

Eurasian jays (*Garrulus glandarius*) show episodic-like memory through the incidental encoding of information

James R. Davies¹, Elias Garcia-Pelegrin², and Nicola S. Clayton¹

¹Department of Psychology, University of Cambridge, Cambridge, CB2 3EB, UK

²Department of Psychology, National University of Singapore, Singapore, 117572

ORCID JRD, 0000-0002-3956-0465; EGP, 0000-0003-0024-9861; NSC, 0000-0003-1835-423X

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Abstract

Episodic memory describes the conscious reimagining of our memories and is often considered to be a uniquely human ability. As these phenomenological components are embedded within its definition, major issues arise when investigating the presence of episodic memory in non-human animals. Importantly, however, when we as humans recall a specific experience, we may remember details from that experience that were inconsequential to our needs, thoughts, or desires at that time. This ‘incidental’ information is nevertheless encoded automatically as part of the memory and is subsequently recalled within a holistic representation of the event. The incidental encoding and unexpected question paradigm represents this characteristic feature of human episodic memory and can be employed to investigate memory recall in non-human animals. However, without evidence for the associated phenomenology during recall, this type of memory is termed ‘episodic-like memory’. Using this approach, we tested seven Eurasian jays (*Garrulus glandarius*) on their ability to use incidental visual information (associated with observed experimenter made ‘caches’) to solve an unexpected memory test. The birds performed above chance levels, suggesting that Eurasian jays can encode, retain, recall, and access incidental visual information within a remembered event, which is an ability indicative of episodic memory in humans.

Introduction

The ability to journey through one’s own subjective time, traveling backwards to remembered events as well as forwards to possible future events, is referred to as mental time travel. When looking backwards and consciously reconstructing personally experienced events, we engage in the form of memory known as episodic memory [1-3]. As such, recalling the past is often differentiated between ‘knowing’ vs ‘remembering’ [1], with episodic memory representing the latter. In contrast, *semantic* memory concerns the recall of factual information with no associated conscious experience, and so can be thought of as simply ‘knowing’. Together, episodic memory and semantic memory make up the declarative, or explicit, memory system which concerns the encoding and storage of long-term memories that can be actively accessed [1, 2].

As the major distinction between semantic and episodic memory is that episodic memory involves a conscious experience during recall, its characteristic phenomenology is intrinsic within its definition [3-5]. This results in major issues when investigating the presence of episodic memory in non-human animals, as evidence for conscious episodic recall in humans is centred around language-based reports and there are currently no agreed upon non-linguistic behavioural markers of consciousness [6]. Whilst many psychologists believe episodic memory (and thus mental time travel) to be a uniquely human ability [3, 7-10], arguing

54 that although animals have a complex semantic knowledge of their environment they cannot
55 consciously recall and re-experience past events as we can [8], it is theoretically impossible
56 to establish if non-humans have episodic memory using this definition. Consequently,
57 researchers have instead focused on behavioural paradigms that represent the characteristics
58 of human episodic memory in non-human animals [11-23]. However, in the absence of
59 evidence for a subjective conscious experience during recall, this type of memory is termed
60 'episodic-like memory' [11].

61 In pioneering research on episodic-like memory, Clayton and colleagues [11-13, 25, 26]
62 conducted a sequence of important experiments with scrub-jays (*Aphelocoma sp.*). As these
63 jays cache long-lasting foods (e.g., nuts) and quickly perishing foods (e.g., insect larvae) for
64 future consumption, it is argued that episodic-like memory has evolved in these birds to
65 facilitate the remembering of the contents, location, and timing of their caches, and therefore
66 the ability to recover these foods before they become inedible [27]. By exploiting this natural
67 phenomenon, these studies demonstrate that jays, when recovering trial-unique caches after
68 varying time intervals, are recalling integrated representations of the 'what' (food type), 'where'
69 (cache location), and 'when' (time of caching relative to retrieval) information and use these
70 memories flexibly to dictate behaviour. Since these seminal studies, other researchers have
71 used the 'what-where-when' paradigm to test species across taxa, including rodents [28-32],
72 great apes [33], other corvids [14], parids [34], and cuttlefish [35].

73 However, it has been suggested that subjects in these experiments could have been
74 successful through the use of non-episodic mechanisms, and thus without necessarily
75 recalling the encoding event in an episodic-like manner [15-19, 23, 36]. As this paradigm
76 requires repeated training to learn the experimental rules (such as the degradation rates of
77 certain foods), the animals may learn to expect an upcoming memory test after the
78 presentation of the encoding situation. Therefore, they may learn that some specific
79 information within the presented event is required to use in the expected upcoming memory
80 test. Subsequently, the animal may be able to retain and carry forward a memory trace
81 representing this information in order to use later in the anticipated memory assessment,
82 without actually remembering back to the original event *upon* presentation of this memory test
83 (as is required for an episodic-like memory account) [37].

84 An alternative paradigm used to test episodic-like memory in non-human animals, and
85 arguably the most convincing [37, 38], is the incidental encoding and unexpected question
86 paradigm [15]. The rationale behind this paradigm is that when we, as humans, engage in
87 episodic memory and recall a specific experience, we may remember details from that event
88 that were inconsequential to our needs, thoughts, or desires at that time. This trivial, or
89 'incidental', information is nevertheless encoded automatically as part of the memory [39] and
90 is subsequently recalled as part of a holistic representation of the event. For example, we may
91 recall incidental visual information when remembering a visit to the supermarket the day
92 before, such as the colour of the cashier's t-shirt or the pattern on the countertop. This
93 paradigm thus aims to behaviourally represent the incidental encoding characteristic of human
94 episodic memory, by 'unexpectedly' asking subjects to recall incidental information about a
95 specific event. As these tests are unexpected to the subjects, they do not learn that any
96 specific information within an encoding trial will later become relevant for an upcoming memory
97 test. If subjects are able to use information, that was irrelevant to solving an encoding trial to
98 obtain success in a subsequent memory test, this demonstrates that they are able to encode,
99 recall and access incidental information within a remembered event, which is a capability
100 characteristic of episodic memory in humans [23]. Researchers have used the incidental
101 encoding and unexpected question paradigm to investigate episodic-like memory in various
102 non-human taxa [15-23].

103 Whilst episodic-like memory has been extensively studied in a few corvid species using
104 the what-where-when memory paradigm [11-14, 25, 26], to our knowledge no researchers
105 have assessed their abilities using the incidental encoding and unexpected question
106 paradigm. Consequently, we tested Eurasian jays (*Garrulus glandarius*), a member of the
107 Corvidae family and relative of the scrub-jay, on their ability to use incidentally encoded
108 information in an unexpected memory task. Like scrub-jays, Eurasian jays habitually cache

109 both perishable and non-perishable foods for later consumption and depend heavily on these
110 caches to sustain them through periods of low food availability [40]. Furthermore, they show
111 evidence for complex cognitive abilities, such as object permanence [41], observational spatial
112 memory [42], and some evidence for the flexible deployment of various cache-protection
113 strategies [43-45] (although these findings were not replicated in later work [46]). Most
114 importantly, however, Eurasian jays have also shown evidence for planning for the future, by
115 overcoming their current desires in order to plan for anticipated future needs [47]. As, in
116 humans, episodic memory is thought to provide the basis from which future orientated
117 thoughts and predictions can be made [48-50], we predicted that Eurasian jays would be able
118 to encode incidental information related to an event, and then subsequently recall this
119 information in order to solve an unexpected memory task.

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122 **Methods**

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124 **Subjects and housing**

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126 Seven Eurasian jays (3 females, 4 males) participated in this study. The sample was made up
127 of all birds that were available and motivated for testing. All the jays were hand-reared in 2015
128 and were socially housed within a large outdoor aviary (approximately 20m long × 10m wide
129 × 3m high) at the Sub-Department of Animal Behaviour, University of Cambridge,
130 Cambridgeshire, UK. The aviary was divided at one end into smaller sections (approximately
131 6 × 2 × 3m) which connected to indoor testing compartments (each 2 x 1 x 2m). The jays were
132 fed a maintenance diet of soaked cat food biscuits, eggs, vegetables, seeds, and fresh fruit
133 and had *ad libitum* access to water (including during testing). To increase their motivation to
134 participate in experiments, the jays' maintenance diet was removed from the aviary 1-hour
135 before testing. Subjects participated on a voluntary basis (maximising motivation) and were
136 individually separated once they entered the testing compartments. The experimenter
137 interacted with the jays via an open window adjacent to the indoor compartments.

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139 **Procedures**

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141 The experiments were reviewed and approved by the University of Cambridge Animal Welfare
142 Ethical Review Body and were conducted under a non-regulated procedure license
143 (NR2021/49). All procedures were non-invasive, purely behavioural and did not require
144 anaesthesia or euthanasia of any subjects. The jays had previous training using cups in
145 previous studies (e.g., [51]). The cups in this study, and other unpublished studies, were
146 always identical and plain red with no other salient and distinctive visual features, as the cups
147 in these experiments simply represented spatial locations that food could be hidden under.
148 Therefore, the jays had no experience with being trained to attend to any visual features
149 (unique or not) on the cups before the onset of this experiment. To confirm their ability to locate
150 food hidden under the cups, a spatial memory training phase was conducted. In this phase,
151 the testing compartment was set up with a platform next to the experimenter window, with a
152 perch placed at the centre. Four identical cups, equally spaced, were arranged in front the
153 perch, parallel to the experimenter window (Fig 1A). The bird entered the compartment and
154 was separated from the rest of the aviary; now only having access to the test compartment
155 and an adjacent closed outside section of the aviary. Whilst remaining on the perch and facing
156 the experimenter, the jays observed as the experimenter turned one of the cups over, placed
157 a mealworm inside, then returned it to its original position (Fig 1A). The birds then made a
158 choice by pulling on a string attached to the top of the cup (S1 Fig) to reveal its contents (Fig
159 1B). Once a choice was made the trial ended, and the bird was encouraged to return to the
160 perch before the procedure was repeated for a subsequent trial. After baiting a cup, the
161 experimenter orientated their head and eyes directly forward and kept their arms by their side

162 in order to limit the possibility of accidental cues directing the bird's choice. The position of the
 163 baited cup was pseudorandomised, in that no single cup contained the mealworm more than
 164 twice in a row. All birds reached training criterion (8/10 successful trials) in a single session of
 165 10 trials.
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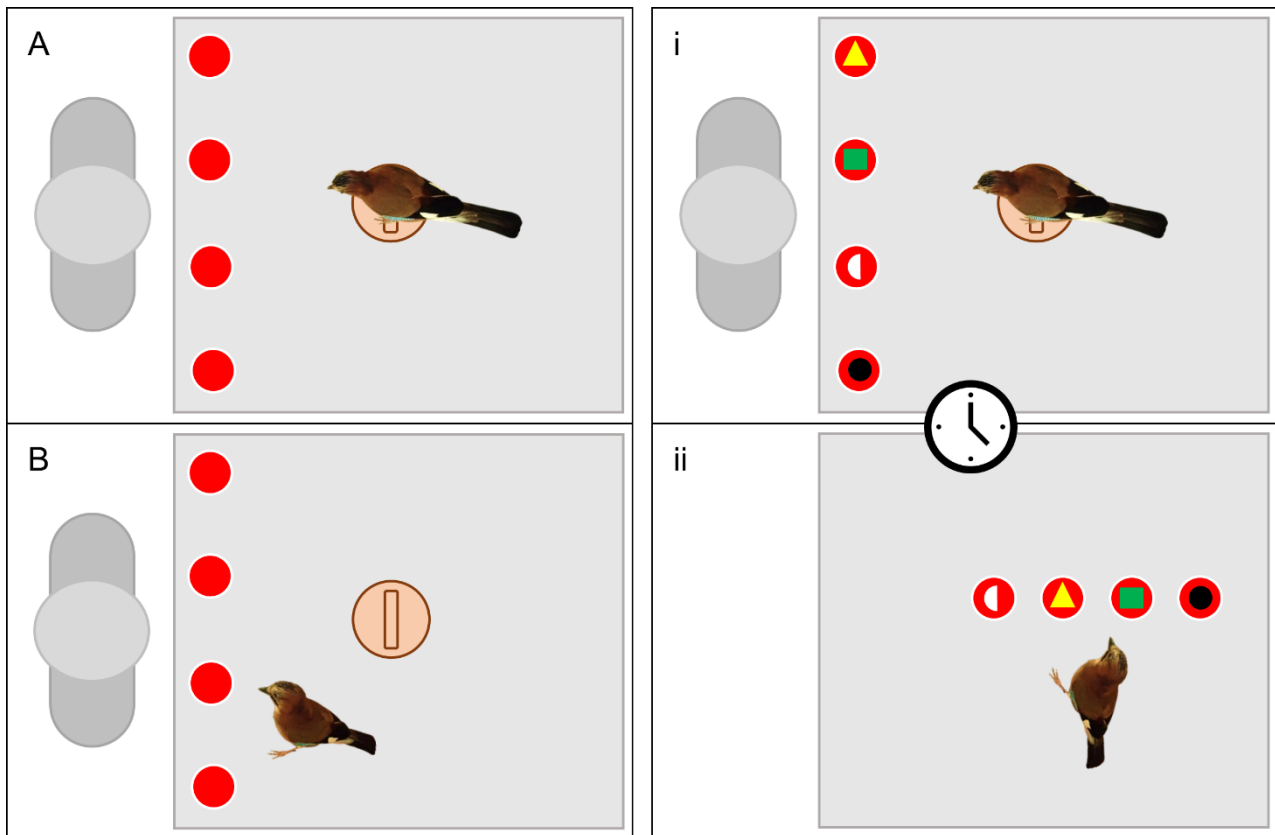


Fig 1. Depiction of the training procedure (A/B) and the experimental stages: i) the encoding phase, ii) the memory phase.

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 168 The set up and procedure of the test phase was almost identical to the training phase,
 169 except for the cups used and the addition of an unexpected delayed long-term memory
 170 assessment. Instead of identical cups, the cups used in test trials each possessed a unique
 171 visual marker as part of an array of different visual elements: either a) coloured card around
 172 the string attached to the top of the cup (S1A Fig); b) a laminated coloured shape attached to
 173 the front of the cup (S1B Fig); or c) a laminated coloured and/or patterned card underneath
 174 the cup (S1C Fig). These visual characteristics were not present during training, and thus did
 175 not represent relevant information associated with solving the original trained task. Each bird
 176 received a single trial per trial type (string, shape, or card), each on different days separated
 177 by at least 24 hours. The order of trials each bird received was pseudorandomised (so that
 178 the position of each trial type in the sequence was counterbalanced across individuals) and
 179 unique (except Stuka and Booster; S1 Table). One bird, Sojka, failed to make a choice in her
 180 string trial within 15 minutes after entering the test compartment and so was excluded from
 181 this trial type. Immediately before each test trial, a minimum of 5 and a maximum of 10 trials
 182 (identical to the training procedure but with the test cups) were conducted to ensure the jays
 183 were still performing accurately with spatial memory and not failing due to other factors
 184 unrelated to the study (e.g., fear, lack of motivation, etc.). As no cup was baited more than the
 185 others, and the bird had immediate access to recover the reward underneath the cup, the
 186 visual characteristics of the cups were again not relevant to solve the task at this stage. As

187 with the training phase, the only information necessary to solve this task was spatial
188 information, meaning the birds only had to use short-term spatial working memory to be
189 successful. Once an individual reached 5 consecutive correct re-training trials, a single test
190 trial was conducted. The first stage of this trial (Fig 1i) was identical to the training procedure,
191 except that 5 mealworms were used to bait the cup (to increase the saliency of the caching
192 event) and the bird was prevented from reaching the cups to prematurely make a choice (a
193 plastic bar was placed over the cups). Once the cup was baited, the bird was removed from
194 the testing compartment (into the outdoor section) and was left alone for 10 minutes without
195 visual access to the cups or the testing compartment. Concurrently, the experimenter moved
196 the cups into a new, distinct location (perpendicular to the test window) and positioned them
197 at random (Fig 1ii). The mealworms were removed from under the cups to control for any
198 visual, auditory, or olfactory cues, thus forcing the birds to rely on memory alone in the
199 succeeding test. Once 10 minutes passed, the bird was brought back into the test
200 compartment and allowed to make a choice. The compartment doors were set up so that the
201 birds faced the cups from the front, and thus were roughly at an equal distance from the jay
202 upon their presentation.

203 As the visual markers were present on the cups during the re-training trials before each
204 test trial, the birds could potentially use two different strategies to solve this task: 1) rely on
205 the spatial information, or 2) rely on the visual information (or a combination of both strategies).
206 Whilst the birds were exclusively trained to use spatial information to solve the training task,
207 although unlikely, the use of the second strategy cannot be ruled out using this methodology
208 alone. Therefore, an additional control task was conducted to determine whether the birds
209 prioritised spatial information over visual and whether they would learn to use visual
210 information when spatial information was no longer relevant, across the same number of trials
211 as the retraining minimum ($n = 5$). This task was identical to the re-training trials, except that
212 before the bird was allowed to make a choice, the cups were quickly rearranged out of sight
213 (behind a visual occluder). This way, the original spatial cues were still present (i.e., there was
214 a cup in the same location as before) but now the use of the first strategy would lead to failure.
215 The position of each cup after rearranging was pseudorandomised so that the baited cup was
216 never in the same spatial position as it was previously. Crucially, if the jay chose the cup with
217 the same visual marker (rather than in the same position), they received the reward
218 underneath it, thus allowing them the opportunity to learn to solve the task using visual
219 information. Each of the 7 jays performed this task following the main testing period, and the
220 visual markers used (trial type) were counterbalanced across subjects (with an extra session
221 of 'shape').
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223 Analysis

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225 All analysis was conducted using RStudio [52]. We conducted binomial generalised linear
226 mixed models (GLMMs) to investigate whether the jays chose the correct cup above chance
227 levels (0.25), with 'individual' as a random effect, for both the main and control test data. To
228 test against the null value of 0.25, we included an offset model (the logit transform of the null
229 value) as a fixed effect. An additional binomial generalised linear model (GLM) was run to
230 assess if the experimental factors had an effect on the birds' performance in the main test,
231 with 'condition' (string, shape, or card) and 'trial number' (the position in the test sequence,
232 i.e., 1, 2 or 3) as fixed effects, including an interaction between these effects. To check our
233 models' assumptions, we used the DHARMA package [53]. The models did not fail to converge
234 and model assumption checks showed no deviation from expected distributions.
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Results and Discussion

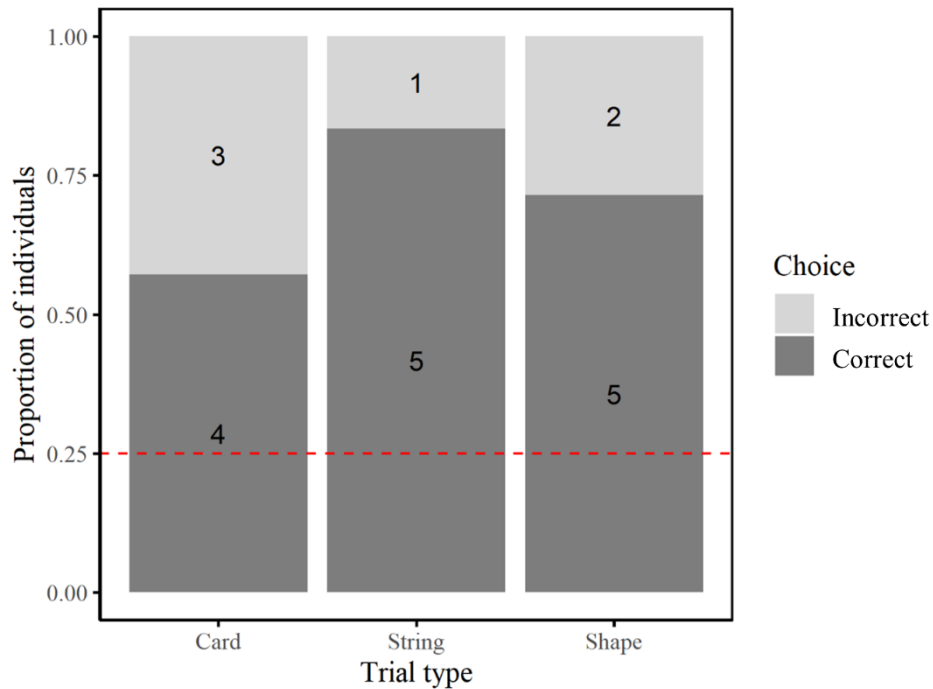


Fig 2. Proportion of individuals (y-axis) and frequency of individuals (inside bars) that made correct or incorrect choices, across trial types. Red line shows performance expected by chance.

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240 The jays chose the correct cup above chance levels in the main test (binomial GLMM, $p <$
 241 0.001 ; Fig 2) and there was no significant effect of condition (binomial GLM, $F_{2,14} = 0.334$, $p =$
 242 0.721 ; Fig 2) or trial number (binomial GLM, $F_{1,14} = 0.476$, $p = 0.501$) on performance, and no
 243 significant interaction between these two factors (binomial GLM, $F_{2,14} = 0.088$, $p = 0.916$). In
 244 the control test, the still jays chose the correct cup above chance levels according to spatial
 245 information, (binomial GLMM, $p < 0.001$; S2 Table), but not according to visual information
 246 (binomial GLMM, $p = 0.151$; S2 Table). As the jays showed a success rate significantly above
 247 chance levels when selecting a cup in the main test memory phase, this suggests that, in line
 248 with our prediction, they were able to encode incidental information within their memories of
 249 the original event during the encoding phase and utilise this information upon the unexpected
 250 re-representation of the cups. Furthermore, as they failed to override the use of spatial
 251 information in the control task, this finding suggests that they were not actively encoding the
 252 visual information regarding the cups in the main test. Taken together, these results
 253 demonstrate evidence for episodic-like memory in Eurasian jays.

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255 Whilst multiple studies have provided evidence in support of other corvids possessing an
 256 episodic-like memory system [11-14], this is the first such evidence in Eurasian jays. Like other
 257 corvids, Eurasian jays habitually cache food in order to sustain them in periods of lower food
 258 availability [40]. Therefore, the temporal characteristics involved in this behaviour may have
 259 selected for the evolution of an episodic-like memory ability [27]. Amongst other corvids,
 260 Eurasian jays are especially reliant on cached food for survival [40], suggesting that this
 261 selection pressure may have been comparatively strong in their lineage. Furthermore,
 262 Eurasian jays frequently pilfer (steal) conspecific caches, which most closely resembles the
 263 experimental situations, as in testing the jays did not cache themselves but instead watched
 264 an experimenter cache. To facilitate pilfering, they possess the ability for observational spatial
 265 memory [42] and it has been suggested that a species dependency on stored food correlates
 266 with their skill at observational spatial memory [36, 54]. Moreover, Eurasian jays have been
 demonstrated to use visual information to locate conspecific caches [42] and seem to, at least

267 in some instances, limit visual information available to competitors when caching themselves
268 [44, 45] (but see [46]).

269 It is important to note, however, that as the birds in the current study were trained to
270 observe the cup baiting event and subsequently use this information to select a cup, an
271 immediate test after baiting likely became expected over training. Whilst, at test, a substantial
272 delay occurred between the baiting event and cup selection, the birds still learned to expect a
273 test at the time of baiting, and therefore the encoding of the relevant information (spatial
274 locations) was likely to be explicit. What is important here, however, is that even if the memory
275 test after the delay was somewhat expected, the nature of the test, i.e., the relevant
276 information and long-term storage required to solve it, was unknown to the jays.

277 Therefore, in order to be successful in this task the jays had to use visual information
278 related to the cups that, at the time of encoding, held no value or relevance to the events
279 unfolding at that time. In the training phase (and the encoding trials), the only information
280 necessary to solve the task and find the food was the spatial position of each cup.
281 Furthermore, this information only needed to be retained for a very short interval as, in this
282 phase, they were allowed to choose a cup almost immediately after the food was hidden.
283 Therefore, only short-term spatial working memory was needed to be successful at this stage
284 of the experiment. However, in the memory phase, after a delay (without visual access to the
285 cups) and once the spatial information no longer existed (as the cups had been moved to
286 distinct locations), the jays had to recall the original event, including the visual characteristics
287 of the cups, in order to solve the task. Whilst these characteristics were present during the
288 short retraining period, meaning there is a possibility that they could have been attended to,
289 without repeated training to specifically learn that these visual characteristics are valuable as
290 cues associated with food (especially when the highly reinforced spatial cues were still
291 available), and without the anticipation of a related memory test for these details, this
292 information was likely to have been encoded incidentally. Indeed, across the same number of
293 trials in the control task the birds did not learn to use visual information when the spatial cues
294 were still present, but were now irrelevant, further suggesting that the visual information of the
295 cups was not explicitly encoded in the main task. The birds' success in the main task, and
296 failure in the control task, therefore demonstrates evidence for the use of episodic-like
297 memory.

298 Whilst tests of episodic-like memory are classically designed to ignore the question of
299 consciousness associated with memory recall, success in this paradigm may shed some light
300 on the contents of a non-human animal's subjective experience. To be successful in the
301 current task, the individual must recall a holistic representation of an event and then target
302 specific incidental information within it in order to solve the unexpected test. Furthermore,
303 recent evidence demonstrates that humans have conscious access to incidentally encoded
304 information within memories and can target this information in order to solve memory tasks
305 [55-58].

306 It must be said, however, that whilst this study does provide convincing evidence to
307 suggest that Eurasian jays can encode, retain, recall, and access incidental visual information
308 within the remembered event, this ability may be restricted to information associated with food
309 caching, and thus does not necessarily represent the domain-general flexibility typical of
310 human episodic memory [59]. As to our knowledge all research investigating episodic-like
311 memory in corvids relies on some form of food caching paradigm, future studies should
312 develop this work by assessing these birds' ability to recall other information, such as social
313 cues, as comparable studies have done with other taxa [23].

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472 **S1 Fig. Depiction of the unique visual markers:** in **A)** 'string' trials (coloured card around
473 the string attached to the top of the cup); **B)** 'shape' trials (a laminated coloured shape attached
474 to the front of the cup); and **C)** 'card' trials (a laminated coloured and/or patterned card
475 underneath the cup).

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478 **S1 Table. Summary of test results showing individual choices for each trial,** including
479 trial number, trial type (shape, string, and card), the number of retraining trials (*RT*) conducted
480 (until 5 in a row correct) and the arrangement in which the cups were presented in both the
481 encoding phase and the memory phase. Letters (e.g., BWGY) represent the main
482 characteristic colour (B = blue, W = white, G = green, Bk = black, P = pink, and Y = yellow)
483 and the order (from left to right) of the cups. Underlined letters represent the baited cup and
484 therefore the correct choice.

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487 **S2 Table. Summary of control test results showing individual choices for each trial,**
488 including trial type (shape, string, and card), trial number, and the arrangement in which the
489 cups were presented in both the initial phase and the second phase after rearranging. Letters
490 (e.g., BWGY) represent the main characteristic colour (B = blue, W = white, G = green, Bk =
491 black, P = pink, and Y = yellow) and the order (from left to right) of the cups. Underlined letters
492 represent the baited cup, and thus the correct choice according to the visual information (the
493 cups' visual features).