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Episodic-like memory during cache recovery by scrub jays

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The recollection of past experiences allows us to recall what a particular event was, and where and when it occurred[1,2], a form of memory that is thought to be unique to humans[3]. It is known, however, that food-storing birds remember the spatial location[4–6] and contents[6–9] of their caches. Furthermore, food-storing animals adapt their caching and recovery strategies to the perishability of food stores[10–13], which suggests that they are sensitive to temporal factors. Here we show that scrub jays (*Aphelocoma coerulescens*) remember 'when' food items are stored by allowing them to recover perishable 'wax worms' (wax-moth larvae) and non-perishable peanuts which they had previously cached in

visuospatially distinct sites. Jays searched preferentially for fresh wax worms, their favoured food, when allowed to recover them shortly after caching. However, they rapidly learned to avoid searching for worms after a longer interval during which the worms had decayed. The recovery preference of jays demonstrates memory of where and when particular food items were cached, thereby fulfilling the behavioural criteria for episodic-like memory in non-human animals.

Scrub jays in the Degrade group were given a series of pretraining trials (see Methods) in which they learned that worms degrade and become unpalatable over time; they therefore learned to avoid recovering these items when a relatively long time (124 h) had elapsed between caching and recovery. The birds then received a further pair of training trials in which they were required to cache peanuts in one side of a distinctive, sand-filled storage tray during one caching phase, and wax worms in the opposite side during the other caching phase (Fig. 1). Different, novel trays were used on every trial throughout the experiment so that the cache sites were trial-unique. The two caching phases were separated by 120 h, and birds were subsequently allowed to recover items from both sides of the caching tray 4 h after the second caching phase. The 4-h and 124-h trial designations refer to the length of the time that elapsed between caching and recovering the wax worms: on the 124-h trial, the birds first stored wax worms 124 h before cache recovery and cached peanuts in the other side of the tray 4 h before recovery; whereas on the 4-h trial, birds cached the wax worms 4 h before recovery, having previously stored peanuts 124 h prior to recovery. As the wax worms were still fresh at recovery on the 4-h trial, and as the fresh worms are their preferred food, the birds directed more of their recovery inspections to the worm side of the storage tray on this trial. By contrast, most of their recovery inspections were directed to the peanut side of the tray on the 124-h trial when the worms were in a decayed state.

During both pretraining and training trials, birds could use the sight and smell of their caches as cues about where to search during cache recovery. To test whether or not jays could remember if it was the worms or the peanuts that had been cached, and where and when they had been cached, each bird received a pair of test trials that differed from the previous pair of training trials in that all food items were removed before the recovery phase of each test trial and fresh sand was placed in the tray. This procedure ensured that the birds had to rely on memory during cache recovery, because olfactory and visual cues about the contents of caches were no longer available to the bird. If jays can remember when and where they stored the two types of food, they should show a preference for
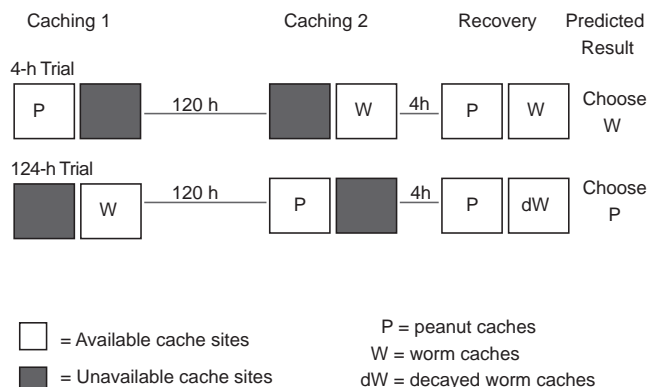

Figure 1 Conditions and contents of the caching tray on different phases of 4-h and 124-h training and trials. The trial designation refers to the length of the time that elapsed between caching and recovering the wax worms. During the caching phases, birds were prevented from storing food items in the shaded halves of the tray by a cover, but they were free to cache in the open, non-shaded halves.

sites at which the worms had recently been cached on the 4-h trial because they should expect the favoured wax worms still to be fresh. We assessed this preference by recording the sites that the birds inspected by probing the sand substrate with their bills. This preference should be reversed on the 124-h trial if the birds can also recall that the wax worms had been cached a relatively long time ago and therefore would have decayed and become unpalatable.

The results of the test trials fulfilled both predictions. Eighty per cent of birds in the Degrade group directed their first inspection to
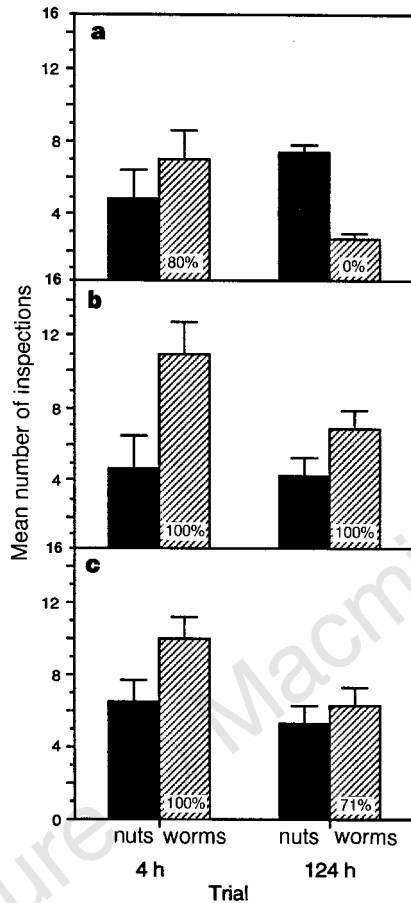

Figure 2 Mean number of inspections directed to the peanut and worm sides of the storage trays (error bars represent mean standard error for these contrasts) during the recovery phase of 4-h and 124-h test trials. All birds inspected the worm side more than the peanut side on the 4-h trial ($F_{1,14} = 9.76, P < 0.01$), a preference that does not differ between the groups ($F_{2,14} = 0.90, P > 0.25$). By contrast, there is a significant interaction between group and side for the number of inspections on the 124-h trial ($F_{2,14} = 9.59, P < 0.01$), and the Degrade group (**a**) inspected the peanut side more than worm side ($F_{1,14} = 12.79, P < 0.01$), whereas the Replenish group (**b**) inspected the worm side more than the peanut side ($F_{1,14} = 4.74$, $P < 0.05$). Birds in the Pilfer group (**c**) showed no significant preference ($F_{1,14} = 0.66, P > 0.25$). The groups also differ in the number of inspections to the worm side of the storage tray ($F_{2,14} = 6.26, P < 0.05$) but not to the peanut side ($F_{2,14} = 1.34, P > 0.25$). A post-hoc Newman–Keuls test reveals that the Degrade group made fewer inspections to the worm side than the other two groups ($P < 0.05$), which did not differ ($P > 0.05$). Also shown is the percentage of birds in each group that made their first inspections to the worm side of the storage tray. There is no difference between the groups in the distribution of first inspections on the 4-h trial ($\chi^2_2 = 2.55, P > 0.20$) and, overall, more first inspections were directed to the worm side than the peanut side (binomial test: $P < 0.01$). The groups differ, however, in their distribution of first inspections on the 124-h trial ($\chi^2_2 = 11.50, P < 0.01$), and one-tail binomial tests reveal that more first inspections were directed at the peanut side by the Degrade group and to the worm side by the Replenish group ($P < 0.05$ in both cases), whereas the Pilfer group showed no significant bias to either side of the caching tray ($P > 0.30$).

the worm side of the caching tray on the 4-h trial, whereas all birds inspected the peanut side first on the 124-h trial (Fig. 2a). A similar pattern was seen for the total number of inspections during cache recovery, with most inspections being directed to the worm side on the 4-h trial but to the peanut side on the 124-h trial (Fig. 2a). This cache recovery pattern suggests that the birds remembered not only where the worms were stored, but also information about the relative time between caching and recovery, in the sense that they searched preferentially in the worm side of the tray when the worms had been cached 4 h previously, but preferred to search in the peanut side when the worms have been cached 124 h before the recovery test.

To check that the preference for peanut caches on the 124-h trial was not due to more rapid forgetting of worm versus peanut caches, we compared the performance of birds in the Degrade group to that of a second, Replenish group. Birds in the Replenish group received the same training as those in the Degrade group except that the stored wax worms were removed immediately after the caching phase and replacing by fresh ones just before the cache recovery phase. Thus, birds in the Replenish group never had the opportunity to learn that worms decay over time. In contrast to the recovery pattern shown by the Degrade group (Fig. 2a), all birds in the Replenish group directed their first inspection to the worm side of the caching tray on both the 4-h and the 124-h test trial (Fig. 2b). Although the total number of inspections to the worm side was reduced on the 124-h trial relative to the 4-h trial, the Replenish group inspected the worm side more frequently than the peanut side during cache recovery on both trials (Fig. 2b), thereby demonstrating that the peanut-side preference shown by the Degrade group on the 124-h trial was not simply due to differential forgetting of worm caches.

We also investigated another ecologically inspired procedure for training the birds to encode and retrieve temporal information about caching. This procedure capitalized on the fact that, in the wild, increasing the time between storage and recovery enhances the likelihood that the caches will be pilfered (stolen) by another animal. In response to pilfering, birds adjust both the locations in which they search for caches and those in which they store food subsequently[14–17]. To teach our birds that the likelihood that the worm caches would be pilfered increased with time since caching, we trained the Pilfer group on a similar procedure to the Degrade group, but in this case the wax worms were removed from the storage tray on the 124-h training trial so that the Pilfer group could recovery only peanut caches. In common with birds in the Replenish and Degrade group, however, birds in the Pilfer group could recover both peanut and worm caches on the 4-h training trial.

During cache recovery on the 4-h test trial, birds in the Pilfer group showed the same preference for the worm sites as the other groups as they all made their first inspection to the worm side (Fig. 2c), a bias that was also expressed in the total number of inspections made to worm and peanut sides (Fig. 2c). The critical results, however, are those for the 124-h test trial. If scrub jays can learn that the probability that caches will be pilfered increases with time that has elapsed between caching and recovery by remembering relatively how long ago they stored the wax worms, then their preference for inspecting the worm sites should be reduced on the 124-h trial relative to that shown by the Replenish group. This prediction was upheld: in contrast to the Replenish group, 29% of the birds in the Pilfer group made their first inspection to the peanut side on the 124-h trial (Fig. 2c), and there was no significant difference in the total number of inspections directed to the two sides of the storage tray (Fig. 2c).

In conclusion, the switch in preference from the worm side on the 4-h trial to the peanut side on the 124-h trial shown by birds in the Degrade group, and to a lesser extent by the Pilfer group, can only be explained by recall of three types of information: (1) 'what' items (peanuts and worms) were cached: (2) 'where' each type of

item was stored (left or right sides); and (3) 'when' (4 h or 124 h ago) the worms were cached. Current theories of human episodic memory refer to autonoetic consciousness[3]—the conscious experience of self—that accompanies episodic recall but, as this state has no obvious manifestation in non-linguistic behaviour[3] it is probably undetectable in many species. In terms of purely behavioural criteria, however, the cache recovery pattern of scrub jays fulfils the three, 'what', 'where' and 'when' criteria for episodic recall and thus provides, to our knowledge, the first conclusive behavioural evidence of episodic-like memory in animals other than humans.   □

Methods

Subjects. Adult, hand-raised scrub jays, which were allocated randomly to the Degrade ($n = 8$), Replenish ($n = 8$) and Pilfer ($n = 7$) groups, were maintained under the same conditions as in the previous studies in which they had participated[8,18]. Six birds (Degrade, $n = 3$; Replenish, $n = 1$; Pilfer, $n = 1$) that failed to store at least one item of both food types during the test trials were omitted from the analysis.

Training and testing. The birds were deprived of their maintenance diet for 4 h before each caching phase of the 4-h and 124-h trials (Fig. 1), and during the 4-h retention interval between the second caching phase and recovery. At the start of each caching phase, a storage tray was placed in the bird's home cage together with a bowl of 50 shelled peanuts or wax worms for 15 min. To provide a storage site that was unique and discriminable on every trial for each bird, the storage tray used on a particular trial was drawn from a large set of sand-filled plastic ice-cube trays (2×7 array of 2.5-cm cube molds), each rendered visuospatially distinct by a surrounding structure of Lego bricks[8]. Access to one side of the storage tray during the first caching phase and the other side during the second caching phase was prevented by a clear Perspex cover. At the end of each caching phase, the number and location of caches were recorded before the food items were removed from the tray. Before each 15-min recovery phase, peanuts were placed in the same ice-cube molds in which they had been cached on the training trials. On 4-h training trials, wax worms were also returned to their original cache locations. On 124-h training trials, decayed worms were placed in those sites for birds for the Replenish group. The worm sites remained empty for the Pilfer group. Furthermore, before all recovery phases the sand substrate was replaced to remove any local visual cues about the location of caches. The procedure was the same on the test trials, except that none of the caches was returned to the storage tray before the recovery phase. The order of the 4-h and 124-h training and test trials was counterbalanced across birds within each group, as was the side of the storage tray in which peanuts and worms were cached. To minimize observer bias, different observers recorded the behaviour during the caching and recovery phases so that the observer during the recovery phase was unaware of the treatment received during caching.

Pretraining. Before the training and test trials, all birds received at least four pairs of pretraining trials. The procedure during pretraining trials differed from that during training trials in three respects. (1) On pretraining trials, peanuts and worms were cached in separate, visuospatially distinct, trial-unique storage trays. Thus during cache recovery, birds were presented with a choice between the two trays on pretraining trials. (2) The second caching phase of a pretraining trial followed immediately after the first one. (3) The cache recovery phase occurred 4 h after the second caching phase on one trial of each pair of pretraining trials and 124 h later on the other pretraining trial. The order in which peanuts and worms were cached was counterbalanced within groups, as was the order of the 4-h and 124-h trials within each pair of pretraining trials.

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Primary motor cortex is involved in bimanual coordination

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Many voluntary movements involve coordination between the limbs[1,2]. However, there have been very few attempts to study the neuronal mechanisms that mediate this coordination. Here we have studied the activity of cortical neurons while monkeys performed tasks that required coordination between the two arms. We found that most neurons in the primary motor cortex (MI) show activity specific to bimanual movements (bimanual-related activity), which is strikingly different from the activity of the same neurons during unimanual movements. Moreover, units in the supplementary motor area (SMA; the area of cortex most often associated with bimanual coordination[3]) showed no more bimanual-related activity than units in MI. Our results challenge the classic view that MI controls the contralateral (opposite) side of the body and that SMA is responsible for the coordination of the arms. Rather, our data suggest that both cortical areas share the control of bilateral coordination.

Common experience and psychophysical studies indicate that the limbs coordinate automatically, and that requirements altering this natural coordination increase task difficulty[1,2,4]. Anatomical, behavioural and electrophysiological evidence indicate that SMA is an important contributor to bimanual coordination[5–9]. However, there are reports of only transient disturbance in interlimb coordination with SMA lesions, suggesting that SMA is not solely responsible for bimanual coordination[4].

We reinvestigated the roles of MI and SMA in bimanual coordination. Monkeys operated two X–Y manipulanda, one with each arm, which moved cursors on a video screen (see Methods and Fig. 1). In bimanual trials the two arms started to move together quite accurately, with an average inter-arm interval (IAI) of 16 ms (s.d. 74 ms) for monkey F and 21 ms (s.d. 56 ms) for monkey G, and