

# 1    **Uncertainty alters the balance between** 2    **incremental learning and episodic memory**

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## 10    **Abstract**

11    A key question in decision making is how humans arbitrate between competing learning and  
12    memory systems to maximize reward. We address this question by probing the balance between  
13    the effects, on choice, of incremental trial-and-error learning versus episodic memories of  
14    individual events. Although a rich literature has studied incremental learning in isolation, the role  
15    of episodic memory in decision making has only recently drawn focus, and little research  
16    disentangles their separate contributions. We hypothesized that the brain arbitrates rationally  
17    between these two systems, relying on each in circumstances to which it is most suited, as  
18    indicated by uncertainty. We tested this hypothesis by directly contrasting contributions of  
19    episodic and incremental influence to decisions, while manipulating the relative uncertainty of  
20    incremental learning using a well-established manipulation of reward volatility. Across two large,  
21    independent samples of young adults, participants traded these influences off rationally,  
22    depending more on episodic information when incremental summaries were more uncertain.  
23    These results support the proposal that the brain optimizes the balance between different forms  
24    of learning and memory according to their relative uncertainties and elucidate the circumstances  
25    under which episodic memory informs decisions.

26

## 27 Introduction

28 Effective decision making depends on using memories of past experiences to inform choices in  
29 the present. This process has been extensively studied using models of learning from trial-and-  
30 error, many of which rely on error-driven learning rules that in effect summarize experiences using  
31 a running average<sup>1-3</sup>. This sort of *incremental learning* provides a simple mechanism for  
32 evaluating actions without maintaining memory traces of each individual experience along the  
33 way, and has rich links to conditioning behavior and putative neural mechanisms for error-driven  
34 learning<sup>4</sup>. However, recent findings indicate that decisions may also be guided by the retrieval of  
35 individual events, a process often assumed to be supported by *episodic memory*<sup>5-14</sup>. Although  
36 theoretical work has suggested a role for episodic memory in initial task acquisition, when  
37 experience is sparse<sup>15,16</sup>, the use of episodes may be much more pervasive, as its influence has  
38 been detected empirically even in decision tasks that are well-trained and can be solved  
39 normatively using incremental learning alone<sup>6,8,10</sup>. The apparent ubiquity of episodic memory as  
40 a substrate for decision making raises questions about the circumstances under which it is  
41 recruited and the implications for behavior.

42 How and when episodic memory is used for decisions relates to a more general challenge in  
43 cognitive control: understanding how the brain balances competing systems for decision making.  
44 An overarching hypothesis is that the brain judiciously adopts different decision strategies in  
45 circumstances for which they are most suited; for example, by determining which system is likely  
46 to produce the most rewarding choices at the least cost. This general idea has been invoked to  
47 explain how the brain arbitrates between deliberative versus habitual decisions and previous work  
48 has suggested a key role for uncertainty in achieving a balance that maximizes reward<sup>17,18</sup>.  
49 Moreover, imbalances in arbitration have been implicated in dysfunction such as compulsion<sup>19,20</sup>,  
50 addiction<sup>21,22</sup>, and rumination<sup>23-25</sup>.

51 Here we hypothesized that uncertainty is used for effective arbitration between decision systems  
52 and tested this hypothesis by investigating the tradeoff between incremental learning and episodic  
53 memory. This is a particularly favorable setting in which to examine this hypothesis due to a rich  
54 prior literature theoretically analyzing, and experimentally manipulating, the efficacy of  
55 incremental learning in isolation. Studies of this sort typically manipulate the volatility, or frequency  
56 of change, of the environment. In line with predictions made by statistical learning models, these  
57 experiments demonstrate that when the reward associated with an action is more volatile, people  
58 adapt by increasing their incremental learning rates<sup>26-32</sup>. In this case, incrementally constructed  
59 estimates reflect a running average over fewer experiences, yielding both less accurate and more  
60 uncertain estimates of expected reward. We therefore reasoned that the benefits of incremental  
61 learning are most pronounced when incremental estimation can leverage many experiences or,  
62 in other words, when volatility is low. By contrast, when the environment is either changing  
63 frequently or has recently changed, estimating reward episodically by retrieving a single, well-  
64 matched experience should be relatively more favorable.

65 We tested this hypothesis using a choice task that directly pits these decision systems against  
66 one another<sup>11</sup>, while manipulating volatility. In particular, we i) independently measured the  
67 contributions of episodic memory vs. incremental learning to choice and ii) altered the uncertainty  
68 about incremental estimates using different levels of volatility. Two large online samples of healthy  
69 young adults (a primary sample with n=254 and a replication sample with n=223) completed three  
70 tasks. The main task of interest combined incremental learning and episodic memory, referred to  
71 throughout as the *deck learning and card memory* task (middle panel, **Figure 1A**). On each trial  
72 of this task, participants chose between an orange and a blue card and received feedback  
73 following their choice. The cards appeared on each trial throughout the task, but their relative  
74 value changed over time (**Figure 1B**). In addition to the color of the card, each card also displayed

75 an object. Critically, objects appeared on a card at most twice throughout the task, such that a  
76 chosen object could re-appear between 9-30 trials after it was chosen the first time, and would  
77 deliver the same reward. Thus, participants could make decisions based on incremental learning  
78 of the average value of the orange vs. blue decks, or based on episodic memory for the specific  
79 value of an object which they only saw once before. Additionally, participants made choices  
80 across two environments: a *high volatility* and a *low volatility* environment. The environments  
81 differed in how often reversals in deck value occurred.

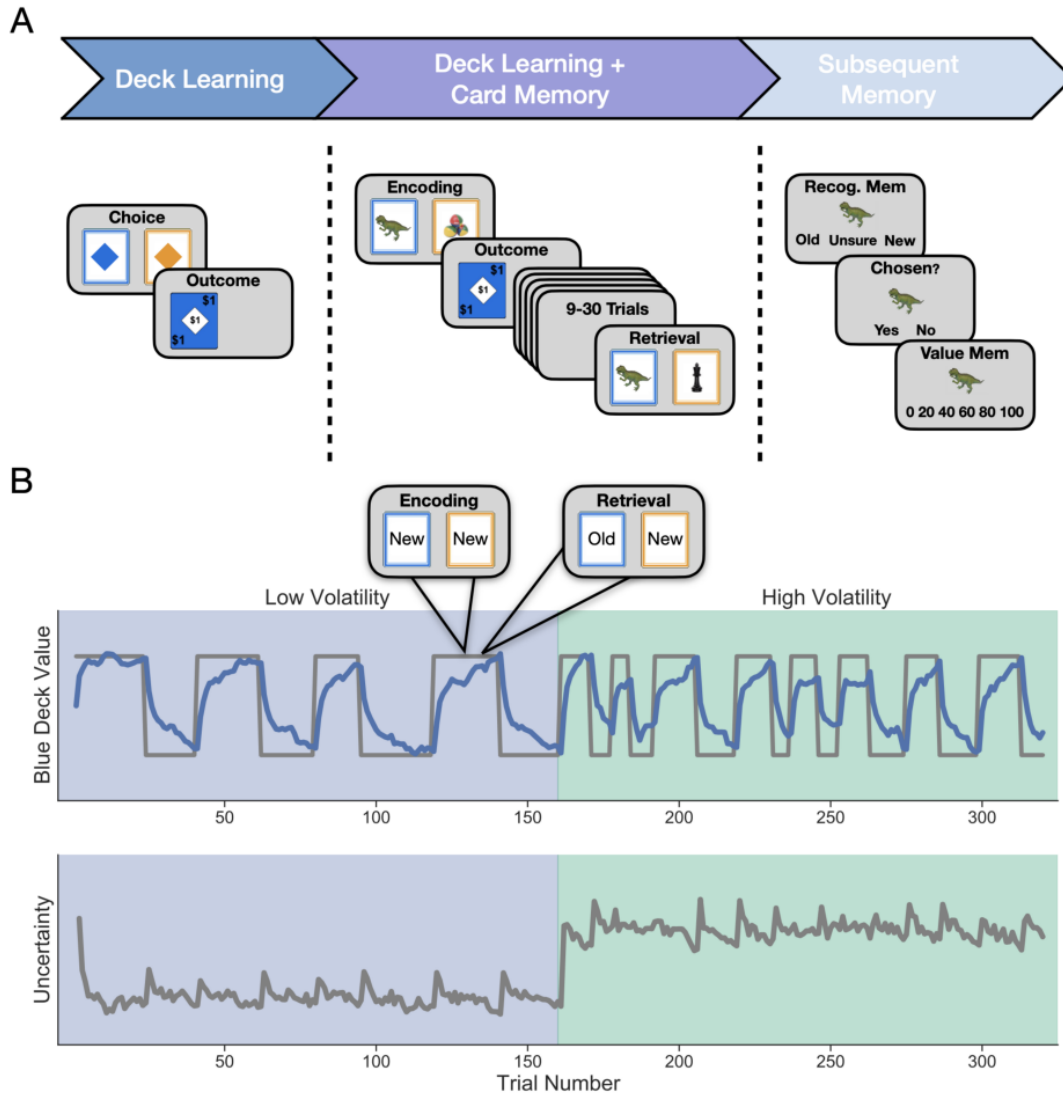
82 In addition to the main task, participants also completed two other simple tasks in the experiment.  
83 First, participants completed a simple *deck learning* task (left panel, **Figure 1A**) to acclimate them  
84 to each environment and quantify the effects of uncertainty. This task included choices between  
85 a blue or orange colored diamond on each trial, without any trial-unique objects. Second, after  
86 the main task, participants completed a standard *subsequent memory* task (right panel, **Figure**  
87 **1A**) designed to assess the effects of uncertainty on later episodic memory for objects and value  
88 they encountered in the main task.

89 We predicted that greater uncertainty about incremental values would be related to increased use  
90 of episodic memory. The experimental design provided two opportunities to measure the impact  
91 of uncertainty both *across* conditions, by comparing between the high and the low volatility  
92 environments, and *within* condition, by examining how learning and choices were impacted by  
93 each reversal.

## 94 **Results**

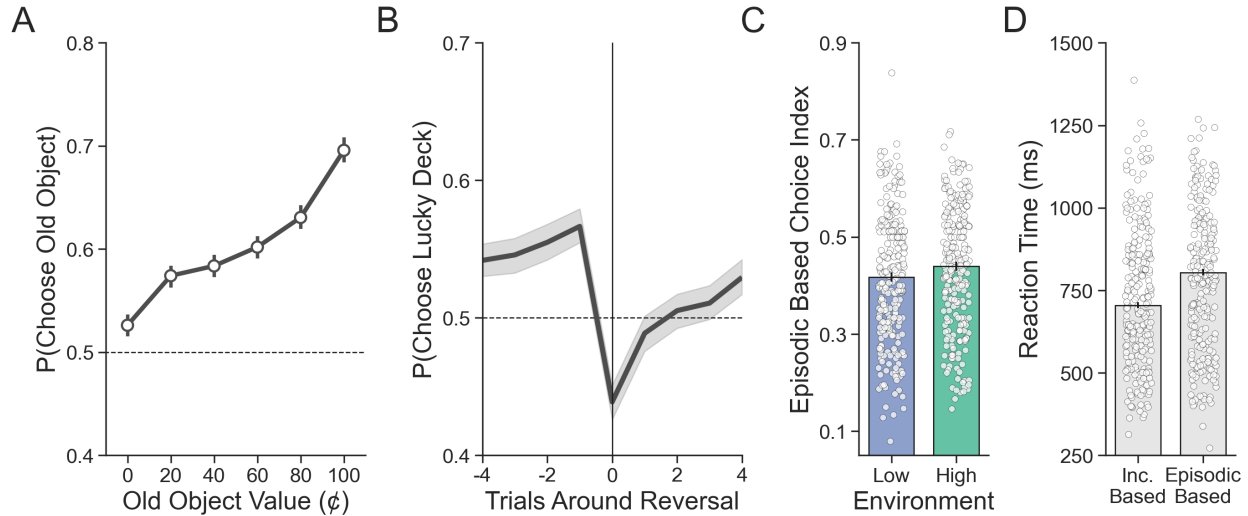
### 95 **Episodic memory is used more under conditions of greater uncertainty about deck value**

96 Participants completed two decision making tasks. The *deck learning* task familiarized them with  
97 the underlying incremental learning task and established an independent measure of sensitivity  
98 to the volatility manipulation. The separate *deck learning and card memory* task measured the  
99 additional influence of episodic memory on decisions (**Figure 1**). In the deck learning task  
100 participants chose between two decks with expected value that changed periodically across two  
101 environments, with one more volatile and the other less volatile. We reasoned that, following each  
102 reversal, participants should be more uncertain about deck value and that this uncertainty should  
103 reduce over time. Because the more volatile environment featured more reversals, this condition  
104 has greater uncertainty overall. In the second deck learning and card memory task, each deck  
105 featured cards with trial-unique objects that could re-appear once after being chosen and were  
106 worth an identical amount at each appearance. We predicted that decisions would be based more  
107 on object value when there was greater uncertainty about deck value. Our logic was that episodic  
108 memory should be deployed when incremental learning is inaccurate and unreliable due to  
109 frequent or recent change. Thus, we expected choices to be more reliant on episodic memory in  
110 the high compared to the low volatility environment and, within an environment, after compared  
111 to before reversals.



112

113 **Figure 1. A) Study Design and Sample Events.** Participants completed three tasks in succession. The  
 114 first was the *deck learning* task which consisted of choosing between two colored cards and receiving an  
 115 outcome following each choice. One color was worth more on average at any given timepoint and this  
 116 mapping changed periodically. Second was the main task of interest, the *deck learning and card memory*  
 117 task, which followed the same structure as the deck learning task but each card also displayed a trial-  
 118 unique object. Cards that were chosen could appear a second time in the task after 9-30 trials and, if they  
 119 re-appeared, were worth the same amount, thereby allowing participants to use episodic memory for  
 120 individual cards in addition to learning deck value from feedback. Lastly, participants completed a  
 121 *subsequent memory* task for objects that may have been seen in the deck learning and card memory task.  
 122 Participants had to indicate whether they recognized an object and, if they did, whether they chose that  
 123 object. If they responded that they had chosen the object they were then asked if they remembered the  
 124 value of that object. **B) Uncertainty manipulation within and across environments.** Uncertainty was  
 125 manipulated by varying the volatility of the relationship between cue and reward over time. Participants  
 126 completed the task in two environments that differed in their relative volatility. The low volatility environment  
 127 featured half as many reversals in deck luckiness as the high volatility environment. *Top:* The true value of  
 128 the blue deck is drawn in gray for an example trial sequence. In blue is estimated blue deck value from the  
 129 reduced Bayesian model.<sup>30</sup> Trials featuring objects appeared only in the deck learning and card memory  
 130 task. *Bottom:* Uncertainty about deck value as estimated by the model is shown in grey. This plot shows  
 131 relative uncertainty, which is the model's imprecision in its estimate of deck value.



132

133 **Figure 2. Evaluating the proportion of incremental and episodic choices.** **A)** Participants' choices  
 134 demonstrate sensitivity to the value of old objects. Group-level averages are shown as points and lines  
 135 represent 95% confidence intervals. **B)** Reversals in deck luckiness altered choice such that the currently  
 136 lucky deck was chosen less following a reversal. The line represents the group-level average and the band  
 137 represents the 95% confidence interval. **C)** On incongruent trials, choices were more likely to be based on  
 138 episodic memory (e.g. high-valued objects chosen and low-valued objects avoided) in the high compared  
 139 to the low volatility environment. Averages for individual subjects are shown as points and lines represent  
 140 the group-level average with a 95% confidence interval. **D)** Median reaction time was longer for incongruent  
 141 choices based on episodic memory compared to those based on incremental learning.

142 We first examined whether participants were separately sensitive to each source of value in the  
 143 deck learning and card memory task: the value of the objects (episodic) and of the decks  
 144 (incremental). Controlling for average deck value, we found that participants used episodic  
 145 memory for object value, evidenced by a greater tendency to choose high-valued old objects than  
 146 low-valued old objects ( $\beta_{Old\ value} = 0.621$ , 95%  $CI = [0.527, 0.713]$ ; **Figure 2A**). Likewise,  
 147 controlling for object value, we also found that participants used incrementally learned value for  
 148 the decks, evidenced by the fact that the higher-valued (lucky) deck was chosen more frequently  
 149 on trials immediately preceding a reversal ( $\beta_{t-4} = 0.038$ , 95%  $CI = [-0.038, 0.113]$ ;  $\beta_{t-3} =$   
 150  $0.056$ , 95%  $CI = [-0.02, 0.134]$ ;  $\beta_{t-2} = 0.088$ , 95%  $CI = [0.009, 0.166]$ ;  $\beta_{t-1} = 0.136$ , 95%  $CI =$   
 151  $[0.052, 0.219]$ ; **Figure 2B**), that this tendency was disrupted by the reversals ( $\beta_{t=0} =$   
 152  $-0.382$ , 95%  $CI = [-0.465, -0.296]$ ), and by the quick recovery of performance on the trials  
 153 following a reversal ( $\beta_{t+1} = -0.175$ , 95%  $CI = [-0.258, -0.095]$ ;  $\beta_{t+2} = -0.106$ , 95%  $CI =$   
 154  $[-0.18, -0.029]$ ;  $\beta_{t+3} = -0.084$ , 95%  $CI = [-0.158, -0.006]$ ;  $\beta_{t+4} = 0.129$ , 95%  $CI =$   
 155  $[0.071, 0.184]$ ).

156 Having established that both episodic memory and incremental learning guided choices, we next  
 157 sought to determine the impact of uncertainty on episodic memory for object value by isolating  
 158 trials on which episodic memory was most likely to be used. To identify reliance on object value,  
 159 we first focused on trials where the two sources of value information were incongruent: i.e. trials  
 160 for which the high-value deck featured an old object that was of low value (<50¢) or the low-value  
 161 deck featured an old object that was of high value (>50¢). We then defined an *episodic based*  
 162 *choice index* by considering a choice as episodic if the old object was, in the first case, avoided  
 163 or, in the second case, chosen. Consistent with our hypothesis, we found greater evidence for  
 164 episodic choices (as defined this way) in the high volatility environment compared to the low  
 165 volatility environment ( $\beta_{Env} = 0.094$ , 95%  $CI = [0.017, 0.17]$ ; **Figure 2C**). Finally, this analysis

166 also gave us the opportunity to test differences in reaction time between incremental and episodic  
167 decisions. Decisions based on episodic value took longer ( $\beta_{EBCI} = 38.573$ , 95%  $CI =$   
168  $[29.703, 47.736]$ ; **Figure 2D**), suggesting that episodic retrieval is more costly in time and perhaps  
169 more effortful overall, when compared to relying on cached incremental value.

### 170 **Uncertainty in incremental values increases sensitivity to episodic value**

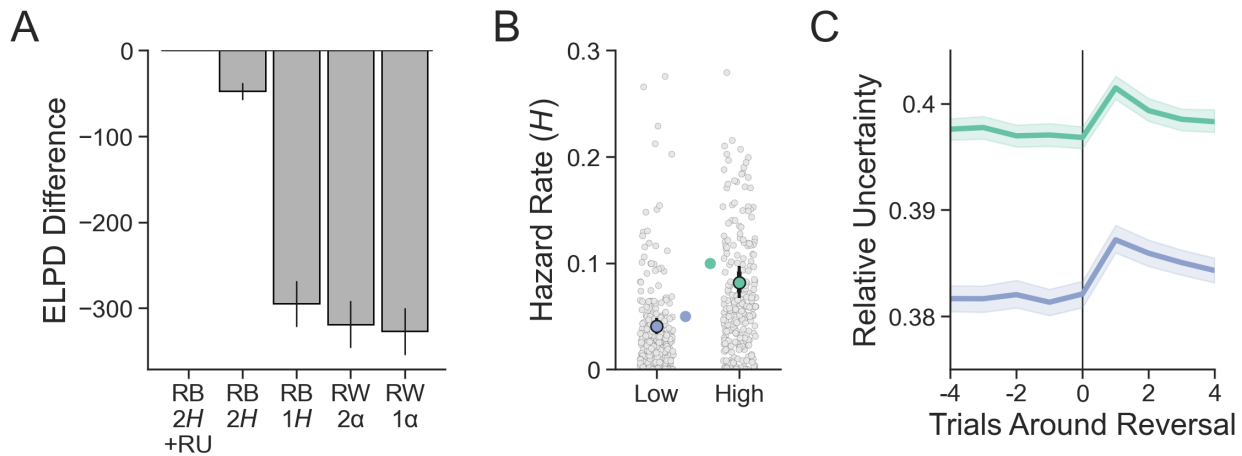
171 To capture uncertainty about deck value on a trial-by-trial basis, we adopted a computational  
172 model that tracks uncertainty during learning. We then used this model to test our central  
173 hypothesis: that episodic memory is used more when posterior uncertainty about deck value is  
174 high.

175 We began by hierarchically fitting two classes of incremental learning models to the behavior on  
176 the deck learning task: a baseline model with a Rescorla-Wagner<sup>2</sup> style update (RW) and a  
177 reduced Bayesian model<sup>30</sup> (RB) that augments the RW learner with a variable learning rate, which  
178 it modulates by tracking ongoing uncertainty about deck value. This approach—which builds on a  
179 line of work applying Bayesian learning models to capture trial-by-trial modulation in uncertainty  
180 and learning rates in volatile environments<sup>26,27,30,32–34</sup>—allowed us to first assess incremental  
181 learning free of any contamination due to competition with episodic memory. We then used the  
182 parameters fit to this task for each participant to generate estimates of subjective deck value and  
183 uncertainty around deck value, out of sample, in the deck learning and card memory task. These  
184 estimates were then used alongside episodic value to predict choices on incongruent trials in the  
185 deck learning and card memory task.

186 We first tested whether participants adjusted their rates of learning in response to uncertainty,  
187 both between environments and due to trial-wise fluctuations in uncertainty about deck value. We  
188 did this by comparing the ability of each combined choice model to predict participants' decisions  
189 out of sample. To test for effects between environments, we compared models that controlled  
190 learning with either a single free parameter (for RW, a learning rate  $\alpha$ ; for RB, a hazard rate  $H$   
191 capturing the expected frequency of reversals) shared across both environments or models with  
192 a separate free parameter for each environment. To test for trial-wise effects within environments,  
193 we compared between RB and RW models: while RW updates deck value with a constant learning  
194 rate, RB tracks ongoing posterior uncertainty about deck value (called relative uncertainty, RU)  
195 and increases its learning rate when this quantity is high.

196 Participants were both sensitive to the volatility manipulation and incorporated uncertainty into  
197 updating their beliefs about deck value. This is indicated by the fact that the RB combined choice  
198 model that included a separate hazard rate for each environment (RB2H) outperformed both RW  
199 models as well as the RB model with a single hazard rate (**Figure 3A**). Further, across the entire  
200 sample, participants detected higher levels of volatility in the high volatility environment, as  
201 indicated by the generally larger hazard rates recovered from this model in the high compared to  
202 the low volatility environment ( $H_{Low} = 0.04$ , 95%  $CI = [0.033, 0.048]$ ;  $H_{High} = 0.081$ , 95%  $CI =$   
203  $[0.067, 0.097]$ ; **Figure 3B**). Next, we examined the model's ability to estimate uncertainty as a  
204 function of reversals in deck luckiness. Compared to an average of the four trials prior to a  
205 reversal, RU increased immediately following a reversal and stabilized over time ( $\beta_{t=0} =$   
206  $0.014$ , 95%  $CI = [-0.019, 0.048]$ ;  $\beta_{t+1} = -0.242$ , 95%  $CI = [-0.276, -0.209]$ ;  $\beta_{t+2} =$   
207  $-0.145$ , 95%  $CI = [-0.178, -0.112]$ ;  $\beta_{t+3} = -0.1$ , 95%  $CI = [-0.131, -0.07]$ ;  $\beta_{t+4} =$   
208  $-0.079$ , 95%  $CI = [-0.108, -0.048]$ ; **Figure 3C**). As expected, RU was also, on average, greater  
209 in the high compared to the low volatility environment ( $\beta_{Env} = 0.015$ , 95%  $CI = [0.012, 0.018]$ ).  
210 Lastly, we were interested in assessing the relationship between reaction time and RU, as we  
211 expected that higher uncertainty may be reflected in more time needed to resolve decisions. In

212 line with this idea, RU was strongly related to reaction time such that choices made under more  
 213 uncertain conditions took longer ( $\beta_{RU} = 1.685$ , 95% CI = [0.823, 2.528]).



214

215 **Figure 3. Evaluating model fit and sensitivity to volatility. A)** Expected log pointwise predictive density  
 216 from each model was calculated from a 20-Fold leave-N-subjects-out cross validation procedure and is  
 217 shown here subtracted from the best fitting model. The best fitting model was the reduced Bayesian (RB)  
 218 model with two hazard rates (2H) and sensitivity to the interaction between old object value and relative  
 219 uncertainty (RU) in the choice function. Error bars represent standard error around ELPD estimates. **B)**  
 220 Participants were sensitive to the relative level of volatility in each environment as measured by the hazard  
 221 rate. Group level parameters are superimposed on individual subject parameters. Wide error bars represent  
 222 80% posterior intervals and skinny error bars represent 95% posterior intervals. The true hazard rate for  
 223 each environment is shown on the interior of the plot. **C)** Relative uncertainty peaks on the trial following a  
 224 reversal and is greater in the high compared to the low volatility environment. Lines represent group means  
 225 and bands represent 95% confidence intervals.

226 Having established that participants were affected by uncertainty around beliefs about deck value,  
 227 we turned to examine our primary question: whether this uncertainty alters the use of episodic  
 228 memory in choices. We first examined effects of RU on our episodic choice index, which  
 229 measures choices consistent with episodic value on trials when it disagrees with incremental  
 230 learning. This analysis verified that episodic memory was used more on incongruent trial  
 231 decisions made under conditions of high RU ( $\beta_{RU} = 2.133$ , 95% CI = [0.7, 3.535]; **Figure 4A**). To  
 232 more directly test the prediction that participants would use episodic memory when uncertainty is  
 233 high, we included trial-by-trial estimates of RU in the RB2H combined choice model, which was  
 234 augmented with an additional free parameter to capture any change with RU in the effect of  
 235 episodic value on choice. Formally, this parameter measured an effect of the interaction between  
 236 these two factors, and the more positive this term the greater the impact of increased uncertainty  
 237 on the use of episodic memory. This new combined choice model further improved out-of-sample  
 238 predictions (RB2H+RU, **Figure 3A**). As predicted, while both incremental and episodic value were  
 239 used overall ( $\beta_{DeckValue} = 0.488$ , 95% CI = [0.411, 0.563];  $\beta_{OldValue} = 0.141$ , 95% CI =  
 240 [0.092, 0.19]), episodic value indeed impacted choices more when relative uncertainty was high  
 241 ( $\beta_{OldValue:RU} = 0.091$ , 95% CI = [0.051, 0.13]; **Figure 4B**). This is consistent with our hypothesis  
 242 that episodic value was relied on more when beliefs about incremental value were uncertain.

243 The analyses above focus on uncertainty present at the time of retrieving episodic value because  
 244 this is what we hypothesized would drive competition in the reliance on either system at choice  
 245 time. However, in principle, reward uncertainty at the time an object is first encountered might  
 246 also affect its encoding, and hence its subsequent use in episodic choice when later retrieved<sup>35</sup>.  
 247 To address this possibility, we looked at the impact of RU resulting from the first time an old

248 object's value was revealed on whether that object was later retrieved for a decision. Using our  
249 episodic based choice index, there was no relationship between the use of episodic memory on  
250 incongruent trial decisions and RU at encoding ( $\beta_{RU} = 0.622$ , 95%  $CI = [-0.832, 2.044]$ ;  
251 **Supplementary Figure 5**). Similarly, we also examined effects of trial-by-trial estimates of RU at  
252 encoding time in the combined choice model by adding another free parameter that captured  
253 change with RU at encoding time in the effect of episodic value on choice. This parameter was  
254 added alongside the effect of RU at retrieval time (from the previous analysis). While there was a  
255 weak effect on choice ( $\beta_{OldValue:RU} = 0.042$ , 95%  $CI = [0.003, 0.079]$ ; **Supplementary Figure 5**),  
256 the inclusion of this parameter did not provide a better fit to subjects' choices than the combined  
257 choice model with only increased sensitivity due to RU at retrieval time (**Supplementary Figure**  
258 **5**), and this result did not replicate in a separate sample ( $\beta_{OldValue:RU} = 0.015$ , 95%  $CI =$   
259  $[-0.026, 0.057]$ ).

## 260 **Episodic and incremental value sensitivity predicts subsequent memory performance**

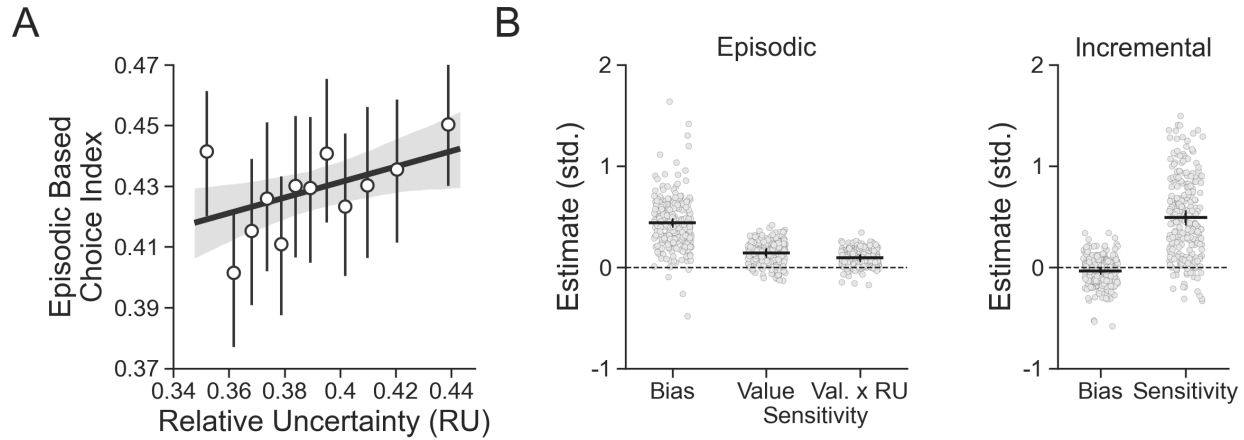
261 Having determined that decisions depended on episodic memory more when uncertainty about  
262 incremental value was higher, we next sought evidence for similar effects on the quality of  
263 episodic memory. Episodic memory is, of course, imperfect, and value estimates derived from  
264 episodic memory are therefore also uncertain. More uncertain episodic memory should then be  
265 disfavored while the influence of incremental value on choice is promoted instead. Although in  
266 the present study we did not experimentally manipulate the strength of episodic memory, as our  
267 volatility manipulation was designed to affect the uncertainty of incremental estimates, we did  
268 measure memory strength in a subsequent memory test. Thus, we predicted that participants who  
269 base fewer decisions on object value and more decisions on deck value should have poorer  
270 subsequent memory for objects seen in the deck learning and card memory task.

271 Participants performed well above chance on the test of recognition memory ( $\beta_0 =$   
272  $1.887$ , 95%  $CI = [1.782, 1.989]$ ), indicating a general ability to discriminate objects seen in the  
273 main task from those that were new. In line with the idea that episodic memory quality also impacts  
274 the relationship between incremental learning and episodic memory, participants with better  
275 subsequent recognition memory were more sensitive to episodic value ( $\beta_{EpSensitivity} =$   
276  $0.373$ , 95%  $CI = [0.273, 0.478]$ ; **Figure 5A**), and these same participants were less sensitive to  
277 incremental value ( $\beta_{IncSensitivity} = -0.276$ , 95%  $CI = [-0.383, -0.17]$ ; **Figure 5B**). This result  
278 provides further evidence for a trade-off between episodic memory and incremental learning, and  
279 provides preliminary support for a broader version of our hypothesis, which is that uncertainty  
280 about value provided by either memory system arbitrates the balance between them.

## 281 **Replication of the main results in a separate sample**

282 We repeated the tasks described above in an independent online sample of healthy young adults  
283 ( $n=223$ ) to test the replicability and robustness of our findings. We replicated all effects of  
284 environment and relative uncertainty on episodic-based choice and subsequent memory (see  
285 **Supplementary Text** and **Supplementary Figures 1-4** for details).



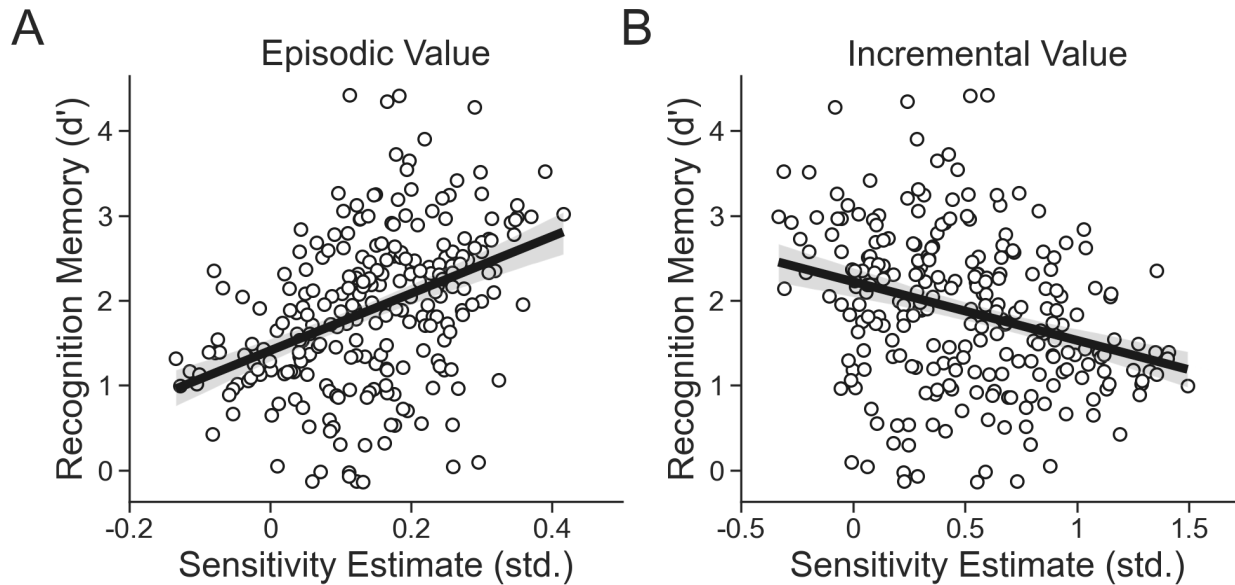


286

287 **Figure 4. Evaluating effects of sensitivity to uncertainty on episodic choices.** A) Participants' degree  
288 of episodic-based choice increased with greater RU as predicted by the combined choice model. Points  
289 are group means and error bars are 95% confidence intervals. B) Estimates from the combined choice  
290 model. Participants were biased to choose previously seen objects regardless of their value and were  
291 additionally sensitive to their value. As hypothesized, this sensitivity was increased when relative  
292 uncertainty was higher. There was no bias to choose one deck color over the other and participants were  
293 highly sensitive to estimated deck value. Group level parameters are superimposed on individual subject  
294 parameters. Wide error bars represent 80% posterior intervals and skinny error bars represent 95%  
295 posterior intervals. Estimates are shown in standard units.

## 296 Discussion

297 Research on learning and value-based decision making has focused on how the brain  
298 summarizes its experiences by error-driven incremental learning rules that, in effect, maintain the  
299 running average of many experiences. While recent work has demonstrated that episodic memory  
300 also contributes to value-based decisions<sup>5-14</sup>, many open questions remain about the  
301 circumstances under which episodic memory is used. Here we used a task which directly  
302 contrasts episodic and incremental influences on decisions and found that participants traded  
303 these influences off rationally, relying more on episodic information when incremental summaries  
304 were less reliable, i.e. more uncertain and based on fewer experiences. We also found evidence  
305 for a complementary modulation of this episodic-incremental balance by episodic memory quality,  
306 suggesting that more uncertain episodic-derived estimates may reduce reliance on episodic  
307 value. Together, these results indicate that reward uncertainty modulates the use of episodic  
308 memory in decisions, suggesting that the brain optimizes the balance between different forms of  
309 learning according to volatility in the environment.



310

311 **Figure 5. Relationship between choice sensitivity and subsequent memory. A)** Participants with  
312 greater sensitivity to episodic value as measured by random effects in the combined choice model tended  
313 to better remember objects seen originally in the card learning and deck memory task. **B)** Participants with  
314 greater sensitivity to incremental value tended to have worse memory for objects from the card learning  
315 and deck memory task. Points represent individual participants, lines are linear fits and bands are 95%  
316 confidence intervals.

317 Our findings add empirical data to previous theoretical and computational work which has  
318 suggested that decision making can greatly benefit from episodic memory for individual estimates  
319 when available data are sparse. This most obviously arises early in learning a new task, but also  
320 in task transfer, high-dimensional or non-Markovian environments, and (as demonstrated in the  
321 current work) during conditions of rapid change<sup>16,36,37</sup>. We investigate these theoretical predictions  
322 in the context of human decision making, testing whether humans rely more heavily on episodic  
323 memory when incremental summaries comprising multiple experiences are relatively poor. We  
324 operationalize this tradeoff in terms of uncertainty, exemplifying a more general statistical scheme  
325 for arbitrating between different decision systems by treating them as estimators of action value.  
326 There is precedent for this type of uncertainty-based arbitration in the brain, with the most well-  
327 known being the tradeoff between model-free learning and model-based learning<sup>17,38</sup>. Control  
328 over decision making by model-free and model-based systems has been found to shift in  
329 accordance with the accuracy of their respective predictions<sup>18</sup>, and humans adjust their reliance  
330 on either system in response to external conditions that provide a relative advantage to one over  
331 the other<sup>39-41</sup>. Tracking uncertainty provides useful information about when inaccuracy is  
332 expected and helps to maximize utility by deploying whichever system is best at a given time. Our  
333 results add to these findings and expand their principles to include episodic memory in this  
334 tradeoff.

335 Indeed, one intriguing possibility is that there is more than just an analogy between the  
336 incremental-episodic balance studied here and previous work on model-free versus model-based  
337 competition. Incremental error-driven learning coincides closely with model-free learning in other  
338 settings<sup>4,17</sup> and, although it has been proposed that episodic control constitutes a “third way”<sup>16</sup>, it  
339 is possible that behavioral signatures of model-based learning might instead arise from episodic  
340 control via covert retrieval of individual episodes<sup>15,42-44</sup>, which contain much of the same  
341 information as a cognitive map or world model. While the present study assesses single-event

342 episodic retrieval more overtly, it remains an open question for future work the extent to which  
343 these same processes, and ultimately the same episodic-incremental tradeoff, might also explain  
344 model-based choice as it has been operationalized in other decision tasks. A related line of work  
345 has emphasized a similar role for working memory in maintaining representations of individual  
346 trials for choice<sup>9,45-47</sup>. Given the capacity constraints of working memory, we think it unlikely that  
347 working memory can account for the effects shown here, which involve memory for dozens of  
348 trial-unique stimuli maintained over tens of trials.

349 Further, our findings help to clarify the impacts of uncertainty, novelty, and prediction error on  
350 episodic memory more broadly. Recent studies found that new episodes are more likely to be  
351 encoded under novel circumstances while prior experiences are more likely to be retrieved when  
352 conditions are familiar<sup>11,12,35,48</sup>. Shifts between these states of memory are thought to be  
353 modulated by one's focus on internal or external sources of information<sup>49,50</sup> and signaled by  
354 prediction errors based in episodic memory<sup>51-54</sup>. Relatedly, unsigned prediction errors, which are  
355 a marker of surprise, improve later episodic memory<sup>55-58</sup>. Findings have even suggested that  
356 states of familiarity and novelty can bias decisions toward the use of single past experiences or  
357 not<sup>11,12</sup>. One alternative hypothesis that emerges from this work is that change-induced  
358 uncertainty and novelty could exert similar effects on memory, such that novelty signaled by  
359 expectancy violations increases encoding in a protracted manner that dwindles as uncertainty is  
360 resolved, or the state of the environment becomes familiar. Our results do not support this  
361 interpretation. Decisions were guided more by individual memories on more uncertain retrieval  
362 trials with little effects of uncertainty at encoding time. It therefore seems likely that uncertainty  
363 and novelty operate in concert but remain largely separate concepts, an interpretation supported  
364 by recent evidence<sup>59</sup>.

365 This work raises further questions about the neurobiological basis of memory-based decisions  
366 and the role of neuromodulation in signaling uncertainty and aiding memory. In particular, studies  
367 have revealed unique functions for norepinephrine (NE) and acetylcholine (ACh) on uncertainty  
368 and learning. These findings suggest that volatility, as defined here, is likely to impact the  
369 noradrenergic modulatory system, which has been found to signal unexpected changes  
370 throughout learning<sup>29,34,60,61</sup>. Noradrenergic terminals densely innervate the hippocampus<sup>62</sup>, and  
371 a role for NE in both explicit memory formation<sup>63</sup> and retrieval<sup>64</sup> has been posited. Future studies  
372 involving a direct investigation of NE or an indirect investigation using pupillometry<sup>29</sup> may help to  
373 isolate its contributions to the interaction between incremental learning and episodic memory in  
374 decision making. ACh is also important for learning and memory, as memory formation is  
375 facilitated by ACh in the hippocampus, which may contribute to its role in separating and storing  
376 new experiences<sup>48,49</sup>. In addition to this role, ACh is heavily involved in incremental learning and  
377 has been widely implicated in signaling expected uncertainty, or noise<sup>60,65</sup>. ACh may therefore  
378 play an important part in managing the tradeoff between incremental learning and episodic  
379 memory. While we held the level of expected uncertainty constant throughout our task, altering  
380 this quantity in future work may prove fruitful.

381 Separately, while in the present study we disadvantaged incremental learning relative to episodic  
382 memory, similar predictions about their balance could be made by instead preferentially  
383 manipulating episodic memory. There are, for instance, clear theoretical benefits to deploying  
384 episodic memory under other task circumstances in which incremental learning is generally ill  
385 suited, such as in environments that are high dimensional or require planning far into the future<sup>15</sup>.  
386 In principle, individual past experiences can be precisely targeted in these situations depending  
387 on the relevance of their features to decisions in the present. Recent advances in computational  
388 neuroscience have, for example, demonstrated that artificial agents endowed with episodic  
389 memory are able to exploit its rich representation of past experience to make faster, more effective  
390 decisions<sup>16,36,37</sup>. While here we provided episodic memory as an alternative source of value to be

391 used in the presence of uncertainty about incremental estimates, future studies making use of  
392 paradigms tailored more directly toward episodic memory's assets will help to further elucidate  
393 how and when the human brain recruits episodic memory for decisions.

394 In conclusion, we have demonstrated that uncertainty induced by volatile environments impacts  
395 whether incremental learning or episodic memory is recruited for decisions. Greater uncertainty  
396 increased the likelihood that single experiences were retrieved for decision making. This effect  
397 suggests that episodic memory aids decision making when simpler sources of value are less  
398 accurate. By focusing on uncertainty, our results tie together disparate findings about when  
399 episodic memory is recruited for decisions and shed light on the exact circumstances under which  
400 the computational expense of episodic memory is worthwhile.

## 401 **Materials and Methods**

### 402 **Experimental Tasks**

403 The primary experimental task used here builds upon a paradigm previously developed by our  
404 lab<sup>11</sup> to successfully measure the relative contribution of incremental and episodic memory to  
405 decisions (**Figure 1A**). Participants were told that they would be playing a card game where their  
406 goal was to win as much money as possible. Each trial consisted of a choice between two decks  
407 of cards that differed based on their color (blue or orange). Participants had two seconds to decide  
408 between the decks and, upon making their choice, a green box was displayed around their choice  
409 until the full two seconds had passed. The outcome of each decision was then immediately  
410 displayed for one second. Following each decision, participants were shown a fixation cross  
411 during the intertrial interval period which varied in length (mean = 1.5 seconds, min = 1 seconds,  
412 max = 2 seconds). Decks were equally likely to appear on either side of the screen (left or right)  
413 on each trial and screen side was not predictive of outcomes. Participants completed a total of  
414 320 trials and were given a 30 second break every 80 trials.

415 Participants were made aware that there were two ways they could earn bonus money throughout  
416 the task, which allowed for the use of incremental and episodic memory respectively. First, at any  
417 point in the experiment one of the two decks was "lucky", meaning that the expected value ( $V$ ) of  
418 one deck color was higher than the other ( $V_{lucky}=73\phi$ ,  $V_{unlucky}=27\phi$ ). Outcomes ranged from \$0  
419 to \$1 in increments of  $20\phi$ . Critically, the mapping from  $V$  to deck color underwent an unsignaled  
420 reversal periodically throughout the experiment (**Figure 1B**), which incentivized participants to  
421 utilize each deck's recent reward history in order to determine the identity of the currently lucky  
422 deck. Each participant completed the task over two environments (with 160 trials in each) that  
423 differed in their relative volatility: a low volatility environment with eight  $V$  reversals, occurring  
424 every 20 trials on average, and a high volatility environment with sixteen  $V$  reversals, occurring  
425 every 10 trials on average. Participants were told that they would be playing in two different  
426 casinos and that in one casino deck luckiness changed less frequently while in the other deck  
427 luckiness changed more frequently. Participants were also made aware of which casino they were  
428 currently in by a border on the screen, with a solid black line indicating the low volatility casino  
429 and a dashed black line indicating the high volatility casino. Environment order was randomized  
430 for each participant.

431 Second, in order to allow us to assess the use of episodic memory throughout the task, each card  
432 within a deck featured an image of a trial-unique object that could re-appear once throughout the  
433 experiment after initially being chosen. Participants were told that if they encountered a card a  
434 second time it would be worth the same amount as when it was first chosen, regardless of whether  
435 its deck color was currently lucky or not. On a given trial  $t$ , cards chosen once from trials  $t - 9$   
436 through  $t - 30$  had a 60% chance of reappearing following a sampling procedure designed to

437 prevent each deck's expected value from becoming skewed by choice, minimize the correlation  
438 between the expected value of previously seen cards and deck expected value, and ensure that  
439 choosing a previously selected card remained close to 50¢.

440 Participants also completed a separate decision making task prior to the combined deck learning  
441 and card memory task that was identical in design but lacked trial-unique objects on each card.  
442 This task, the deck learning task, was designed to isolate the sole contribution of incremental  
443 learning to decisions and to allow participants to gain prior experience with each environment's  
444 volatility level. Participants completed the combined deck learning and card memory task  
445 immediately following completion of the deck learning task. Instructions were presented  
446 immediately prior to each task and participants completed five practice trials and a comprehension  
447 quiz prior to starting each.

448 Following completion of the combined deck learning and card memory task, we tested  
449 participants' memory for the trial-unique objects. Participants completed 80 (up to) three part  
450 memory trials. An object was first displayed on the screen and participants were asked whether  
451 or not they had previously seen the object and were given five response options: Definitely New,  
452 Probably New, Don't Know, Probably Old, Definitely Old. If the participant indicated that they had  
453 not seen the object before or did not know, they moved on to the next trial. If, however, they  
454 indicated that they had seen the object before they were then asked if they had chosen the object  
455 or not. Lastly, if they responded that they had chosen the object, they were asked what the value  
456 of that object was (with options spanning each of the six possible object values between \$0-1).  
457 Of the 80 trials, 48 were previously seen objects and 32 were new objects that had not been seen  
458 before. Of the 48 previously seen objects, half were sampled from each environment (24 each)  
459 and, of these, an equal number were taken from each possible object value (with 4 from each  
460 value in each environment). As with the decision-making tasks, participants were required to pass  
461 a comprehension quiz prior to starting the memory task.

462 All tasks were programmed using the jsPsych JavaScript library<sup>66</sup> and hosted on a Google Cloud  
463 server running Apache and the Ubuntu operating system. Object images were selected from  
464 publicly available stimulus sets<sup>67,68</sup> for a total of 665 unique objects that could appear in each run  
465 of the experiment.

## 466 **Participants**

467 A total of 418 participants between the ages of 18 - 35 were recruited for our main sample through  
468 Amazon Mechanical Turk using the Cloud Research Approved Participants feature<sup>69</sup>. Recruitment  
469 was restricted to the United States and nine dollars of compensation was provided following  
470 completion of the 50 minute experiment. Participants were also paid a bonus in proportion to their  
471 final combined earnings on both the training task and the combined deck learning and card  
472 memory task (total earnings / 100). Before starting each task, all participants were required to  
473 score 100% on a quiz that tested their comprehension of the instructions and were made to repeat  
474 the instructions until this score was achieved. Informed consent was obtained with approval from  
475 the Columbia University Institutional Review Board.

476 From the initial pool of participants, we excluded those who did not meet our pre-defined  
477 performance criteria. Participants were excluded from analysis on the deck learning and card  
478 memory task if they i) responded to fewer trials than the group average minus one standard  
479 deviation on the deck learning and card memory task, ii) responded faster than the group average  
480 minus one standard deviation on this task, or iii) did not demonstrate faster learning in the high  
481 compared to the low volatility environment on the independent deck learning task. Our reasoning  
482 for this latter decision was that it is only possible to test for effects of volatility on episodic memory

483 recruitment in participants who were sensitive to the difference in volatility between the  
484 environments, and it is well-established that a higher learning rate should be used in more volatile  
485 conditions<sup>26</sup>. Further, our independent assessment of deck learning was designed to avoid issues  
486 of selection bias in this procedure. We measured the effect of environment on learning by fitting  
487 a mixed effects logistic regression model to predict if subjects chose the lucky deck up to five  
488 trials after a reversal event in the deck learning task. For each subject  $s$  and trial  $t$ , this model  
489 predicts the probability that the lucky deck was chosen:

$$490 \quad p(\text{ChooseLucky}) = \sigma(\beta_0 + b_{0,s[t]} + T\text{SinceRev}_t \times Env_t(\beta_1 + b_{1,s[t]}))$$
$$491 \quad \sigma(x) = \frac{1}{1 + e^{-x}}$$

492 where  $\beta$ s are fixed effects,  $b$ s are random effects,  $T\text{SinceRev}$  is the trial number coded as distance  
493 from a reversal event (1-5), and  $Env$  is the environment a choice was made in coded as -0.5 and  
494 0.5 for the low and high volatility environments respectively. Participants with positive values of  
495  $b_1$  can be said to have chosen the lucky deck more quickly following a reversal in the high  
496 compared to the low volatility environment, and we included only these participants in the rest of  
497 our analyses. A total of 254 participants survived after applying these criteria.

#### 498 **Deck Learning and Card Memory Task Behavioral Analysis**

499 We first analyzed the extent to which previously seen (old) objects were used in the combined  
500 deck learning and card memory task by fitting the following mixed effects regression model to  
501 predict whether an old object was chosen:

$$502 \quad p(\text{ChooseOld}) = \sigma(\beta_0 + b_{0,s[t]} + OldVal_t(\beta_1 + b_{1,s[t]}) + TrueDeckVal_t(\beta_2 + b_{2,s[t]}))$$

503 where  $OldVal$  is the centered value (between -0.5 and 0.5) of an old object. We additionally  
504 controlled for the influence of deck value on this analysis by adding a regressor,  $TrueDeckVal$ ,  
505 which is the centered true average value of the deck on which each object was shown. Trials not  
506 featuring old objects were dropped from this analysis.

507 We then similarly assessed the extent to which participants engaged in incremental learning  
508 overall by looking at the impact of reversals on incremental accuracy directly. To do this, we  
509 grouped trials according to their distance from a reversal, up to four trials prior to ( $t = -4: -1$ ),  
510 during ( $t = 0$ ), and after ( $t = 1: 4$ ) a reversal occurred. We then dummy coded them to measure  
511 their effects on incremental accuracy separately. We also controlled for the influence of old object  
512 value in this analysis by including in this regression the coded value of a previously seen object  
513 (ranging from 0.5 if the value was \$1 on the lucky deck or \$0 on the lucky deck to -0.5 if the value  
514 was \$0 on the lucky deck and \$1 on the unlucky deck), for a total of 18 estimated effects:

$$515 \quad p(\text{ChooseLucky}) = \sigma(T_{-4:4}(\beta_{1:9} + b_{1:9,s[t]}) + T_{-4:4} \times OldVal_t(\beta_{10:18} + b_{10:18,s[t]}))$$

516 To next focus on whether there was an effect of environment on the extent to which the value of  
517 old objects was used for decisions, we restricted all further analyses involving old objects to  
518 “incongruent” trials, which were defined as trials on which either the old object was high valued  
519 (>50¢) and on the unlucky deck or low valued (<50¢) and on the lucky deck. To better capture  
520 participants’ beliefs, deck luckiness was determined by the best-fitting incremental learning model  
521 (see next section) rather than using the experimenter-controlled ground truth: whichever deck had  
522 the higher model-derived value estimate on a given trial was labeled the lucky deck. Our logic in  
523 using only incongruent trials was that choices that stray from choosing whichever deck is more  
524 valuable should reflect choices that were based on the episodic value for an object. Lastly, we

525 defined our outcome measure of episodic based choice index (EBCI) to equal 1 on trials where  
526 the “correct” episodic response was given (i.e. high valued objects were chosen and low valued  
527 object were avoided), and 0 on trials where the “correct” incremental response was given (i.e. the  
528 opposite was true). A single mixed effects logistic regression was then used to assess possible  
529 effects of environment *Env* on EBCI:

$$530 \quad p(EBCI) = \sigma(\beta_0 + b_{0,s[t]} + Env_t(\beta_1 + b_{1,s[t]}))$$

531 where here *Env* was coded identically to the above analyses.

532 To assess the effect of episodic-based choices on reaction time (RT), we used the following mixed  
533 effects linear regression model:

$$534 \quad RT_t = \beta_0 + b_{0,s[t]} + EBCI_t(\beta_1 + b_{1,s[t]}) + Switch_t(\beta_2 + b_{2,s[t]}) + ChosenVal_t(\beta_3 + b_{3,s[t]})$$

535 where *EBCI* was coded as -0.5 for incremental-based trials and 0.5 for episodic-based trials. We  
536 also included covariates to control for two other possible effects on RT. The first, *Switch*, captured  
537 possible RT slowing due to switching from choosing one deck to the other and was coded as -0.5  
538 if a stay occurred and 0.5 if a switch occurred. The second, *ChosenVal*, captured any effects due  
539 to the value of the option that may have guided choice, and was set to be the value of the  
540 previously seen object on episodic-based trials and the running average true value on  
541 incremental-based trials.

542 For these regression models as well as those described in the following sections, fixed effects are  
543 reported in the text as the median of each parameter’s marginal posterior distribution alongside  
544 95% credible intervals, which indicate where 95% of the posterior density falls. Parameter values  
545 outside of this range are unlikely given the model, data, and priors. Thus, if the range of likely  
546 values does not include zero, we conclude that a meaningful effect was observed.

## 547 **Incremental Learning Models**

548 We next assessed the performance of several reinforcement learning models on our task in order  
549 to best capture incremental learning. A detailed description of each model can be found in the  
550 Supplementary Methods. In brief, these included one model that performed Rescorla-Wagner<sup>2</sup>  
551 style updating with both a single (RW1 $\alpha$ ) and a separate (RW2 $\alpha$ ) fixed learning rate for each  
552 environment, and two reduced Bayesian (RB) models<sup>30</sup> with both a single (RB1 $H$ ) and a separate  
553 hazard rate for each environment (RB1 $H$ ). Models were fit to the deck learning task (see  
554 **Posterior Inference** and **Supplementary Methods**) and used to generate subject-wise  
555 estimates of deck value, and where applicable, uncertainty in the combined deck learning and  
556 card memory task.

## 557 **Combined Choice Models**

558 After fitting the above hierarchical models to the deck learning task, parameter estimates for each  
559 subject were then used to generate trial-by-trial timeseries for deck value and uncertainty (where  
560 applicable) throughout performance on the combined deck learning and card memory task. Mixed  
561 effects Bayesian logistic regressions for each incremental learning model were then used to  
562 capture the effects of multiple memory-based sources of value on incongruent trial choices in this  
563 task. For each subject *s* and trial *t*, these models can be written as:

$$p(\text{ChooseOrange}) = \sigma(\beta_0 + b_{0,s[t]} + \text{DeckVal}_t(\beta_1 + b_{1,s[t]}) + \text{Old}_t(\beta_2 + b_{2,s[t]}) + \text{OldVal}_t(\beta_3 + b_{3,s[t]}))$$

564  
565 where the intercept captures a bias toward choosing either of the decks regardless of outcome,  
566 *DeckVal* is the deck value estimated from each model, the effect of *Old* captures a bias toward  
567 choosing a previously seen card regardless of its value, and *OldVal* is the coded value of a  
568 previously seen object (ranging from 0.5 if the value was \$1 on the orange deck or \$0 on the blue  
569 deck to -0.5 if the value was \$0 on the orange deck and \$1 on the blue deck). An additional fifth  
570 regression that also incorporated our hypothesized effect of increased sensitivity to old object  
571 value when uncertainty about deck value is higher was also fit. This regression was identical to  
572 the others but included an additional interaction effect of uncertainty and old object value:  
573  $\text{OldVal}_t \times \text{Unc}_t(\beta_4 + b_{4,s[t]})$  and used the RB2H model's *DeckVal* estimate alongside its estimate  
574 of relative uncertainty (RU) to estimate the effect of  $\text{OldVal} \times \text{Unc}$ . RU was chosen over CPP  
575 because it captures the reducible uncertainty about deck value, which is the quantity we were  
576 interested in for this study. Prior to fitting the model, all predictors were z scored in order to report  
577 effects in standard units.

## 578 **Relative Uncertainty Analyses**

579 We conducted several other analyses that tested effects on or of relative uncertainty (RU)  
580 throughout the combined deck learning and card memory task. RU was mean-centered in each  
581 of these analyses. First, we assessed separately the effect of RU at retrieval time on EBCI using  
582 a mixed effects logistic regression:

$$583 \quad p(\text{EBCI}) = \sigma(\beta_0 + b_{0,s[t]} + \text{RU}_t(\beta_1 + b_{1,s[t]}) + \text{RU}_t^2(\beta_2 + b_{2,s[t]}))$$

584 An additional binomial term was included in this model to allow for the possibility that the effect of  
585 RU is nonlinear, although this term was found to have no effect. The effect of RU at encoding  
586 time was assessed using an identical model but with RU at encoding included instead of RU at  
587 retrieval.

588 Next, to ensure that the RB model captured uncertainty related to changes in deck luckiness, we  
589 tested for an effect of environment on RU using a mixed effects linear regression:

$$590 \quad \text{RU}_t = \beta_0 + b_{0,s[t]} + \text{Env}_t(\beta_1 + b_{1,s[t]})$$

591 We then also looked at the impact of reversals on RU. To do this, we calculated the difference in  
592 RU on reversal trials and up to four trials following a reversal from the average RU on the four  
593 trials immediately preceding a reversal. Then, using a dummy coded approach similar to that used  
594 for the model testing effects of reversals on incremental accuracy, we fit the following mixed  
595 effects linear regression with 5 effects:

$$596 \quad \text{RUDifference}_t = T_{0:4}(\beta_{1:5} + b_{1:5,s[t]})$$

597 We also assessed the effect of RU on reaction time using another mixed effects linear regression:

$$598 \quad \text{RT}_t = \beta_0 + b_{0,s[t]} + \text{RU}_t(\beta_1 + b_{1,s[t]})$$



## 599 **Subsequent Memory Task Behavioral Analysis**

600 Performance on the subsequent memory task was analyzed in two ways. First, recognition  
601 memory was assessed by computing the signal detection metric  $d'$  for each participant  
602 adjusted for extreme proportions using a log-linear rule<sup>70</sup>. The relationship with  $d'$  and  
603 sensitivity to both episodic value and incremental value was then determined using simple linear  
604 regressions of the form  $d'_{prime_s} = \beta_0 + Sensitivity_s(\beta_1)$  where *Sensitivity* was either the random  
605 effect of episodic value from the combined choice model for each participant or the random effect  
606 of incremental value from the combined choice value for each participant.

## 607 **Posterior Inference and Model Comparison**

608 Parameters for all incremental learning models were estimated using hierarchical Bayesian  
609 inference such that group-level priors were used to regularize subject-level estimates. This  
610 approach to fitting reinforcement learning models improves parameter identifiability and predictive  
611 accuracy<sup>71</sup>. The joint posterior was approximated using No-U-Turn Sampling<sup>72</sup> as implemented in  
612 Stan<sup>73</sup>. Four chains with 2000 samples (1000 discarded as burn-in) were run for a total of 4000  
613 posterior samples per model. Chain convergence was determined by ensuring that the Gelman-  
614 Rubin statistic  $\hat{R}$  was close to 1. A full description of the parameterization and choice of priors for  
615 each model can be found in the **Supplementary Methods**. All regression models were fit using  
616 No-U-Turn Sampling in Stan with the same number of chains and samples. Default weakly-  
617 informative priors implemented in the rstanarm package<sup>74</sup> were used for each regression model.  
618 Model fit for the combined choice models was assessed by separating each dataset into 20 folds  
619 and performing a cross validation procedure by leaving out N/20 subjects per fold where N is the  
620 number of subjects in each sample. The expected log pointwise predictive density (ELPD) was  
621 then computed and used as a measure of out-of-sample predictive fit for each model.

## 622 **Replication**

623 We identically repeated all procedures and analyses applied to the main sample on an  
624 independently collected replication sample. A total of 401 participants were again recruited  
625 through Amazon Mechanical Turk and 223 survived exclusion procedures carried out identically  
626 to those used for the main sample.

## 627 **Citation race and gender diversity statement**

628 The gender balance of papers cited within this work was quantified using databases that store  
629 the probability of a first name being carried by a woman. Excluding self-citations to the first and  
630 last authors of the current paper, the gender breakdown of our references is 12.16%  
631 woman(first)/woman(last), 6.76% man/woman, 23.44% woman/man, and 57.64% man/man. This  
632 method is limited in that a) names, pronouns, and social media profiles used to construct the  
633 databases may not, in every case, be indicative of gender identity and b) it cannot account for  
634 intersex, non-binary, or transgender people. Second, we obtained predicted racial/ethnic category  
635 of the first and last author of each reference using databases that store the probability of a first  
636 and last name being carried by an author of color. By this measure (and excluding self-citations),  
637 our references contain 9.55% author of color (first)/author of color(last), 19.97% white  
638 author/author of color, 22.7% author of color/white author, and 47.78% white author/white author.  
639 This method is limited in that a) using names and Florida Voter Data to make the predictions may  
640 not be indicative of racial/ethnic identity, and b) it cannot account for Indigenous and mixed-race  
641 authors, or those who may face differential biases due to the ambiguous racialization or  
642 ethnicization of their names.

643 **Data Availability**

644 All code, data, and software needed to reproduce the manuscript can be found here:  
645 <https://codeocean.com/capsule/2024716/tree/v1>

646 **Contributions**

647 J.N., D.S., and N.D.D. designed the study. J.N. conducted the experiments and analyzed the  
648 data. J.N., D.S., and N.D.D. wrote the manuscript.

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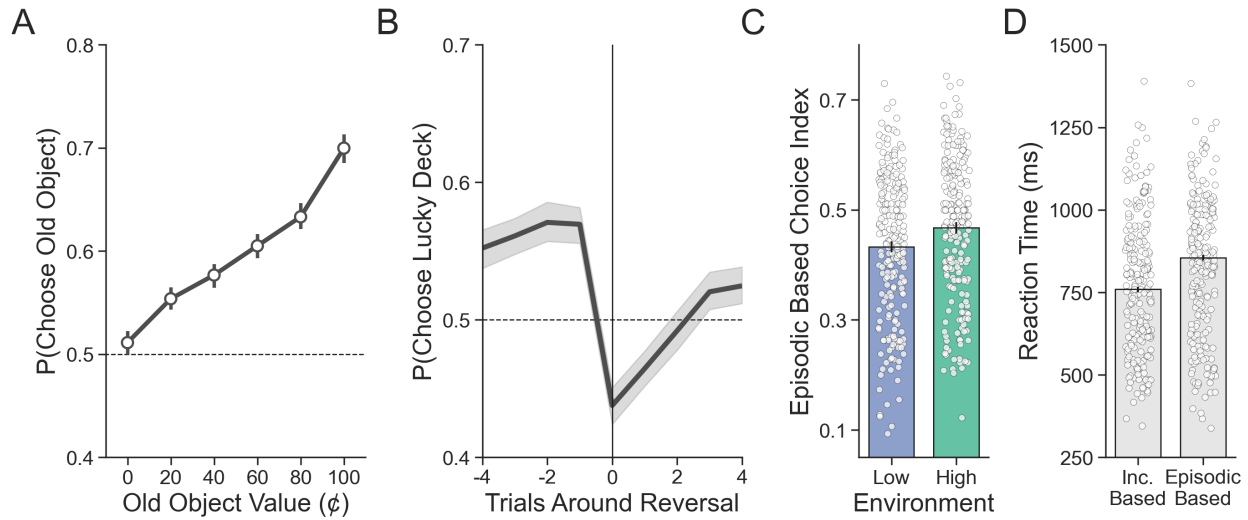
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819 **Uncertainty alters the balance between**  
820 **incremental learning and episodic memory**

821 **Supplementary Text**

822

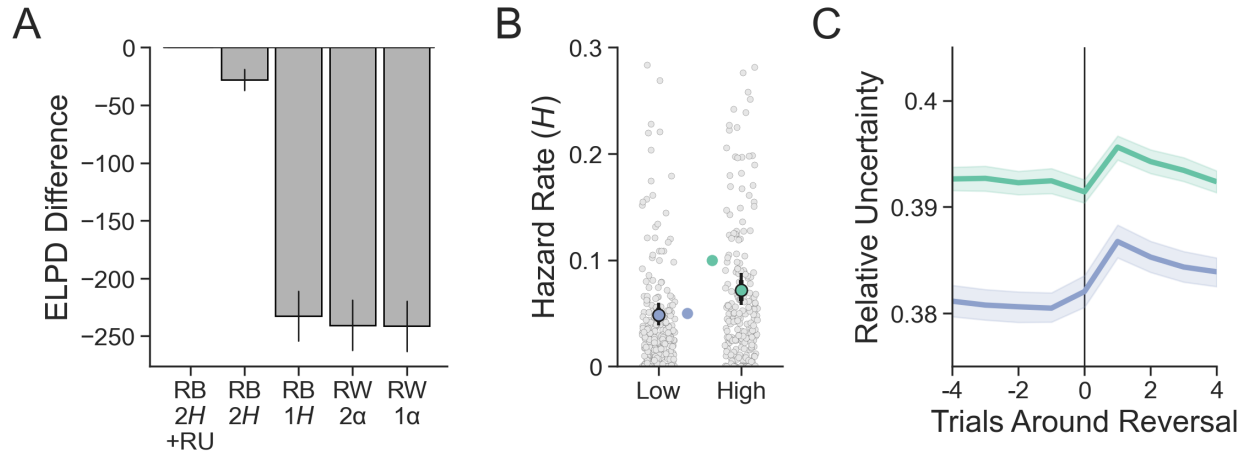




823

824 **Supplementary Figure 1.** Recreation of Figure 2 in the main text using the replication dataset. **A)**  
825 Participants' choices demonstrate sensitivity to the value of old objects. **B)** Reversals in deck luckiness  
826 altered choice such that the currently lucky deck was chosen less following a reversal. **C)** On incongruent  
827 trials, choices were more likely to be based on episodic memory in the high compared to the low volatility  
828 environment. **D)** Reaction time was longer for incongruent choices based on episodic memory compared  
829 to those based on incremental learning.

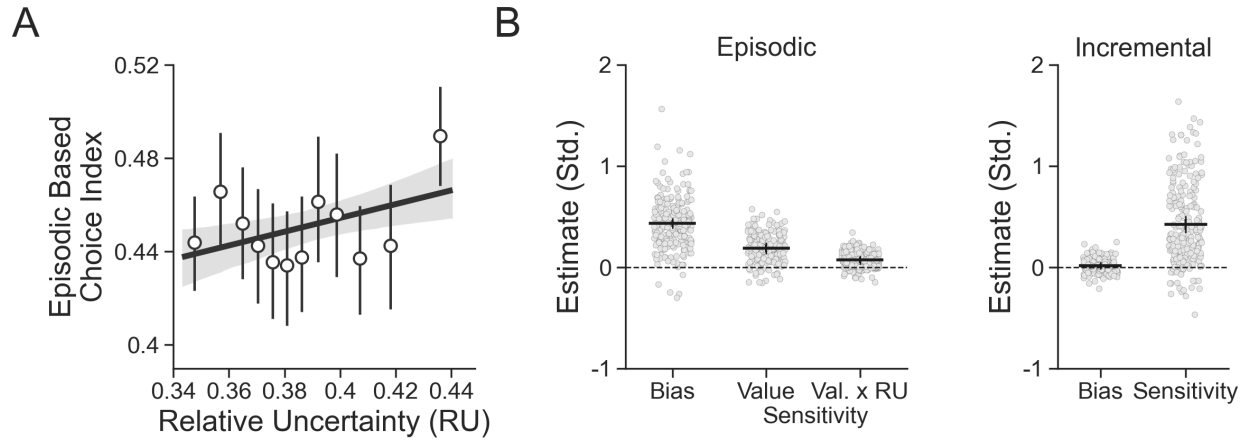
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832 **Supplementary Figure 2.** Recreation of Figure 3 in the main text using the replication dataset. **A)** The best  
833 fitting model was again the reduced Bayesian (RB) model with two hazard rates (2H) and sensitivity to the  
834 interaction between old object value and relative uncertainty (RU) in the choice function. **B)** Participants  
835 were affected by the relative level of volatility in each environment as measured by the hazard rate. Group  
836 level parameters are superimposed on individual subject parameters. **C)** Relative uncertainty peaks on the  
837 trial following a reversal and is greater in the high compared to the low volatility environment.

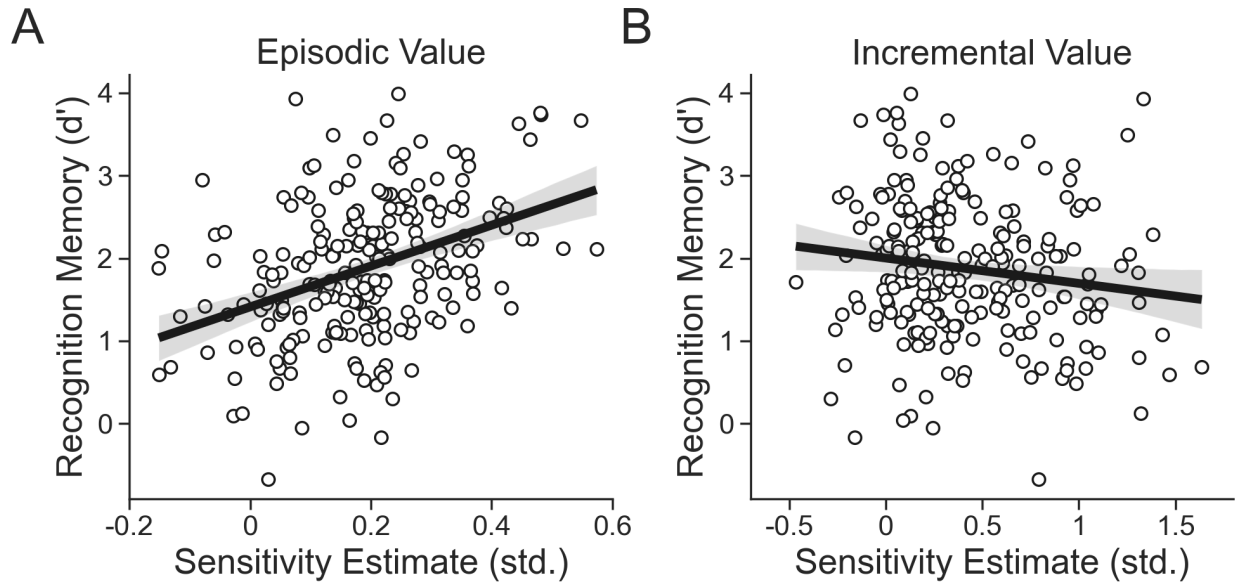
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840 **Supplementary Figure 3.** Recreation of Figure 4 in the main text using the replication dataset. **A)**  
841 Participants' degree of episodic-based choice increases with greater RU. **B)** Estimates from the combined  
842 choice model. Participants were biased to choose previously seen objects regardless of their value and  
843 were additionally sensitive to their value. As hypothesized, this sensitivity was increased when relative  
844 uncertainty was higher. There was no bias to choose one deck color over the other and participants were  
845 highly sensitive to estimated deck value.

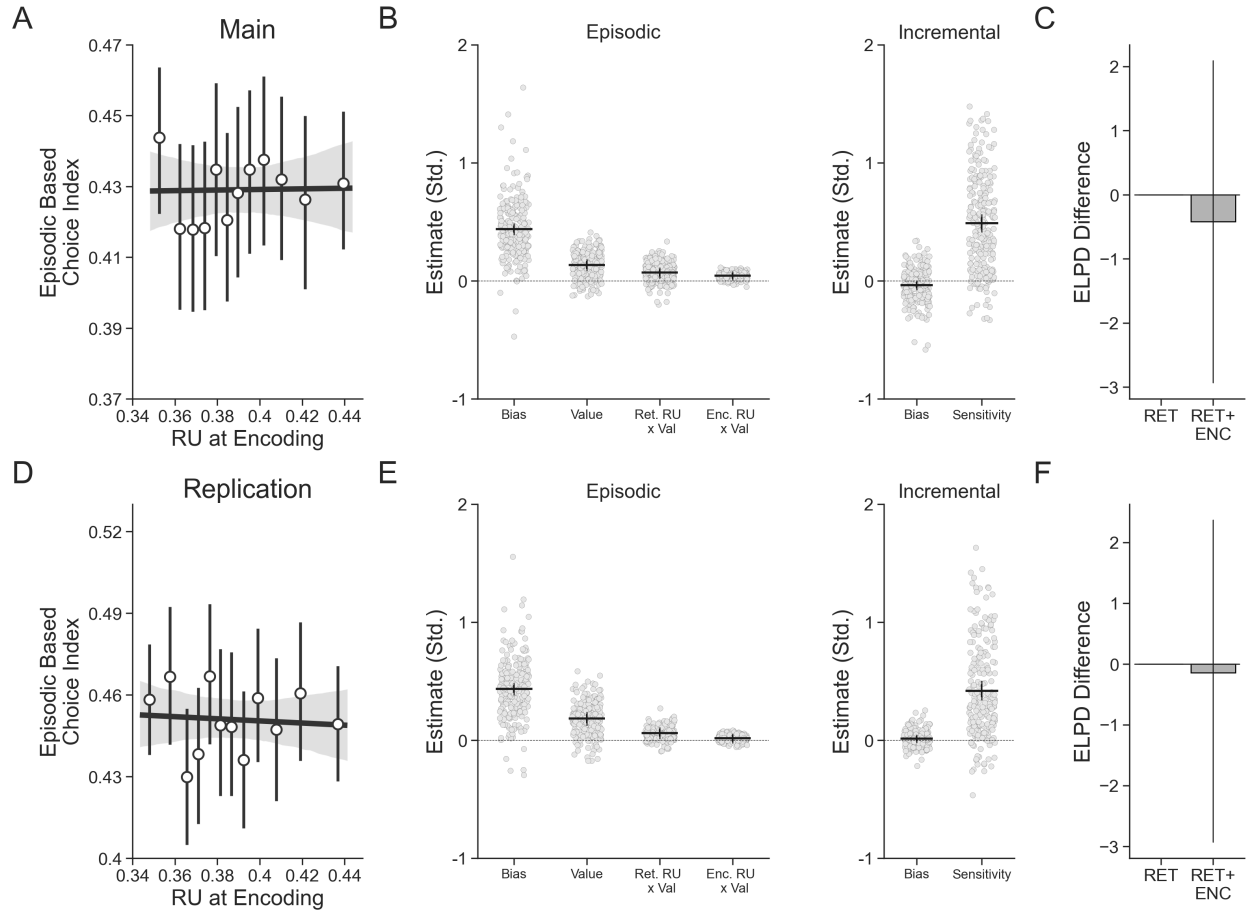
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848 **Supplementary Figure 4** Recreation of Figure 5 in the main text using the replication dataset. **A)**  
849 Participants with greater sensitivity to episodic value tended to better remember objects from the deck  
850 learning and card memory task. **B)** Participants with greater sensitivity to incremental value tended to have  
851 worse memory for objects from the card learning and deck memory task.

852



853

854 **Supplementary Figure 5.** Results of relative uncertainty (RU) at encoding time on episodic-based choice  
 855 in the main (A,B,C) and replication (D,E,F) sample. **A)** There was no relationship between RU at encoding  
 856 and the degree to which participants based decisions on episodic value. **B)** Estimates from the combined  
 857 choice model including both effects of RU at retrieval time and RU at encoding time. Relative to the effect  
 858 of the interaction between RU at retrieval time and old object value, the equivalent effect for RU at encoding  
 859 time was small in the main sample. **C)** Expected log pointwise predictive density for the combined choice  
 860 model including only an effect of the interaction between RU at retrieval time and old object value (presented  
 861 in the text) and the model also including the interaction between RU at encoding time and old object value.  
 862 Including RU at encoding time did not improve model performance. **D)** There was again no relationship  
 863 between RU at encoding and episodic-based choice in the replication sample. **E)** In the replication sample,  
 864 there was no effect of the interaction between RU at encoding and old object value on choice behavior. **F)**  
 865 Including RU at encoding time again did not improve model performance in the replication sample.

866

## 867 Replication Results

868 Here we repeat and describe all analyses reported in the main text with replication sample. All  
869 results are reported in the same order as in the main text.

### 870 Episodic memory is used more under conditions of greater uncertainty

871 Participants in the replication sample were substantially more likely to chose high-valued old  
872 objects compared to low-valued old objects ( $\beta_{OldValue} = 0.723$ , 95%  $CI = [0.624, 0.827]$ ;  
873 **Supplementary Figure 1A**). Participants also altered their behavior in response to reversals in  
874 deck value. The higher-valued (lucky) deck was chosen more frequently on trials immediately  
875 preceding a reversal ( $\beta_{t-4} = 0.095$ , 95%  $CI = [0.016, 0.176]$ ;  $\beta_{t-3} = 0.128$ , 95%  $CI =$   
876  $[0.047, 0.213]$ ;  $\beta_{t-2} = 0.168$ , 95%  $CI = [0.085, 0.251]$ ;  $\beta_{t-1} = 0.161$ , 95%  $CI = [0.075, 0.25]$ ;  
877 **Supplementary Figure 1B**). This tendency was then disrupted by trials on which a reversal  
878 occurred ( $\beta_{t=0} = -0.373$ , 95%  $CI = [-0.464, -0.286]$ ), with performance quickly recovering as  
879 the newly lucky deck became chosen more frequently on the trials following a reversal ( $\beta_{t+1} =$   
880  $-0.256$ , 95%  $CI = [-0.337, -0.175]$ ;  $\beta_{t+2} = -0.144$ , 95%  $CI = [-0.22, -0.064]$ ;  $t + 3$ :  $\beta_{t+3} =$   
881  $-0.024$ , 95%  $CI = [-0.102, 0.053]$ ;  $\beta_{t+4} = 0.113$ , 95%  $CI = [0.055, 0.174]$ ). Thus, participants in  
882 the replication sample were also sensitive to reversals in deck value, thereby indicating that they  
883 engaged in incremental learning throughout the task.

884 Participants in the replication sample also based more decisions on episodic value in the high  
885 volatility environment compared to the low volatility environment ( $\beta_{Env} = 0.145$ , 95%  $CI =$   
886  $[0.063, 0.229]$ ; **Supplementary Figure 1C**). Furthermore, decisions based on episodic value  
887 again took longer ( $\beta_{EBCI} = 41.38$ , 95%  $CI = [30.823, 51.707]$ ; **Supplementary Figure 1D**).

### 888 Uncertainty increases sensitivity to episodic value

889 In the replication sample, the reduced Bayesian model with two hazard rates was again the best  
890 fitting model (**Supplementary Figure 2A**). Participants detected higher levels of volatility in the  
891 high compared to the low volatility environment, as indicated by the generally larger hazard rates  
892 recovered from the high compared to the low volatility environment ( $\beta_{Low} = 0.048$ , 95%  $CI =$   
893  $[0.038, 0.06]$ ;  $\beta_{High} = 0.071$ , 95%  $CI = [0.058, 0.088]$ ; **Supplementary Figure 2B**). Compared to  
894 an average of the four trials prior to a reversal, RU also increased immediately following a reversal  
895 and stabilized over time ( $\beta_{t=0} = 0.021$ , 95%  $CI = [-0.014, 0.056]$ ;  $\beta_{t+1} = -0.22$ , 95%  $CI =$   
896  $[-0.253, -0.185]$ ;  $\beta_{t+2} = -0.144$ , 95%  $CI = [-0.178, -0.11]$ ;  $\beta_{t+3} = -0.098$ , 95%  $CI =$   
897  $[-0.129, -0.064]$ ;  $\beta_{t+4} = -0.05$ , 95%  $CI = [-0.083, -0.019]$ ; **Supplementary Figure 2C**). RU  
898 was again also, on average, greater in the high compared to the low volatility environment ( $\beta_{Env} =$   
899  $0.01$ , 95%  $CI = [0.007, 0.013]$ ) and related to reaction time such that choices made under more  
900 uncertain conditions took longer ( $\beta_{RU} = 1.364$ , 95%  $CI = [0.407, 2.338]$ ).

901 Episodic memory was also used more on incongruent trial decisions made under conditions of  
902 high RU ( $\beta_{RU} = 2.718$ , 95%  $CI = [1.096, 4.436]$ ; **Supplementary Figure 3A**). We again fit the  
903 combined choice model to the replication sample and found the following. Participants again used  
904 both sources of value throughout the task: both deck value as estimated by the model  
905 ( $\beta_{DeckValue} = 0.42$ , 95%  $CI = [0.336, 0.505]$ ; **Supplementary Figure 3B**) and the episodic value  
906 from old objects ( $\beta_{OldValue} = 0.188$ , 95%  $CI = [0.13, 0.245]$ ) strongly impacted choice. Lastly,  
907 episodic value again impacted choices more when relative uncertainty was high ( $\beta_{OldValue:RU} =$   
908  $0.069$ , 95%  $CI = [0.024, 0.113]$ ).

909 Finally, there was again no relationship between the use of episodic memory on incongruent trial  
910 decision and RU at encoding ( $\beta_{RU} = 0.99$ , 95%  $CI = [-0.642, 2.576]$ ; **Supplementary Figure 5**).

911 Unlike in the main sample, however, including a sixth parameter to assess increased sensitivity  
912 to old object value due to RU at encoding time did not have an effect in the combined choice  
913 model ( $\beta_{OldValue:RU} = 0.015$ , 95%  $CI = [-0.026, 0.057]$ ; **Supplementary Figure 5**), which is also  
914 reported in the main text. As with the main sample, including this parameter did not provide a  
915 better fit to subjects' choices than the combined choice model with only increased sensitivity due  
916 to RU at retrieval time.

## 917 **Episodic and Incremental value sensitivity predicts subsequent memory performance**

918 Participants in the replication sample again performed well above chance on the test of  
919 recognition memory ( $\beta_0 = 1.874$ , 95%  $CI = [1.772, 1.977]$ ). Participants with better subsequent  
920 recognition memory were again more sensitive to episodic value ( $\beta_{EpSensitivity} = 0.334$ , 95%  $CI =$   
921  $[0.229, 0.44]$ ; **Supplementary Figure 4A**), and these same participants were again less sensitive  
922 to incremental value ( $\beta_{IncSensitivity} = -0.124$ , 95%  $CI = [-0.238, -0.009]$ ; **Supplementary**  
923 **Figure 4B**).

## 924 **Supplementary Methods**

### 925 **Description of Incremental Learning Models**

#### 926 **Rescorla Wagner (RW)**

927 The first model we considered was a standard model-free reinforcement learner that assumes a  
928 stored value ( $Q$ ) for each deck is updated over time.  $Q$  is then referenced on each decision in  
929 order to guide choices. After each outcome  $o_t$ , the value for the orange deck  $Q_O$  is updated  
930 according to the following rule<sup>1</sup> if the orange deck chosen:

$$931 \quad Q_{O,t+1} = Q_{O,t} + \alpha(o_t - Q_{O,t})$$

932 And is not updated if the blue deck is chosen:

$$933 \quad Q_{O,t+1} = Q_{O,t}$$

934 Likewise, the value for the blue deck  $Q_B$  is updated equivalently. Large differences between  
935 estimated value and outcomes therefore have a larger impact on updates, but the overall degree  
936 of updating is controlled by the learning rate,  $\alpha$ . Two versions of this model were fit, one with a  
937 single learning rate (RW1 $\alpha$ ), and one with two learning rates (RW2 $\alpha$ ),  $\alpha_{low}$  or  $\alpha_{high}$ , depending  
938 on which environment the current trial was completed in. These parameters are constrained to lie  
939 between 0 and 1. A separate learning rate was used for each environment in the (RW2 $\alpha$ ) version  
940 to capture the well-established idea that a higher learning rate should be used in more volatile  
941 conditions<sup>2</sup>.

#### 942 **Reduced Bayesian (RB)**

943 The second model we considered was the reduced Bayesian (RB) model developed by Nassar  
944 and colleagues<sup>3</sup>. This model tracks and updates its belief that the orange deck is lucky based on  
945 trialwise outcomes,  $o_t$ , using the following prediction error-based update:

$$946 \quad B_{t+1} = B_t + \alpha_t(o_t - B_t)$$

947 This update is identical to that used in the RW model, however the learning rate  $\alpha_t$  is itself updated  
948 following each outcome according to the following rule:

$$949 \quad \alpha_t = \Omega_t + (1 - \Omega_t)\tau_t$$

950 where  $\Omega_t$  is the probability that a change in deck luckiness has occurred on the most recent trial  
951 (the change point probability or CPP) and  $\tau_t$  is the imprecision in the model's belief about deck  
952 value (the relative uncertainty or RU). The learning rate therefore increases whenever CPP or RU  
953 increase. CPP can be written as:

$$954 \quad \Omega_t = \frac{U(o_t|0,1)H}{U(o_t|0,1)H + \mathcal{N}(o_t|B_t, \sigma^2)(1-H)}$$

955 where  $H$  is the hazard rate or probability of a change in deck luckiness. Two versions of this model  
956 were fit, one with a single hazard rate (RB1H), and one with two hazard rates (RB2H),  $H_{low}$  and  
957  $H_{high}$ , depending on the environment the current trial was completed in. In this equation, the  
958 numerator represents the probability that an outcome was sampled from a new average deck  
959 value, whereas the denominator indicates the combined probability of a change and the  
960 probability that the outcome was generated by a Gaussian distribution centered around the most  
961 recent belief about deck luckiness and the variance of this distribution,  $\sigma^2$ . Because CPP is a  
962 probability, it is constrained to lie between 0 and 1. In our implementation,  $H$  was a free parameter  
963 (see Posterior Inference section below) and  $\Omega_1$  was initialized to 1.

964 RU, which is the uncertainty about deck value relative to the amount of noise in the environment,  
965 is quite similar to the Kalman gain used in Kalman filtering<sup>4</sup>:

$$966 \quad k_t = \Omega_t \sigma^2 + (1 - \Omega_t) \tau_t \sigma^2 + \Omega_t (1 - \Omega_t) ((o_t - B_t)(1 - \tau_t))^2$$
$$967 \quad \tau_{t+1} = \frac{k_t}{k_t + \sigma^2}$$

968 where  $\sigma^2$  is the observation noise and was here fixed to the true observation noise (0.33).  $k_t$   
969 consists of three terms: the first is the variance of the deck value distribution conditional on a  
970 change point, the second is the variance of the deck value distribution conditional on no change,  
971 and the third is the variance due to the difference in means between these two distributions. These  
972 terms are then used in the equation for  $\tau_{t+1}$  to provide the uncertainty about whether an outcome  
973 was due to a change in deck value or the noise in observations that is expected when a change  
974 point has not occurred. Because this model does not follow the two-armed bandit assumption of  
975 our task (that is, that outcomes come from two separate decks), all outcomes were coded in terms  
976 of the orange deck. For example, this means that an outcome worth \$1 on the orange deck is  
977 treated the same as an outcome worth \$0 on the blue deck by this model. While this description  
978 represents a brief overview of the critical equations of the reduced Bayesian model, a full  
979 explanation can be found in Nassar et al., 2010<sup>3</sup>.

## 980 **Softmax Choice**

981 All incremental learning models were paired with a softmax choice function in order to predict  
982 participants' decisions on each trial:

$$983 \quad \theta_t = \frac{1}{1 + e^{-(\beta_0 + \beta_1 V_t)}}$$

984 where  $\theta_t$  is the probability that the orange deck was chosen on trial  $t$ . This function also consists  
985 of two inverse temperature parameters:  $\beta_0$  to model an intercept and  $\beta_1$  to model the slope of the  
986 decision function related to deck value. The primary difference for each model was how  $V_t$  is  
987 computed: RW ( $V_t = Q_{O,t} - Q_{B,t}$ ); RB ( $V_t = B_t$ ). In each of these cases, a positive  $V_t$  indicates  
988 evidence that the orange deck is more valuable while a negative  $V_t$  indicates evidence that the  
989 blue deck is more valuable.



## 990 **Posterior Inference**

991 For all incremental learning models, the likelihood function can be written as:

$$992 \quad c_{s,t} \sim \text{Bernoulli}(\theta_{s,t})$$

993 where  $c_{s,t}$  is 1 if subject  $s$  chose the orange deck on trial  $t$  and 0 if blue was chosen. Following  
994 the recommendations of Gelman and Hill, 2006<sup>5</sup> and van Geen and Gerraty, 2021<sup>6</sup>,  $\beta_s$  is drawn  
995 from a multivariate normal distribution with mean vector  $\mu_\beta$  and covariance matrix  $\Sigma_\beta$ :

$$996 \quad \beta_s \sim \text{MultivariateNormal}(\mu_\beta, \Sigma_\beta)$$

997 where  $\Sigma_\beta$  is decomposed into a vector of coefficient scales  $\tau_\beta$  and a correlation matrix  $\Omega_\beta$  via:

$$998 \quad \Sigma_\beta = \text{diag}(\tau_\beta) \times \Omega_\beta \times \text{diag}(\tau_\beta)$$

999 Weakly-informative hyperpriors were then set on the hyperparameters  $\mu_\beta, \Omega_\beta$  and  $\tau_\beta$ :

$$1000 \quad \mu_\beta \sim \mathcal{N}(0, 5)$$

$$1001 \quad \tau_\beta \sim \text{Cauchy}^+(0, 2.5)$$

$$1002 \quad \Omega_\beta \sim \text{LKJCorr}(2)$$

1003 These hyperpriors were chosen for their respective desirable properties: the half cauchy is  
1004 bounded at zero and has a relatively heavy tail which is useful for scale parameters, the LKJ prior  
1005 with shape = 2 concentrates some mass around the unit matrix thereby favoring less correlation<sup>7</sup>,  
1006 and the normal is a standard choice for regression coefficients.

1007 Because sampling from heavy tailed distributions like the Cauchy is difficult for Hamiltonian Monte  
1008 Carlo<sup>8</sup>, a reparameterization of the Cauchy distribution was used here.  $\tau_\beta$  was thereby defined as  
1009 the transform of a uniformly distributed variable  $\tau_{\beta\_u}$  using the Cauchy inverse cumulative  
1010 distribution function such that:

$$1011 \quad F_x^{-1}(\tau_{\beta\_u}) = \tau_\beta \left( \pi \left( \tau_{\beta\_u} - \frac{1}{2} \right) \right)$$

$$1012 \quad \tau_{\beta\_u} \sim \mathcal{U}(0, 1)$$

1013 In addition, a multivariate non-centered parameterization specifying the model in terms of the  
1014 Cholesky factorized correlation matrix was used in order to shift the data's correlation with the  
1015 parameters to the hyperparameters, which increases the efficiency of sampling the parameters  
1016 of hierarchical models<sup>8</sup>. The full correlation matrix  $\Omega_\beta$  was replaced with a Cholesky factorized  
1017 parameter  $L_{\Omega_\beta}$  such that:

$$1018 \quad \Omega_\beta = L_{\Omega_\beta} \times L_{\Omega_\beta}^T$$

$$1019 \quad \beta_s = \mu_\beta + (\text{diag}(\tau) \times L_{\Omega_\beta} \times z)^T$$

$$1020 \quad L_{\Omega_\beta} \sim \text{LKJCholesky}(2)$$

$$1021 \quad z \sim \mathcal{N}(0, 1)$$

1022 where multiplying the Cholesky factor of the correlation matrix by the standard normally distributed  
1023 additional parameter  $z$  and adding the group mean  $\mu_\beta$  creates a  $\beta_s$  vector distributed identically  
1024 to the original model.

1025 While the choice function is identical for each model, the parameters used in generating deck  
1026 value differ for each. All were fit hierarchically and were modeled with the following priors and  
1027 hyperpriors:

1028 Rescorla Wagner with a single learning rate (RW1 $\alpha$ ):

$$\alpha \sim \beta(a1, a2)$$

1029  $a1 \sim \mathcal{N}(0,5)$

$$a2 \sim \mathcal{N}(0,5)$$

1030 Rescorla Wagner with two learning rates (RW2 $\alpha$ ):

$$\alpha_{low} \sim \beta(a1_{low}, a2_{low})$$

$$\alpha_{high} \sim \beta(a1_{high}, a2_{high})$$

1031  $a1_{low} \sim \mathcal{N}(0,5)$

$$a2_{low} \sim \mathcal{N}(0,5)$$

$$a1_{high} \sim \mathcal{N}(0,5)$$

$$a2_{high} \sim \mathcal{N}(0,5)$$

1032 Reduced Bayes with a single hazard rate (RB1 $H$ ):

$$H \sim \beta(h1, h2)$$

1033  $h1 \sim \mathcal{N}(0,5)$

$$h2 \sim \mathcal{N}(0,5)$$

1034 Reduced Bayes with two hazard rates (RB2 $H$ ):

$$H_{low} \sim \beta(h1_{low}, h2_{low})$$

$$H_{high} \sim \beta(h1_{high}, h2_{high})$$

1035  $h1_{low} \sim \mathcal{N}(0,5)$

$$h2_{low} \sim \mathcal{N}(0,5)$$

$$h1_{high} \sim \mathcal{N}(0,5)$$

$$h2_{high} \sim \mathcal{N}(0,5)$$

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