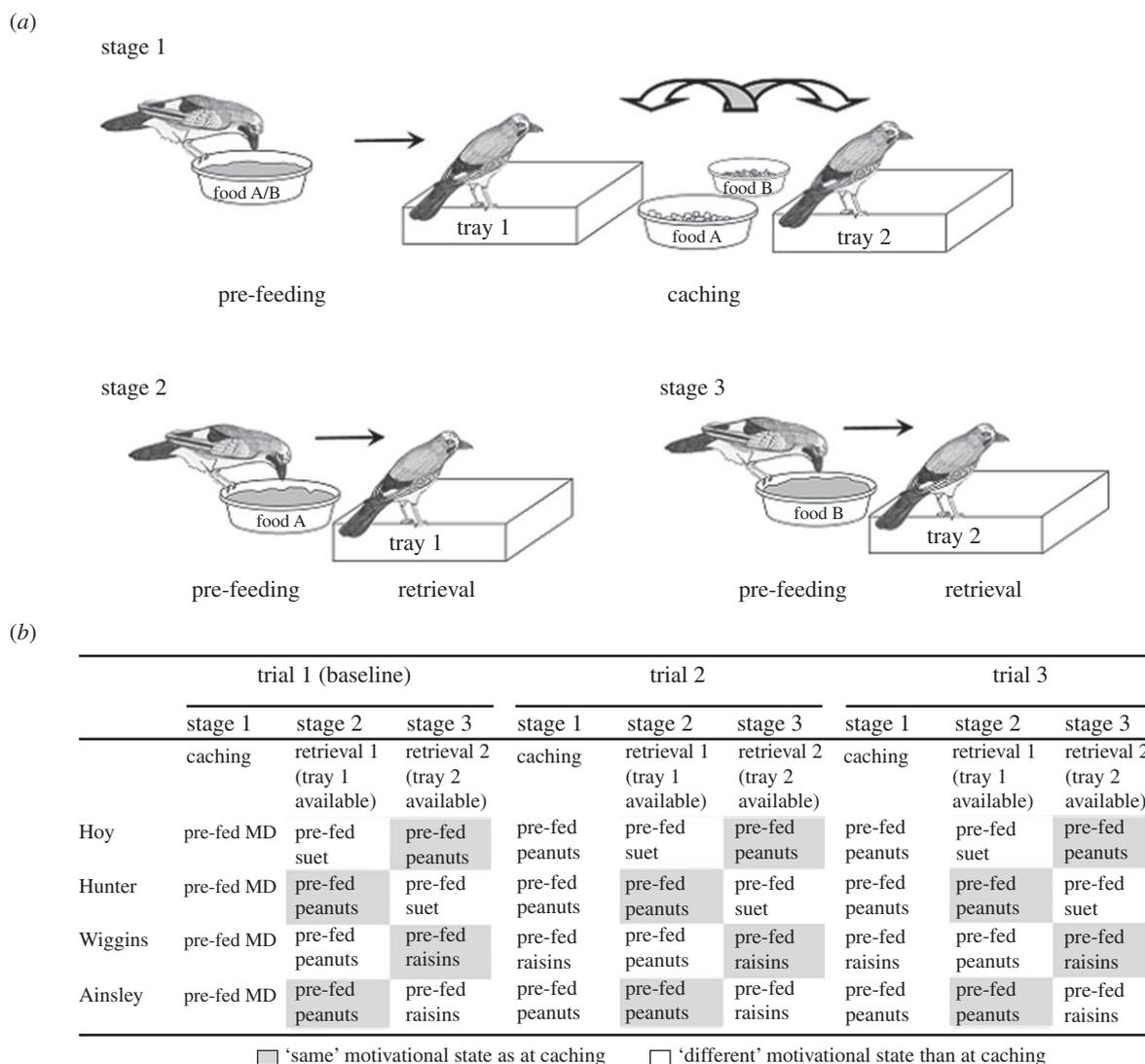☐ 'same' motivational state as at caching   ☐ 'different' motivational state than at caching

Figure 1. (a) Experimental procedure. In stage 1, birds are pre-fed then cache foods A and B in trays 1 and 2. In stage 2, birds are pre-fed one food, then allowed to retrieve from tray 1. In stage 3, birds are pre-fed the other food and allowed to retrieve from tray 2. (b) Experimental timetable, pre-feeding orders and counterbalancing. MD, maintenance diet.

allowed to cache and eat for 15 min. Bowls and trays were then removed, birds reunited and MD returned. Trays were checked for caches out of sight of the birds.

Stage 2: retrieval 1. Food deprivation for stage 2 began 3 h after the end of stage 1. Subjects were pre-fed one of the test foods (powdered/liquidized) for 15 min before caching trays were returned. Retrieval lasted for 15 min during which time tray 2 was blocked by a transparent cover and tray 1 was accessible. Birds were then reunited and MD returned.

Stage 3: retrieval 2. Stage 3 occurred the following day, at the same time of day as stage 2. Stage 3 was the same as stage 2, except that the birds were pre-fed the other test food, and tray 1 was blocked while tray 2 was accessible.

Thus, one of the trays was accessible when the birds were in the same motivational state as at caching (the 'same' tray) and one was accessible when birds were in a different motivational state (the 'different' tray).

(c) *Analysis*

Data were analysed using two-tailed repeated-measures ANOVAs with alpha set at 0.05.

3. RESULTS

(a) *Specific satiety*

Birds showed specific satiety by eating and caching less of the pre-fed food than the non-pre-fed food. There was a significant effect of the food type pre-fed on

the birds' subsequent overall and caching food preferences (repeated-measures ANOVA: overall: $F_{1,3} = 12.4$, $p = 0.039$; caching: $F_{1,3} = 10.45$, $p = 0.048$), whereas eating preferences approached, but did not reach significance ($F_{1,3} = 9.8$, $p = 0.052$). The effect did not differ between eating and caching, suggesting that both behaviours responded similarly to pre-feeding ($F_{1,3} = 0.97$, $p = 0.400$).

(b) *Planning*

Birds cached both foods in equal amounts in both trays in trial 1 but then developed a differential preference between the trays, preferentially caching in each tray the type of food that they would desire when retrieving from it (figure 2b). There was no general preference for one food ($F_{1,3} = 0.66$, $p = 0.480$) or tray ($F_{1,3} = 5.55$, $p = 0.100$), and birds did not reduce caching overall over the experiment ($F_{2,2} = 0.26$, $p = 0.800$). Crucially, there was a significant trial × tray × food interaction ($F_{2,2} = 24.95$, $p = 0.039$) suggesting that birds altered their caching behaviour according to what they would desire at retrieval. Note that there was no tray × food interaction in trial 1 (baseline: $F_{1,3} = 3.0$, $p = 0.180$),
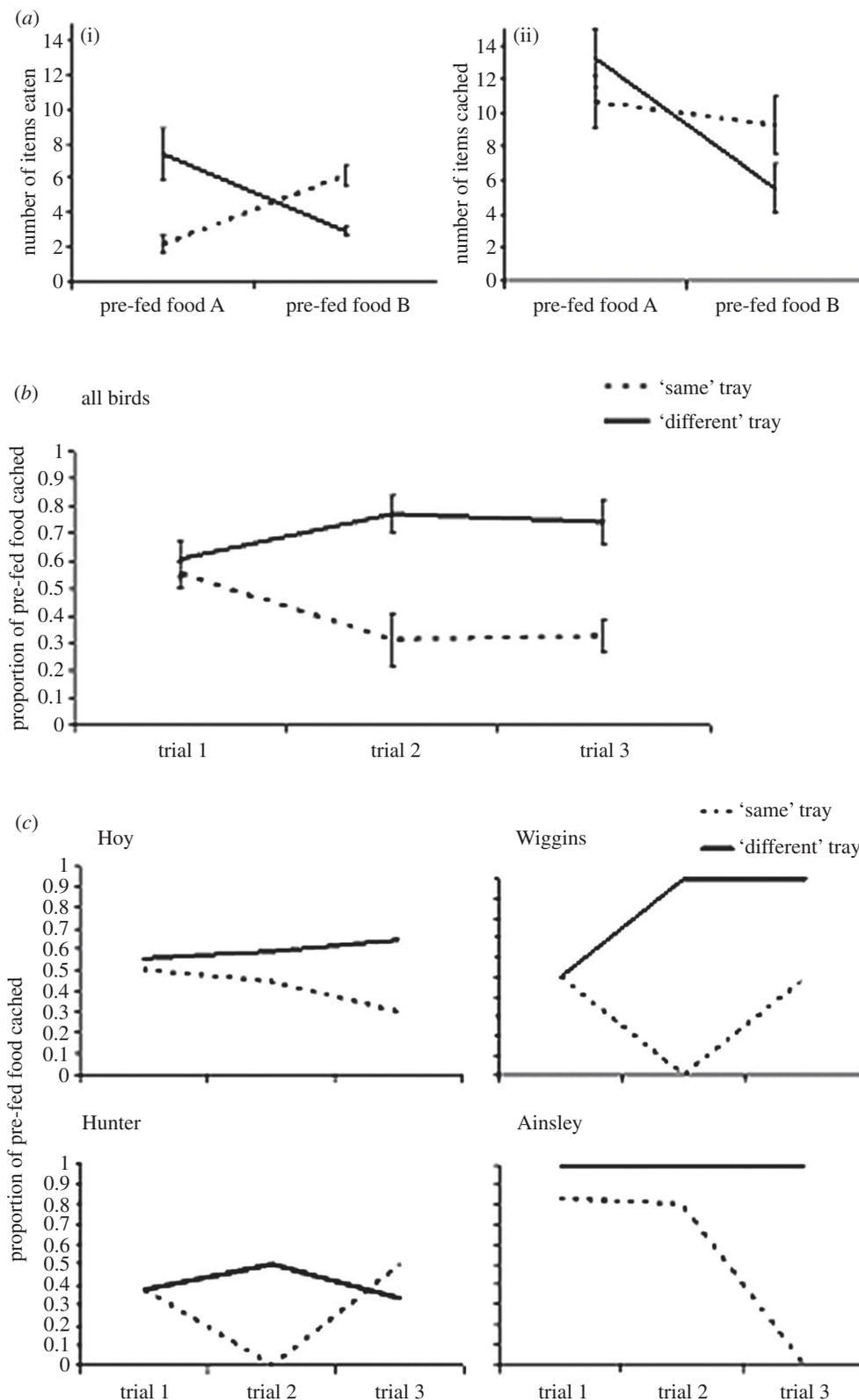
Figure 2. (*a*) Performance in specific satiety experiment: (i) eating; (ii) caching (dashed line, food A; solid line, food B). (*b*) Planning experiment. Proportion of total cached food in each individual tray that was the pre-fed food (dashed line, same tray; solid line, different tray). (*c*) Performance of individual birds in planning experiment (dashed line, same tray; solid line, different tray). Proportion of total cached food in each individual tray that was the pre-fed food.

but such an interaction was present in trial 2 ($F_{1,3} = 14.24$, $p = 0.030$). In trial 3, this interaction was lost ($F_{1,3} = 2.258$, $p = 0.230$), while behaviour in trials 1 and 2 was consistent across birds, the loss of significance may be owing to the behaviour of a single bird (Hunter) whose preference disappeared in trial 3 (figure 2*c*). When

the data were analysed without her, the effect approached significance ($F_{1,3} = 15.429$, $p = 0.059$).

The birds' consumption of foods A and B in stage 1 (caching) of trials 2 and 3 showed a specific satiety effect that approached significance and was comparable with that shown in the specific satiety experiment

($F_{1,3} = 9.64$, $p = 0.053$). Importantly, in contrast to the specific satiety experiment, the birds' caching behaviour differed from their eating behaviour ($F_{1,3} = 19.99$, $p = 0.021$). The birds were thus responding to their current specific satiety in their eating, but not in their caching behaviour (see electronic supplementary material).

4. DISCUSSION

We have demonstrated that Eurasian jays distribute their caches according to their future, rather than current, desires. This within-subjects design addresses many of the criticisms of the original scrub-jay study [7]. Not only are these birds capable of planning for a future desire, but also in planning for two temporally distinct future desires.

Three out of four birds showed a reliable pattern, across both trials 2 and 3, of choosing where to cache each food type according to what they would desire when retrieving caches from those locations. One bird, Hunter, lost this preference on the third trial. It is possible that this bird used a different strategy. Instead of adapting her caching to account for food consumed immediately before cache-retrieval, she may have decided *not to eat* before cache-retrieval. This would be a valid strategy, particularly if she preferred whole to powdered peanuts. Such a strategy cannot be fully investigated here as we lacked sufficiently sensitive weighing equipment to confirm if powdered food had been consumed, but visual observations (of bill-probes, food spillage) indicated that while the other birds had eaten the pre-feeding powder in trial 3, Hunter had not. This warrants investigation in future studies.

The major critique of previous work on scrub-jays [7] was that the jays could have 'learned not to cache items that turned out to be of little value' [8, p. 1]. However, it is not clear by which learning mechanism this could occur [9], or how such a criticism could be extended to the work presented here. In the current study, while it is possible to form an association between outcomes and cache-locations, this association would need to have a sufficiently powerful impact on the bird's motivational state so as to overcome its current desires; this is very difficult even for humans [10].

Humans are able to purposefully construct potential outcomes in their minds, and to make future-oriented decisions based on these constructions. However, it may be that a simpler mechanism could have preceded such an ability. MTT may be uniquely useful in providing a means by which associative learning processes can be recruited in contexts in which they would not normally be effective; to provide, through re-experience, the potential outcome of an action *at the time of the action itself*. Boyer [11] argues that a crucial part of MTT is the re-experience of *emotions* and that often these emotional experiences clash with current goals. Boyer suggests that this clash may represent the function of MTT; to give an action's (temporally distant) consequences emotional salience in the present and act as a counter-motivation against current desires. This process would be entirely outside cognitive control as it would be triggered without deliberate construction. Given that caching birds have been shown to have

semi-independent motivational systems for eating and caching [12], they would be ideally placed to exploit such a mechanism. While Boyer himself does not do so, this theory can be couched in associative learning terminology: MTT may provide a means for temporal contiguity of action and outcome to be artificially increased to allow learning of its potential consequences. A similar account, the 'mnemonic associative theory' [13,14] suggests that, rather than previous outcomes being re-experienced at the time of action, previous actions are re-experienced at the time of the outcome, and that this leads to the formation of an association between action and outcome which drives future behaviour in similar contexts. Thus, 'future-oriented' action is performed in response to previously formed associations rather than from cognitive decision-making in response to a retrieved memory. Fundamentally, both accounts suggest the possibility that when an episodic memory of an event is retrieved at the time of another event, an association can be formed between the two events, and that this may be a mechanism for long-delay associative learning.

We have demonstrated that jays overcome their default motivation to cache currently desired food and instead cache according to future value. Whether jays 'pre-experience' the future remains an open question, but our results provide strong evidence that they can act for a future motivational state that is different from their current one, and do so flexibly (i.e. based on learned contingencies, not 'instincts'). This evidence directly challenges the BKH. However, if Boyer is correct and MTT allows future motivational states to be experienced in the present, then MTT may have developed in some animals *precisely because* the BKH is correct. If an individual can only act on a current motivational state, then the only way for them to be prospective is by *changing* that motivational state, rather than disengaging from it.

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