

Beneficial and detrimental effects of schema incongruence on memory for contextual events

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<u>Abstract</u>

Mental schemas provide a framework into which new information can easily be integrated. In a series of experiments, we examined how incongruence that stems from a prediction error (van Kesteren, Ruiter, Fernández, & Henson, 2012) modulates memory for multicomponent events that instantiated pre-existing schemas. Each event consisted of four stimulus pairs with overlapping components, presented in four blocks (A-B, B-C, C-D, D-A). A-B pairs elicited contextual expectations (A: Farm, B: Tractor) that were either met by a congruent C component (C: Farmer) or violated by an incongruent one (C: Lawyer). The baseline condition included unrelated pairs, where the C component was neither congruent nor incongruent. In experiment 2, events were presented in successive trials instead of blocks, and eye movements were recorded to analyse allocation of attention. Memory was tested through old-new item recognition followed by cued recall. Across experiments, recognition and recall performance for incongruent components was reduced compared to congruent components. Incongruent items were in some cases more accurately retrieved compared to unrelated ones, depending on task demands. Additionally, better recall was observed in the incongruent D-A pairs, compared to congruent and unrelated ones, because of reduced interference from C components. Eye-tracking revealed an increased number of fixations on C components in the incongruent and unrelated conditions. These results suggest that the integration of incongruent items into an episode is impaired, compared to congruent items, despite the contextual surprise and increased attention they elicited at encoding. However, there was a beneficial effect of prediction error on memory performance, compared to a baseline, depending on the task employed.

Keywords: congruence effects, schema, prediction error, event integration

Abstract word count: 259 words

1 Introduction

2 Schemas and their role in supporting memory have been a topic of intensive research over 3 several decades (Bartlett, 1932). Schema effects can benefit memory in two ways; firstly, the 4 mere existence of a schema could enhance learning of new information. Previous research 5 suggests memory performance is improved when the items can be assimilated into an 6 existing schema (McClelland, 2013; Tse et al., 2007, 2011). Secondly, performance can be 7 assessed across congruent and incongruent information. A common observation, referred to 8 as the congruency effect, is that schema-congruent information is better recognised and 9 recalled than incongruent information (Atienza, Crespo-Garcia, & Cantero, 2010; Craik & 10 Tulving, 1975; Staresina, Gray, & Davachi, 2009; van Kesteren, Rijpkema, Ruiter, & 11 Fernandez, 2010). However, van Kesteren and colleagues (2012) proposed a model (SLIMM) 12 showing schemas can enhance memory for both congruent and incongruent information, via 13 different mechanisms. The key modulator in this model is the prediction error elicited by the 14 incongruent item (Greve, Cooper, Kaula, Anderson, & Henson, 2017). A prominent aspect 15 that remains elusive is to what extent memory is enhanced by the prediction error (e.g. 16 whether memory performance is equivalently good for congruent and incongruent items). 17 Here, we test behavioural predictions of this model by combining contextual surprise with 18 schema-incongruent items, embedded in multi-component events (Horner, Bisby, Bush, Lin, 19 & Burgess, 2015; Horner & Burgess, 2013).

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SLIMM posits that incongruence could lead to superior memory when the contextual schema provides a strong constraint (van Kesteren et al., 2012). In such cases, the incongruent item elicits a prediction error, leading to better memory through the creation of new representations. Importantly, the degree to which incongruence benefits memory, compared to a schema-less, baseline level, remains unclear. The model also accounts for congruency effects, as encountering congruent information results in medial prefrontal

27 cortex (mPFC) activation of the schema, which in turn facilitates encoding in the medial 28 temporal lobe (MTL; for similar ideas see Brod, Werkle-Bergner, & Shing, 2013; Preston & Eichenbaum, 2013). A key aspect of the SLIMM model is that the fate of incongruent 29 30 information in memory is determined by the context it is embedded in. Most of the studies 31 examining schema effects build upon pre-experimental knowledge (Bayen & Kuhlmann, 32 2011; Bein, Reggev, & Maril, 2014; van Kesteren et al., 2010) and the relationship between a 33 pair of items, or their level of semantic relatedness (Bein et al., 2014; Staresina et al., 2009; 34 van Kesteren et al., 2013). For example, purple-banana would be an incongruent pair, 35 whereas yellow-banana constitutes a congruent one. However, this design does not 36 necessarily allow for predictions to develop at encoding. Subsequently, during retrieval, 37 there is no episodic contextual setting that would reinstate the schema (van Kesteren et al., 38 2012).

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40 Incongruence that stems from a prediction error should be accompanied by better 41 retention, supported by MTL engagement (Greve et al., 2017; van Kesteren et al., 2012). 42 Importantly, for a prediction to be wrong, it must first be elicited (Kumaran & Maguire, 43 2007). We therefore utilised interleaved learning of events comprising pairs of components, 44 to allow for predictions to be developed and violated. Previous research suggests such multi-45 component events are well suited for this purpose, as they promote binding of components 46 into contextual events (Horner et al., 2015; Horner & Burgess, 2013). Therefore, the first pair 47 of components presented can be used to implicitly set the schema-related predictions 48 (Schlichting & Preston, 2015). Additionally, this paradigm makes it possible to test how 49 incongruent components affect the rest of the contextual event. Specifically, whether 50 incongruent components can be integrated into an otherwise congruent event (Bein et al., 51 2015), relying on interactions between mPFC and MTL (Schlichting & Preston, 2015, 2017). 52 Thus, we can measure not only the independent recollection of incongruent components,

but also their indirect effect on adjacent congruent components. According to SLIMM (van Kesteren et al., 2012), if incongruent representations are reactivated at retrieval (similarly to congruent ones), we would expect equivalent levels of interference from incongruent and congruent C components in adjacent A-B and D-A pairs.

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58 In the studies reported here, we used events consisting of four pairs. Each pair shared a 59 common component (A-B, B-C, C-D, D-A), to promote retrieval of the previous pair during 60 study (Caplan, Rehani, & Andrews, 2014), as well as to allow for components to be 61 integrated into an event (Burton, Lek, & Caplan, 2017; Schlichting & Preston, 2017). We 62 extend previous literature on schema effects by actively eliciting contextual predictions that 63 stem from existing schemas, as opposed to relying solely on the level of relatedness of two 64 items. On this basis, we hypothesised that incongruence will modulate memory both of the 65 incongruent components and the event they are incorporated in. Whilst SLIMM predicts 66 memory enhancement of incongruent components (van Kesteren et al., 2012), it remains 67 unclear to what extent. By including an unrelated 'baseline' condition, where there is no 68 schema, we will test not only whether the presence of a prediction error supports schema-69 related memory, but also to what extent. For example, congruent and incongruent items 70 could be equally better than unrelated ones, show a graded response (congruent > 71 incongruent > unrelated), or be equivalent to unrelated events.

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To assess differences in memory performance between congruent and incongruent items, compared to an unrelated baseline, we used contextual events (see Experiment 1a in the Supplementary Materials for comparison between congruent-incongruent alone). The first pair in the event is location-object, as it easily instantiates the schema (or lack thereof) for the following items (farm-tractor immediately brings to mind other farm-related items, whereas golf course-torch does not intrinsically belong to a specific context or schema, see

| 79 | Bar & Aminoff, 2003). Both congruent and incongruent events had three components that |
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| 80 | were schema-congruent (A,B,D; see Figure 1 for examples). In the schema-based conditions, |
| 81 | A-B pairs elicited contextual expectations that were either met by a congruent C component |
| 82 | or violated by an incongruent one. In unrelated events, components did not share any |
| 83 | common contextual information. Memory was tested in two steps, first a yes/no item |
| 84 | recognition task for each component, followed by a cued recall for the adjacent component |
| 85 | (e.g. B-? or ?-D, see Figure 1). Cued recall was tested only for initially recognised |
| 86 | components. Multiple retrieval trials were employed to test effects of task demand |
| 87 | (recognition vs. recall, forward vs. backward cued recall). |

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- 89 90

Figure 1 about here

91 Experiment 1

92 Results and Discussion

Item recognition. A three (congruence: congruent, incongruent, unrelated) by two 93 94 (components: A, B, C, D) repeated measures ANOVA (Figure 2c) was conducted for corrected 95 recognition responses (hits – false alarms). Greenhouse-Geisser correction for the sphericity 96 assumption of ANOVAs are reported where appropriate, and all post-hoc analyses reported 97 are Bonferroni corrected. When multiple t-tests were computed, a threshold p value is 98 reported for all of them (e.g. all p's < .05). Despite near-ceiling recognition performance 99 (overall average of 93% accuracy), a main effect of congruence was found F(2,60) = 3.87 p = .026, $\eta_p^2 = .113$, with follow-up paired t-tests indicating congruent components were more 100 101 easily recognised than incongruent ones t(30) = 2.95, p = .006, Cohen's d = .53, and 102 unrelated cues t(30) = .258, p = .015, Cohen's d = .464. No differences were observed 103 between incongruent and unrelated components t(30) = .851, p = .4.

105 *Cued recall.* We first tested whether there were any effects of order on trials (AB - forward, 106 BA - backward) from the same pair (A-B). The three (congruence) by four (pair) by two 107 (order) repeated measures ANOVA yielded both a main effect of order F(1,30) = 11.2, p = .002, η_{p}^{2} = .272 and a significant three-way interaction F(6,180) = 4.2, p = .008, η_{p}^{2} = .123. This 108 109 suggests there were different patterns of performance in each condition between the 110 forward and backwards trials (see Figures 2a and 2b). Therefore, we carried out two 111 separate three (congruence) by four (pair) ANOVAs, one for each order (forward X - ?, and 112 backward ? - X). The forward ANOVA (Figure 2a) revealed a significant interaction between congruence and pairs F(6,180) = 5.37, p < .001, η_0^2 = .152. Similarly, the ANOVA for backward 113 pairs (Figure 4b) revealed an interaction effect F(6,180) = 4.01, p < .001, $\eta_p^2 = .118$. 114

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116 Planned comparisons between the congruence conditions for each trial were carried out to 117 examine differences between conditions. Congruent BC and CD trials (forward order) were 118 better recalled than incongruent and unrelated ones (all p's \leq .011). No significant 119 differences were observed between incongruent and unrelated components in these two 120 trials (all p's \geq .32). In the backward order trials, a benefit of incongruent over unrelated 121 trials was found for DC t(30) = 2.774, p = .009, Cohen's d = .5, and a trend towards it was 122 observed in CB trials t(30) = 1.75, p = .091, Cohen's d = .31. These results show the order 123 effect was due to a graded pattern (congruent > incongruent > unrelated) in the backward, 124 but not forward order. Finally, in DA and AD trials, incongruent components were better 125 recalled than unrelated and congruent ones and incongruent AB were more accurately 126 retrieved compared to congruent ones (all $p's \le .01$).

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Figure 2 about here

130 Interference analysis. To further elucidate the benefit of incongruence on D-A and A-B pairs, 131 we examined the erroneous answers for cued recall trials (Figure 2d). We inspected both 132 trials comprising the D-A pairing (AD and DA) together, to have a sufficient number of trials 133 and participants included (due to order effects in previous analysis we also carried out this 134 analysis separated by order, which showed similar results despite a lower number of trials 135 and participants included, see Supplementary Materials). We examined how many of the 136 errors were due to interference from C items, compared to a baseline (erroneous recall of 137 B/D). One out of the 31 participants had missing values for one pair, therefore data from 30 138 participants were analysed. A three (congruence: congruent, incongruent and unrelated) by 139 two (item: C and D/B) by two (pair: A-B and D-A) repeated measures ANOVA revealed interaction effects of congruence by item F(2,58) = 7.37, p = .001, η_p^2 = .203, and item by pair 140 F(1,29) = 10.36, p = .003, $\eta_p^2 = .263$. The three-way interaction effect was not significant 141 142 F(2,58) = 1.1, p = .34.

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144 Post-hoc tests revealed more C errors in congruent D-A and A-B pairs compared to 145 incongruent and unrelated ones (all p's < .004). There were also more C errors in 146 incongruent D-A and A-B pairs compared to unrelated ones (all p's < .038). When comparing 147 interference between C items and baseline B/D items, in D-A pairs we observed less 148 interference from incongruent C compared to incongruent B components (t(29) = 2.14, p =149 .041, Cohen's d = .391). In A-B trials, on the other hand, interference to incongruent pairs is 150 equivalent between C and D items (t(29) = .084, p = .934), but there is more interference 151 from congruent C items compared to congruent D ones (t(29) = 2.43, p = .021, Cohen's d =152 .444).

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154 The results described above show that memory performance for congruent components is 155 superior to incongruent and unrelated ones, in all testing formats. Incongruent items are, in

156 backward cued recall, more accurately retrieved than unrelated ones. The interference 157 analysis showed better recall performance for congruence-matched pairs (A-B, D-A) of incongruent events is due to reduced interference from C components, suggesting they are 158 159 less integrated into the event. Additionally, incongruent C items caused more interference 160 than unrelated ones, showing a similar pattern of responses as in backward cued recall. 161 Overall, these findings suggest that congruence benefits memory performance across the 162 board, but memory for incongruent components was modulated by task demands. 163 Differences in performance between incongruent and unrelated pairs, stemming from the 164 prediction error associated with incongruence, were observed in backward cued recall and 165 the interference analysis. In both cases, a graded response was observed (congruent > 166 incongruent > unrelated). In the recognition and forward recall, on the other hand, memory 167 for incongruent components was equivalent to unrelated ones.

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169 Experiment 2

170 To address the integration account of reduced performance for incongruent components, 171 we devised Experiment 2 to allow for easier integration of the pairs into a cohesive event. To 172 do so, events were presented as trial-by-trial pairs, rather than across blocks. Trial-by-trial 173 presentation differs in the contextual setting of learning. In Experiment 1, each pair was 174 compared to other pairs of the same kind (i.e. B-C pairs from different events were always 175 studied together). In Experiment 2, on the other hand, the 'reference point' is the previous 176 pair from the same event (B-C will follow A-B from the same event). This change would 177 allow for a quicker build-up of predictions, as the event pairs would now be temporally 178 closer than in the previous experiments. We added an associative inference task between A 179 and C items, which were not shown together, to test differences in integration levels. To 180 examine whether unexpected pairs are processed differently at encoding, we measured eye-181 movements during this stage. We reasoned that changes in fixation patterns observed at

- 182 encoding would indicate a different allocation of resources to components that are more183 difficult to encode and integrate into the event.
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185 Eye-tracking results

186 We first subjected the number of fixations to a three (congruence) by four (pair) by 2 (area 187 of interest, AOI) ANOVA (Figure 3a), which showed a significant main effect of pair F(2.1,56.73) = 73.6, p < .001, $\eta_p^2 = .732$, a congruence by pair interaction F(6,162) = 5.63, p 188 189 <.001, η_p^2 = .173 and a significant AOI by pair interaction F(2.23,60.32) = 25.7, p < .001, η_p^2 = 190 .49. Post-hoc comparisons showed the least amount of fixations on the B item of unrelated 191 A-B pairs, when compared to the congruent and incongruent conditions (all p's \leq .008). 192 Additionally, unrelated B-C pairs were associated with fewer fixations on B, when compared 193 to congruent and incongruent pairs (all p's < .001). For the C components in the B-C pairs, 194 congruent components were associated with the lowest number of fixations compared to 195 incongruent and unrelated ones (all p's \leq .008). A similar analysis for fixation durations 196 (Figure 3b) revealed significant main effects of pair F(1.53, 42.91) = 76.33, p < .001, η_p^2 = .732 and AOI F(1,28) = 13.21, p = .001, η_p^2 = .321, as well as a pair by congruence interaction 197 F(6,168) = 5.9, p < .001, $\eta_p^2 = .174$, and a pair by AOI interaction F(3.84) = 19.98, p < .001, 198 η_p^2 = .416. Planned comparisons indicated that in unrelated B-C pairs, fixations on the B 199 200 components were shortest and those on C components were longest, compared to 201 congruent and incongruent pairs (all p's \leq .003).

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Figure 3 about here

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205 Behavioural Results

Item recognition. A three (congruence: congruent, incongruent, unrelated) by four
(component: A, B, C, D) repeated measures ANOVA was conducted for corrected recognition

responses. Again, a main effect of congruence was found F(2,54) = 14.83 p < .001, $\eta_p^2 = .355$, with follow-up paired t-tests indicating congruent components were more easily recognised than incongruent and unrelated ones (all p's \leq .002). No differences were observed between incongruent and unrelated components (p > .2).

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213 Cued recall. We first tested whether there were any effects of order. Similar to Experiment 214 1, the three (congruence) by four (pair) by two (order) repeated measures ANOVA yielded a significant three-way interaction F(6,162) = 4.39, p < .001, η_p^2 = .14. This suggests there were 215 216 different patterns of performance in each condition between the forward and backwards 217 orders. Therefore, we performed two separate three (congruence) by four (pair) ANOVAs, 218 one for each presentation order (forward X - ?, and backward ? - X). The forward ANOVA (Figure 4a) revealed a significant congruence by pair interaction F(4.14, 112) = 5.67, p < .001, 219 η_p^2 = .174. The ANOVA for backward trials (Figure 4b) was akin to that for the forward trials, 220 221 with an interaction between congruence and pair F(6,162) = 9.37, p < .001, η_p^2 = .258.

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223 Planned comparisons between the congruence conditions for each trial were then carried 224 out. For AB and DA trials a similar pattern emerged, whereby there were no significant 225 differences between congruent trials and any of the other conditions (all p's \ge .02), but a 226 significant benefit of incongruent trials over unrelated ones was observed (all p's \leq .002). 227 Unrelated BA trials were associated with reduced recall performance compared to 228 congruent and incongruent ones (all p's \leq .006). For BC, CB, CD and DC trials there were 229 again similar findings, with congruent trials associated with better recall compared to 230 incongruent and unrelated trials (all p's \leq .013), but no difference was observed between 231 incongruent and unrelated trials (all p's \geq .668). These results suggest that performance for 232 trials that are part of incongruent events tracks their level of relatedness.

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Figure 4 about here

236 Associative inference retrieval task (A-C). A three (congruence) by two (component: A vs. C) 237 ANOVA yielded a significant main effect of congruence F(1.57, 40.97) = 105.46, p < .001, η_p^2 238 = .802 (Figure 4c). The main effect of component was not significant F(1,26) = .016, p = .901, 239 as was the interaction effect F(1.43, 37.23) = .58, p = .508. Post-hoc tests revealed that 240 congruent components were associated with better performance compared to incongruent 241 and unrelated ones, and a benefit of incongruent components over unrelated ones (all p's < 242 .001). 243 244 Interference analysis. . A three (congruence: congruent, incongruent and unrelated) by two 245 (component: C and D/B) by two (pair: A-B and D-A) repeated measures ANOVA (Figure 4d) 246 revealed a significant interaction between congruence and item F(2,54) = 34.8, p < .001, n_p^2 247 = .563). The other two-way interactions, as well the three-way interaction were not 248 significant (all p's > .248). Planned comparisons showed increased interference from 249 congruent C components in A-B and D-A pairs, compared to incongruent and unrelated 250 components (all p's < .001). There were no significant differences between incongruent and 251 unrelated C components (all p's > .528). Additionally, there was more interference from 252 incongruent B/D (baseline) components, compared to incongruent C components, in D-A 253 pairs (t(27) = 4.45, p < .001, Cohen's d = .841) and A-B pairs, respectively (t(27) = 3.44, p =254 .002, Cohen's d = .778).

255

256 General Discussion

In a series of experiments, we found that unexpected incongruent components were lesslikely to be recognised and recalled, compared to congruent ones. This pattern was observed

259 both when events were presented across blocks, to allow for predictions to develop 260 gradually, and when events were constructed trial-by-trial, to promote easier integration. 261 Examination of fixation patterns during encoding of such events revealed increased fixations 262 on the first unexpected incongruent component, compared to their congruent counterparts, 263 suggesting they were more difficult to encode. Our results suggest the presence of a 264 prediction error in incongruent pairs did not enhance memory to the level observed in 265 congruent events. However, depending on task demands, it did benefit memory compared 266 to unrelated components (showing a graded pattern of responses). Finally, a beneficial 267 effect of incongruence was observed in A-B and D-A pairs, which were only indirectly related 268 to the incongruent C component.

269

270 The advantageous role of schema congruence on memory performance, compared to both 271 incongruent and unrelated items, is in line with the congruency effect. Previous findings, and 272 predictions from SLIMM, suggest congruent items benefit from the existing strong 273 representation of the schema (Craik & Tulving, 1975; Staresina et al., 2009; van Kesteren et 274 al., 2012). Previous experiences of similar associations (e.g. farm-tractor) are reactivated by 275 the mPFC (Brod et al., 2013; Preston & Eichenbaum, 2013; Schlichting & Preston, 2015), and 276 proposed to be more readily available during retrieval (Hemmer & Steyvers, 2009; 277 Moscovitch & Craik, 1976; Steyvers & Hemmer, 2012). This notion is in line with our finding 278 that congruent A-B and D-A pairs are more prone to interference from C components, 279 showing reduced recall accuracy. Incongruent components, and unrelated ones even more 280 so, are more difficult to integrate into the event (Bein et al., 2015; Craik & Tulving, 1975), 281 resulting in less associative competition (Caplan et al., 2014), or a more constrained search 282 space (Anderson, 1981) for retrieving A-B and D-A.

283

284 Further evidence for the reduced integration of incongruent C components can be found in 285 forward-order trials in Experiment 1, as well as in all retrieval trials in Experiment 2. 286 Incongruent components show comparable results, in memory performance and eye-287 fixation patterns, to those of their unrelated counterparts. The eye-tracking results indicate 288 increased effort invested in encoding incongruent items, but this effort does not come into 289 fruition later in retrieval performance. The encoding part of this effect can be attributed to 290 MTL-driven function, showing the prediction error associated with an incongruent 291 component promotes more elaborate encoding. During retrieval, congruent information 292 seems to be dominating, especially in trials where a congruent item (B or D) cues retrieval of 293 an incongruent item. In this case, mPFC involvement would potentially direct retrieval 294 towards congruent representations (Preston & Eichenbaum, 2013; van Kesteren et al., 295 2012). Although previous studies have shown similar encoding and retrieval effects 296 independently (van Kestern et al., 2010, 2013), future neuroimaging studies could examine 297 the co-occurrence of such effects. Additionally, due to the use of bidirectional cued-recall 298 tests, we could not directly correlate fixations at encoding with later retrieval performance, 299 but this would be an interesting effect to examine.

300

301 Incongruent components also served as worse cues for their associates (Schulman, 1974), 302 showing impaired recall performance (equivalent to unrelated pairs). This finding is more 303 difficult to interpret in light of SLIMM's predictions (van Kesteren et al., 2012), as successful 304 retrieval in this case requires reactivation of a congruent item. We argue this finding points 305 to difficulty in binding the incongruent component into the event (Craik & Tulving, 1975; 306 Bein et al., 2015; Packard et al., 2017), as also indicated by increased fixations. Given that 307 schemas facilitate gist extraction and abstraction of commonalities (Gilboa & Marlatte, 308 2017), the presence of an incongruent component in the event could interrupt this process. 309 This would therefore result in reduced schema instantiation to support binding of the

incongruent C component to its congruent pairwise associates, explaining impairedperformance on C-B and C-D pairs.

312

313 Interestingly, in the backward order retrieval trials and interference analysis (Experiment 1), 314 as well as in the A-C inference task (Experiment 2), a graded pattern of responses was 315 observed (congruent > incongruent > unrelated). To our knowledge, this is the first study to 316 show such pattern. Although van Kesteren and colleagues (2012) postulated memory for 317 both congruent and incongruent items would be enhanced, the extent to which this effect 318 varies between conditions was unclear. Previous findings pertaining to congruency effects 319 have not used an unrelated baseline condition, making it difficult to account for such 320 differences. Here, we find that whilst components from congruent events were 321 unequivocally better recalled, incongruent components showed better performance 322 compared to unrelated ones. This pattern of results suggests a prediction error can enhance 323 memory performance (compared to unrelated items), though not to the same extent as 324 congruence does. Interestingly, this result was observed only under specific circumstances, 325 suggesting this effect could be susceptible to task demands (Ghosh & Gilboa, 2014).

326

327 In Experiment 1, events were created across blocks, thus online comparisons were between 328 B-C pairs from different events. Conversely, in Experiment 2 comparisons were made with A-329 B pairs from the same event. This difference in temporal context during encoding, could 330 have biased processing of incongruent pairs in Experiment 1 compared to Experiment 2 331 (Howard & Kahana, 2002). Although overall memory performance in Experiment 1 was 332 symmetric between forward and backward trials, graded responses were observed only in 333 backward trials. Asymmetry in memory recall has been suggested to depend on the 334 relationship between paired associates (Greene & Tussing, 2001; Li & Lewandowsky, 1995; 335 Yang et al., 2013) and to engage the anterior hippocampus (Giovanello, Schnyer, &

336 Verfaellie, 2009). Forward recall is believed to be schema-driven (Geiselman & Callot, 1990) 337 and more susceptible to disruptions during formation of associations at encoding (Li & 338 Lewandowsky, 1995). In line with this, we find superior memory for congruent components, 339 with no differences between incongruent and unrelated pairs in the forward order. 340 Backward recall, on the other hand, is suggested to be more data-driven (Geiselman & 341 Callot, 1990) and thus more susceptible to contextual details at encoding. We therefore 342 suggest backward retrieval in our task promoted the beneficial effect of prediction error, 343 mediated by hippocampal engagement (van Kesteren et al., 2012).

344

345 Graded responses were also obtained in the associative inference task in Experiment 2. 346 Successful performance on such tasks is often used as a marker for schematic organisation 347 of representations in memory, as it supports novel integration of indirectly related items 348 (Kumaran, Summerfield, Hassabis, & Maguire, 2009; Preston & Eichenbaum, 2013; Tse et al., 349 2007; Zeithamova, Dominick, & Preston, 2012). In this task, incongruent and unrelated pairs 350 were matched on relatedness and differed only on the build-up of expectations from the 351 event's schema. Thus, the presence of a prediction error here could have mediated 352 enhanced inference in this task. Alternatively, the mere existence of a schema in the 353 incongruent condition, as opposed to the unrelated one, could have supported this 354 inference (Kumaran, 2013; McClelland, 2013; Preston & Eichenbaum, 2013; Tse et al., 2011; 355 Zeithamova et al., 2012). Future research on schema effects would benefit from further 356 exploring these effects, specifically in relation to how task demands can modulate memory 357 for incongruent information.

358

Our main aim was to test behavioural predictions outlined by SLIMM (van Kesteren et al., 2012). We thus utilised a paradigm that allows expectations to gradually develop by using interleaved learning of paired associates. The findings reported above provide some support

362 to the notion prediction errors can enhance memory for incongruent items. An alternative 363 interpretation is that the amount of prediction error associated with incongruent 364 components in our studies was not large enough to result in conclusively improved 365 performance. Critically, our task was designed to implicitly set participants' predictions. This 366 was done in order to capture the inherent aspect of predictions as they arise in daily life, and 367 to avoid any artificial allocation of attention towards this manipulation. As a result of this 368 manipulation, we could not quantify the amount of prediction error elicited by incongruent 369 components, but only indirectly assert contextual predictions were elicited by the stimuli 370 used (Bar & Aminoff, 2003).

371

372 In conclusion, our results provide further evidence for the notion that schemas aid memory 373 by providing a structured representation into which congruent information can easily fit. The 374 findings reported here also shed light on the extent to which prediction errors in 375 incongruent items support its presence in memory. Although it requires more effortful 376 encoding, retrieval success of incongruent items is always reduced compared to congruent 377 components. The extent to which incongruent items are better remembered compared to 378 unrelated components, on the other hand, is modulated by task demands. Future research 379 looking into schema-mediated memory may build on the approach and findings highlighted 380 above to better understand factors contributing to these effects.

381

382 Methods

383 Experiment 1

Participants. 35 participants (12 males) gave informed consent to take part in the
experiment. Four participants whose recognition performance was either above or below
three times the IQR were excluded from any further analysis. Thus, data from 31 participants
between the ages 18-27 (M = 19.8, SD = 2.91) were analysed.

388

389 Materials. The experiment was controlled using E-Prime 1 (Psychology Software Tools). 390 Stimuli were 30 four-components events (10 congruent, 10 incongruent 10 unrelated 391 events). Each event contained a location (component A, e.g. farm), two objects (components 392 B and D, haystack and a tractor) and a person's profession (component C, farmer). Items 393 were presented as images with labels above them (see Figure 1 for examples). Congruent 394 and incongruent events were constructed to elicit strong contextual predictions, meaning 395 that their components are most likely to appear in the given context, as established by 396 previous work (Bar & Aminoff, 2003). Ten of the events were assigned to be in the 397 incongruent condition, such that the person (C component) was unexpected in the context 398 (a lawyer in the context of a farm with a haystack and a tractor). Another 10 were 399 congruent, meaning the person was expected given the context (a farmer in a farm). The 400 final 10 events included objects with low contextual value (Bar & Aminoff, 2003), meaning 401 they can be found in in a variety of contexts. The allocation of events to conditions was 402 counterbalanced across participants. Images were obtained from freely available online 403 resources labelled with a Creative Commons License.

404

405 Procedure. The experiment consisted of three phases: encoding, distraction and retrieval 406 (see Figure 1). The encoding phase was interleaved and took place over 4 blocks, one block 407 for each pairwise association (A-B, B-C, C-D, D-A). Critically, A-B and D-A pairs are not directly 408 associated with the C component (which defines whether an event is assigned to a 409 congruent or incongruent condition). These pairs are congruent in both congruent and 410 incongruent conditions, thus providing an opportunity for testing the effect of incongruence 411 on the rest of the event. Each block consisted of 30 randomised-order trials, resulting in a 412 total of 120 trials in the encoding phase. Each trial began with a one-second fixation cross, 413 followed by presentation of one pair of labelled images for three seconds. Participants were

- 414 instructed to imagine the components interacting together, as vividly as they could, while415 being aware of their respective location on the screen (right and left).
- 416

To prevent participants from actively rehearsing the encoded information, a distractor task involving solving arithmetic problems was used for five minutes. Participants were instructed to be as accurate as possible and were informed that if they failed to reach a certain performance threshold their data would be excluded from further analysis. Following this task, the retrieval phase began, where items were presented in a pseudo-randomised order, based on 10 pre-made lists. Two retrieval tasks were employed, a recognition task for each component, followed by a cued-recall task only for the recognised components.

424

425 Participants were first presented with the yes/no recognition task. They had a maximum of 426 10 seconds to complete this task. If they responded 'yes', a second cued-recall task took 427 place immediately. For this task, the recognised component was coded as 'cue' and the 428 recalled component as 'target'. Participants were asked to recall which item appeared with 429 the previously recognised item (a source recall task, retrieve the item in the location 430 indicated on the screen). Each pairwise association from each event was tested in both 431 directions in a randomised order (for example, forward A-? and backward ?-B). A cued-recall 432 answer was scored as correct if it was identical to the item presented at encoding, if it was a 433 specific case of the same category (for example, 'car mechanic' instead of 'mechanic') or 434 semantically similar ('gymnast' instead of 'acrobat'). If the participant failed to give an 435 answer within 20 seconds of the cue being presented, the trial was scored as incorrect. In 436 addition to the 120 items that were encoded, 30 additional items, making up six events, 437 were used as foils.

438

439 Experiment 2

440 Experiment 2 was identical to Experiment 1, with the following modifications:

Participants. 35 participants (9 males) gave informed consent to take part in the experiment.
Data from seven participants were removed from any further analysis due to technical
failure of the eye-tracker (one participant), poor eye-tracking data (three participants;
inclusion of these participants in the behavioural analysis did not change the results) and
poor memory performance, above or below three times the IQR (three participants). Thus,
data from 28 participants between the ages 18-28 (M = 20.8, SD = 2.78) were analysed.

447

Materials and apparatus. The materials were identical to those used in Experiment 1. To examine fixation patterns during encoding, eye movements were recorded during encoding, using an ASL infrared eye tracker (Eye-Trac 6000, Applied Science Laboratories) at a sampling rate of 60 Hz. The desktop-mounted camera was placed under the presentation screen, 70cm away from the participant. A chin-rest was used to minimise participants' movement.

453

454 Procedure. Before the experiment started, eye calibration was performed using a 9-point 455 matrix. During the encoding phase in Experiment 2, events were presented sequentially, 456 trial-by-trial, rather than across blocks as was done in Experiment 1. Each of the four pairs 457 comprising an event was presented for three seconds, with a 1s fixation cross between 458 them. Following the last pair of the event, a fixation cross was displayed for 2s, until a new 459 event had started. To examine whether reduced performance for the incongruent C 460 components was due to a difficulty in integrating them as part of the events, an additional 461 retrieval inference task was employed. Following the cued-recall task, participants were 462 presented with a location or a person (A or C components) for a maximum of 10 seconds 463 and were asked to recall its counterpart person or location from the same event, 464 respectively.

465

| 466 | Eye tracking analysis. Eyeneal software (Applied Science Laboratories) was used to convert |
|-----|--|
| 467 | the raw gaze coordinates to fixation points. The start of a fixation point was defined as six |
| 468 | sequential gaze points with a standard deviation smaller than 0.5 visual degrees. The end of |
| 469 | a fixation was marked when three consecutive gaze points were at least one visual degree |
| 470 | away from the initial fixation location. The fixation points reported below are the average |
| 471 | point of the start and end fixation locations. Two areas of interest (AOI) were defined in the |
| 472 | Fixplot software (Applied Science Laboratory), one for each of the images displayed on the |
| 473 | screen. Statistical analyses were conducted on the number of fixations and fixation duration |
| 474 | for each AOI. |
| 475 | |
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- 478
- 479 *Author Contributions Statement*:
- 480 D.F., D.M., B.W., and D.T. designed the experiment, D.F collected and analysed data, D.F.,
- 481 D.M., B.W. and D.T. wrote the manuscript.
- 482
- 483 *Competing financial interest statement:*
- 484 The author(s) declare no competing financial interests.

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| 616 | |

617 Figures



618

619 Figure 1 | Experimental Design. A) Encoding phase. Participants 120 paired associates, over four blocks, one for each pairwise association from every event. 620 They imagined each pair interacting in a meaningful way for 3s. Each pair was 621 preceded by a 1s fixation cross. B) Retrieval phase. Participants were presented with 622 623 a cue and asked to indicate whether they remember seeing it at encoding. If they 624 responded 'yes' they were asked to recall one of the other components from the 625 same event, based on the spatial location of the cue. Inference association task was 626 used in Experiment 2. Labels in parentheses are for illustration and were not 627 presented during the experiment.





Figure 2 | Results Experiment 1. A) Cued recall performance forward pairs (e.g. A-?). 630 B) Cued recall performance backward pairs (e.g. ?-B). In both orders performance 631 tracks levels of relatedness of pairs, such that most incongruent and unrelated pairs 632 are equivocal. C) Item recognition, Congruent C components show better accuracy 633 634 compared to incongruent ones. D) Interference analysis, percentage of erroneously 635 recalled C items in the cued recall task. Most interference from congruent items, 636 followed by incongruent and then unrelated. Unless otherwise states, error bars represent standard error of mean. * $p \le .05$, ** $p \le .01$, *** $p \le .001$ 637



Figure 3 | Eye tracking results Experiment 2. A) Number of fixations on each item, per pair. Increased fixations on first presentation of incongruent and unrelated items. B) Total time spent fixating on each item of the pair during the 3s encoding trial. More time spent fixating on unrelated C items. * $p \le .05$, ** $p \le .01$, *** $p \le$.001

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Figure 4 | Behavioural results Experiment 2. A) Cued recall performance forward 645 pairs (e.g. A-?), incongruent items on par with unrelated ones. B) Cued recall 646 performance backward pairs (e.g. ?-B), similarly to forward order, incongruent and 647 648 unrelated items associated with reduced performance. C) Associative inference, 649 recall of A cued by C and vice versa. Near-ceiling performance for congruent items, 650 followed by incongruent items associated with better performance than unrelated ones D) Interference analysis, higher percentage of erroneously recalled congruent C 651 items in the cued recall task. * $p \le .05$, ** $p \le .01$, *** $p \le .001$ 652