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Competitive state of actions during planning predicts sequence execution accuracy.

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19   collected the data; M.M. and K.K. designed the analysis; G.H. and K.K. designed the
20   computational model; M.M., T.I. and K.K. performed the analysis; M.M., T.I., G.H. and
21   K.K. wrote the paper. All authors contributed to editing of the manuscript.

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Abstract

Humans can learn and retrieve novel skilled movement sequences from memory, yet the content and structure of sequence planning are not well understood. Previous computational and neurophysiological work suggests that actions in a sequence are planned as parallel graded activations and selected for output through competition (competitive queuing; CQ). However, the relevance of CQ during planning to sequence fluency and accuracy, as opposed to sequence timing, is unclear. To resolve this question, we assessed the competitive state of constituent actions behaviourally during sequence preparation. In three separate multi-session experiments, 55 healthy participants were trained to retrieve and produce 4-finger sequences with particular timing from long-term memory. In addition to sequence production, we evaluated reaction time (RT) and error rate increase to constituent action probes at several points during the preparation period. Our results demonstrate that longer preparation time produces a steeper CQ activation and selection gradient between adjacent sequence elements, whilst no effect was found for sequence speed or temporal structure. Further, participants with a steeper CQ gradient tended to produce correct sequences faster and with a higher temporal accuracy. In a computational model, we hypothesize that the CQ gradient during planning is driven by the width of acquired positional tuning of each sequential item, independently of timing. Our results suggest that competitive activation during sequence planning is established gradually during sequence planning and predicts sequence fluency and accuracy, rather than the speed or temporal structure of the motor sequence.

Keywords:

motor sequence; preparation; reaction time; finger accuracy; competitive queuing

Introduction

Producing a variety of movement sequences from memory fluently is an essential capacity of primates, in particular humans. It enables a skilled and flexible interaction with the world for a range of everyday activities - from tool-use, speech and gestural communication, to sports and music. Key to fluent sequence production is sequence planning before the initiation of the first movement[1,2], with longer preparation time benefitting sequence execution, i.e. reducing initiation time after a 'Go' cue and improving accuracy[3]. However, the underlying nature and content of sequence planning is still debated[4].

Computational models of sequence control, such as competitive queuing (CQ) models, suggest that preparatory activity reactivates sequence segments *concurrently* by means of a parallel activation gradient in the parallel planning layer[5]. Here the neural activation pattern for each sequence segment is weighted according to its temporal position in the sequence[6,7]. A rich literature indirectly supporting CQ in sequence control stems from observations of serial recall including transposition of neighbouring items and items occupying the same position in different chunks[6,8,9], and excitability of forthcoming items during sequence production[10]. Moreover, the CQ account has also been substantiated directly at the neurophysiological level in the context of well-trained finger sequences[11,12], saccades[13] and drawing geometrical shapes[14]. Importantly, these results have demonstrated that the neural gradient during planning is relevant to subsequent execution. In particular, response separation in the competitive gradient during sequence planning is predictive of sequence production accuracy[11,14]. Together, these data suggest that skilled sequence production involves the concurrent planning of several movements in advance before sequence initiation to achieve fluent performance.

While neural CQ during planning has been shown to predict subsequent production, it remains unclear which properties of the sequence this preparatory pattern encapsulates – the accuracy of the sequence (fluency of initiation and production quality), or the temporal structure of the sequence (speed and temporal grouping). Some CQ models assume the presence of a temporal context layer and that the activity gradients are learned by associations of the latter to each sequence element in the parallel planning layer, e.g. through Hebbian learning[7]. The form of activity in the context layer can be as simple as a decaying start signal[15], a combination

88   of start and end signals[5,16] or a sequence of overlapping states[7,17]. Although primarily

89   encoding serial order of sequence items, models utilizing overlapping states can

90   implement effects of temporal grouping or sequence rhythm[7]. Therefore, it is possible

91   that the competitive activation of actions during sequence planning encodes the

92   temporal structure of the upcoming sequence.

93   In order to investigate the nature of sequence preparation and its relation to

94   subsequent performance, we have developed a behavioural paradigm to capture the

95   preparatory state of each item during planning of a well-learned sequence. Following

96   training, participants prepared a motor sequence from memory following an abstract

97   visual stimulus associated with a particular sequence of finger presses performed with

98   a particular temporal structure and speed. In half of the trials during the test phase,

99   the 'Go' cue was replaced by a finger press cue probing presses occurring at different

100   positions of the sequence. We used reaction time (RT) and finger press accuracy to

101   these 'probes' to compute as measures of the relative activation of planned actions

102   during sequence planning.

103   We hypothesized that if competitive queuing primarily reflected the accuracy of

104   the sequence plan, we would on average observe an enhancement of the CQ gradient

105   with longer preparation time, as well as a correlation of the gradient with measures of

106   sequence fluency and skill, specifically more rapid sequence initiation of correct

107   sequences after the 'Go' cue, more accurate timing and fewer finger press errors. If,

108   however, the gradient reflected the temporal structure – the speed and temporal

109   grouping of the sequence, we should see that it is less pronounced for sequences

110   twice as fast (speed manipulation), and shortened vs lengthened inter-press-intervals

111   (IPI; temporal structure manipulation), because the actions are closer together in time.

112   We find that the relative level of activation of probed actions at the end of the

113   planning period accords with their intended serial position. Contrary to the timing

114   hypothesis, we found no reliable association with speed or temporal structure of the

115   sequences. In contrast, we report that the corresponding CQ gradient is enhanced

116   with longer preparation time, and is correlated with faster initiation of correct

117   sequences and better temporal accuracy. Our data suggests that the competitive

118   queuing gradient during planning primarily encodes the intended order of actions and

119   the accuracy of a sequence plan, and not its overall speed or temporal structure.

120   Based on this data, we propose a computational model that explains how the width of

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121 purely positional tuning could act on the relative activation state of actions during

122 sequence planning independently of timing to enable accurate and fluent sequence

123 performance.

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125   **Preparation** 500/1000/1500 ms
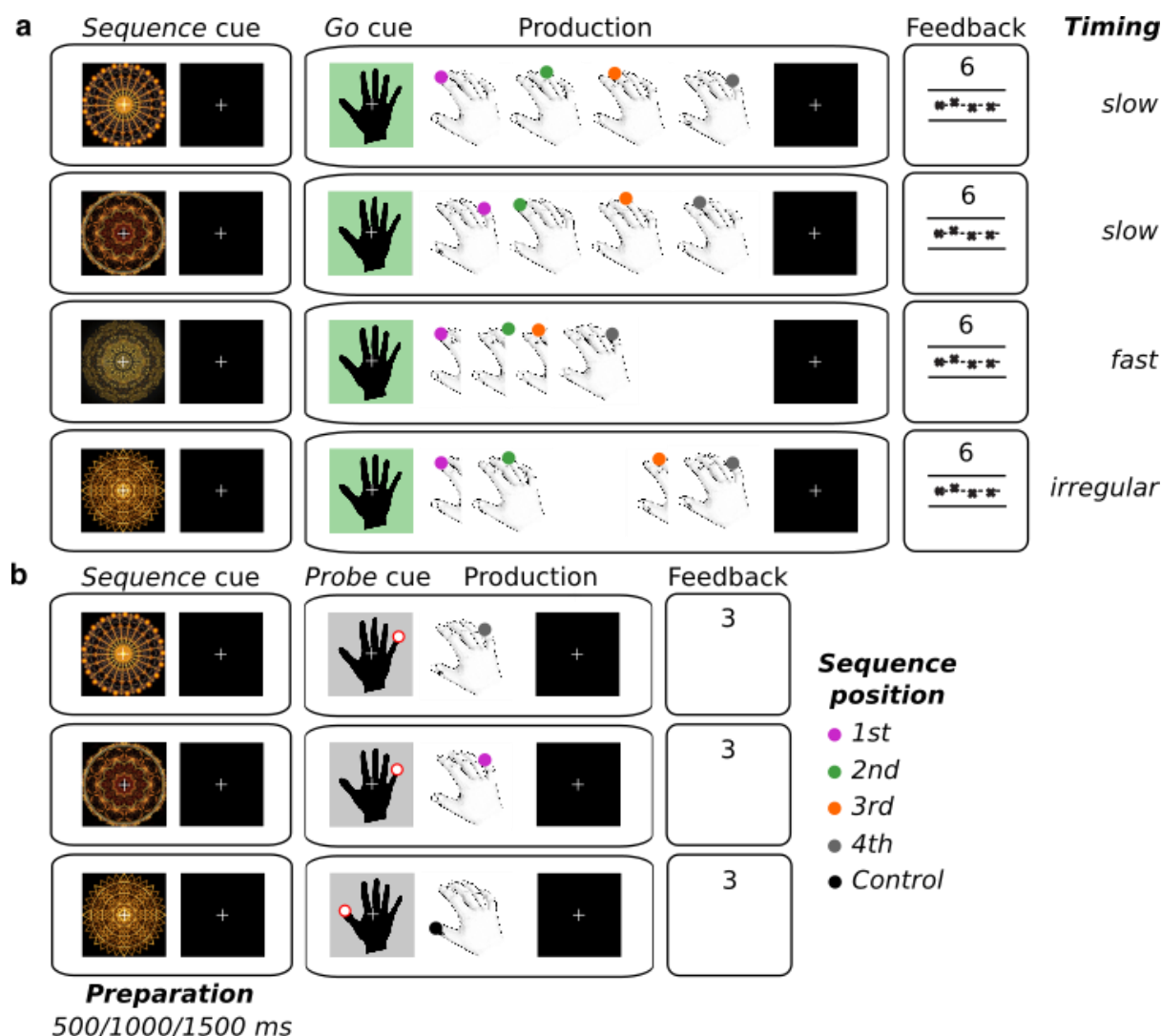
Figure 1 | Experimental conditions. a. Participants were trained to produce 4-element finger sequences following a *Go* cue from memory. Each finger sequence or timing corresponded to a unique abstract visual *Sequence* cue presented up to 1500 ms before the Go cue (Preparation period). Experiment 1 cued the production of sequences with two different finger press orders. Here we manipulated the duration of the Preparation period (500, 1000 or 1500 ms). Experiments 2 and 3 had a fixed preparation duration of 1500 ms, but *Sequence* cues prompted the production of sequences with a different temporal structure (slow, fast and irregular). Participants received visual feedback in each trial on the accuracy of the press order and their timing, and received points based on press accuracy, temporal accuracy and initiation time (cf. Methods section). **b**. In all experiments, we introduced *Probe* trials, in which following the preparation period the *Go* cue was replaced with a *Probe* cue prompting a particular finger digit to be pressed, corresponding to each sequence position or control (thumb, which did not feature in any sequence production). This condition was used to obtain the reaction time (RT) and error rate for each position at the end of the preparation period. They received points for accurate production and fast RTs.

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128   **Results**

129   ***Finger press accuracy in sequences produced from memory was***
130   ***matched across conditions***

131   Across three experiments, participants were trained for two days to associate
132   two or three abstract visual cues with a particular four-element finger sequence
133   performed with a particular temporal structure (Timing: slow, fast or irregular) following
134   a brief preparation period (Delay between *Sequence* and *Go* cue onsets: short / 500ms,
135   intermediate / 1000 ms and long / 1500 ms). In the test phase on the third day, they
136   produced the respective sequences entirely from memory (Figure 1, all panels).

137   The finger error rate in sequence production from memory was higher in
138   Experiment 1 than in Experiments 2 and 3. This is likely due to Experiment 1 involving
139   the production of two different finger sequences produced with the same timing, and
140   Experiments 2 and 3 involving the production of one finger sequence with different
141   timings. The mean occurrence of finger errors, as indicated by either incorrect finger
142   order or incomplete sequences, ranged from 0% to 26.6% in the short ($M = 5.6\%$, *SD*
143    $= 6.9$), 0% to 21.9% in the intermediate ($M = 5.7\%$ *SD* $= 6$), and from 0% to 15.6% in
144   the long Delay condition ($M = 4.6\%$, $SD = 4.5$) in Experiment 1. In Experiment 2, finger
145   error rate varied between 0% and 5.5% at the slow timing ($M = 2.2\%$, $SD = 2.1$),
146   between 0% and 8.5% at the fast timing ($M = 2.2\%$, $SD = 2.5$), and between 0% and
147   7% at the irregular timing ($M = 2.3\%$, $SD = 2.7$). Error performance in Experiment 3
148   showed a rate between 0% and 13.3% at the slow timing ($M = 2.6\%$, $SD = 3.4$),
149   between 0% and 7.5% at the fast timing ($M = 2.8\%$, $SD = 2.5$), and between 0% and
150   9.2% at the irregular timing ($M = 2.4\%$, $SD = 2.6$).

151   Neither Delay (Experiment 1, $F_{(2, 36)} = .993$, $p = .451$, $\eta p^2 = .052$) between
152   the *Sequence* and the *Go* cue, nor the sequence Timing condition affected finger press
153   accuracy during sequence production (Experiment 2, $F_{(2, 34)} = .006$, $p = .994$,
154    $\eta p^2 = .000$; Experiment 3, $F_{(1.458, 24.787)} = .249$, $p = .711$, $\eta p^2 = .014$, Greenhouse-
155   Geisser corrected, $\chi_2 (2) = 7.436$, $p = .024$, Figure 2c). This means that participants
156   learned and prepared the finger order of all target sequences with the same finger
157   accuracy, regardless of the preparation time or the temporal structure of the planned
158   sequence.

159   ***Participants produced sequences from memory with correct relative***
160   ***timing***

161   When producing the sequences from memory during the test phase,
162   participants had a general tendency to produce faster versions of the finger press
163   sequences (Figure 2a), similar to the effects found in previous work[18]. The produced
164   sequence duration was shorter than the target duration by 28.4% (SD = 10.7%), 38.6%
165   (SD = 20.6%) and 46.2% (SD = 17.4%) in Experiment 1, 2 and 3, respectively (Figure
166   2a). However, the goal of our experimental design was to train participants to either
167   retain or to modulate the *relative* timing across conditions according to the target
168   relative IPIs, respectively (Figure 2b). Importantly, the majority of participants
169   produced the sequences with the correct relative timing across conditions – on
170   average the same temporal structure (slow) across preparation durations in
171   Experiment1, and three different temporal structures (slow, fast, irregular) in
172   Experiments 2 and 3 (Figure 2b).

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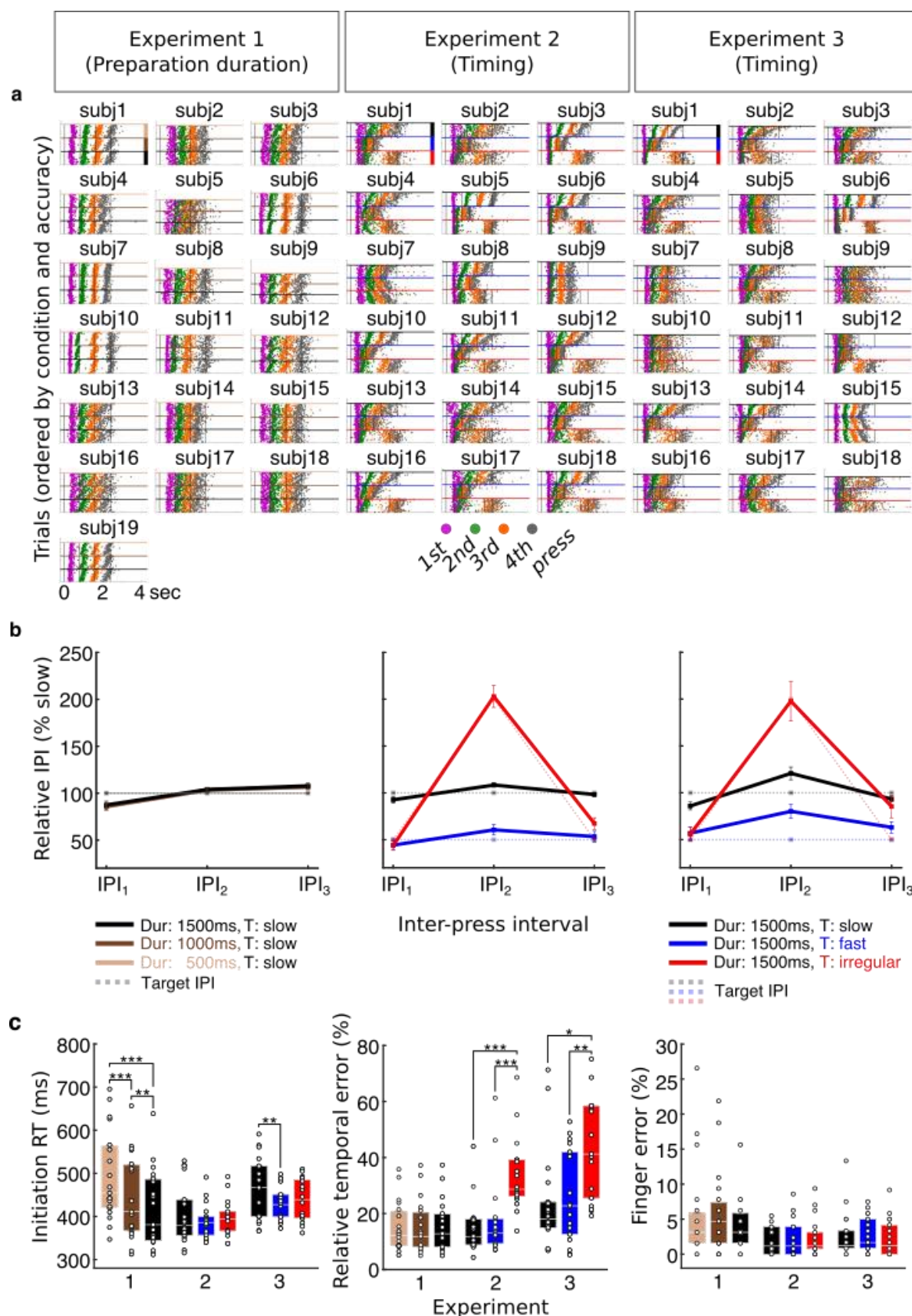
Figure 2 | Sequence production. a. Individual participants' raster plots show the timing of single button presses for each correct sequence trial produced from memory after the *Go* cue (t = 0) following training (target timing superimposed, grey lines). The colour code of the button presses corresponds to the

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press position in Figures 1 and 5. Within each condition, trials are ordered from most accurate to least accurate with regard to target onset (colour coding for conditions, cf. side bars in first participant panels, respectively). **b.** On average IPI production followed the target IPI structure, with a slow, twice as fast and an irregular sequence. IPIs were normalized across trials relative to slow isochronous condition. Preparation duration did not modulate IPI production of slow sequences, in contrast to the timing conditions. Error bars represent standard errors. **c.** Sequence initiation RT (Go cue to first press latency) decreased with preparation time (foreperiod effect). Relative temporal error was elevated for the irregular sequence in both experiments 2 and 3, in which it occurred. There was no effect of any of the conditions on finger press error rate, defined as proportion of incorrect trials. | * P ≤ 0.05 | ** P ≤ 0.01 | *** P ≤ 0.001.

174   Despite a largely overlapping sequence timing across preparation durations in

175   Experiment 1 (Figure 2b, left), we found a small, but significant IPI × Delay interaction

176   (3×3 repeated measures ANOVA: $F_{(4, 72)} = 2.528$, $p = .048$, $\eta p^2 = .123$) explained by

177   a modulation of 9 ms. Post-hoc comparisons (Bonferroni-corrected for nine tests)

178   revealed a significant shortening of the 1_{st} interval in the short ($p = .002$) and in the

179   intermediate delay ($p = .002$) compared to the long delay conditions. Additionally, the

180   3_{rd} interval was larger in the long delay than at the intermediate delay ($p = .004$). This

181   shows that there was a tendency to slightly compress the 1_{st} interval with shorter

182   preparation time and slightly expand the 3_{rd} interval with longer preparation time.

183   However, the size of this temporal modulation in Experiment 1 was 97% smaller than

184   the temporal structure modulation induced in Experiments 2 and 3. Any potential

185   sequence timing effect on CQ activation of actions during preparation should thus be

186   vastly augmented in Experiments 2 and 3.

187   As expected, Experiment 2 showed a significant IPI × Timing interaction (3×3

188   repeated measures ANOVA: $F_{(1.260, 21.417)} = 59.485$, $p < .001$, $\eta p^2 = .778$,

189   Greenhouse-Geisser corrected, $\chi_2 (9) = 97.832$, $p < .001$). The pairwise comparisons

190   (Bonferroni-corrected for nine tests) of the produced intervals confirmed that the

191   participants modulated their relative interval production according to the trained target

192   interval structure. In accordance with the target sequence, in the slow timing condition

193   the 1_{st} interval was significantly longer than in the fast ($p < .001$) and the irregular

194   timing conditions ($p < .001$), while there was no difference between the fast and

195   irregular conditions ($p = 1.000$) for the latter. The 2_{nd} interval length increased slightly,

196   yet proportionally for both the slow and the fast conditions, retaining the significant

197   difference ($p < .001$) and doubled in length for irregular relative to the slow timing

198   condition ($p < .001$). Finally, the 3_{rd} interval exhibited a very similar profile to the 1_{st}

199   interval (slow *vs* fast, $p < .001$; slow *vs* irregular, $p < .001$), but showed a slightly lower

200   percent interval for the fast compared to the irregular conditions ($p = .027$). Overall,

201   the IPI production data shows that the fast sequence was on average half as long as

202   the slow sequence, and the irregular timing condition changed the relative interval

203   structure from regular slow to an irregular short–long–short pattern of the same

204   sequence duration. Experiment 3 replicated the findings of Experiment 2 showing a

205   significant IPI × Timing interaction (3×3 repeated measures ANOVA: $F_{(1.558, 26.485)}$

206   = 17.369, $p < .001$, $\eta p^2 = .505$, Greenhouse-Geisser corrected, $\chi^2 (9) = 61.311$, p

207      $< .001$). Again, post-hoc pairwise comparisons (Bonferroni-corrected for nine tests)

208   confirmed that the 1st interval of the slow condition was longer than that of the fast

209   ($p = .001$) and irregular ($p = .003$) conditions, while no difference was found between

210   fast and irregular conditions ($p = 1.000$). The 2nd interval was significantly longer in the

211   slow compared to the fast condition ($p = .001$), but shorter compared to the irregular

212   condition ($p = .005$). Similarly, the fast condition was half as long in the irregular

213   condition ($p < .001$). The 3rd interval was twice as long for the slow relative to the fast

214   condition ($p < .001$), but failed to show a significant shortening for the irregular relative

215   to the regular slow sequence conditions ($p = 1.000$), and there was only a marginally

216   significant difference between fast and irregular conditions ($p = .096$). Overall, our

217   findings demonstrate that, on average, participants retrieved and produced the finger

218   sequences form memory with distinct temporal structures according to the relative

219   timing of slow, fast and irregular target intervals.

220   ***Longer preparation duration speeds up sequence initiation***

221   The time to initiate a correct action sequence after the *Go* cue can be taken as

222   a marker of the state of action planning after the preparatory delay[3,19,20]. We found a

223   significant difference in mean initiation RT with Delay (Experiment 1, one-way

224   repeated measures ANOVA: $F_{(1.382, 24.877)} = 52.809$, $p < .001$, $\eta p^2 = .746$,

225   Greenhouse-Geisser corrected, $\chi^2 (2) = 10.074$, $p = .006$) (Figure 2c, left). Pairwise

226   comparisons (Bonferroni-corrected for three tests) confirmed that initiation time for the

227   intermediate and long delay conditions was significantly shorter than following the

228   short delay (intermediate *vs* short delay, $p < .001$; long *vs* short delay, $p < .001$).

229   Similarly, sequence initiation following a long delay performed at significantly faster

230   mean RT as compared to the intermediate delay period ($p = .005$). Notably, this effect

231   is also in line with the classic foreperiod effect identified for single actions showing

232   faster RTs for longer foreperiod durations [21,22] suggesting that temporal expectation of

233   the *Go* cue may also contribute to faster sequence initiation in addition to the state of

234   sequence planning.

235   In contrast to the effect of preparation time, the planned temporal structure of

236   the sequence did not consistently affect sequence initiation RT (Figure 2c, left). There

237   was no main effect of sequence Timing in Experiment 2 (one-way repeated measures

238   ANOVA: $F(1.407, 23.917) = 1.700$, $p = .207$, $\eta p^2 = .091$, Greenhouse-Geisser

239   corrected, $\chi_2(2) = 8.759$, $p = .013$), but a main effect of Timing in Experiment 3 (one-

240   way repeated measures ANOVA: $F(1.294, 21.993) = 11.590$, $p = .001$, $\eta p^2 = .405$,

241   Greenhouse-Geisser corrected, $\chi_2(2) = 12.632$, $p = .002$). Specifically, as explained

242   by pairwise comparisons (Bonferroni-corrected for three tests), participants in

243   Experiment 3 were slower at initiating a slow regular sequence when compared to a

244   fast regular sequence ($p = .006$) and an irregular sequence ($p = .010$) whilst there was

245   no difference in initiation RT between the fast regular and the irregular conditions (p

246    $= .118$).

247   ***Sequences involving irregular inter-press-intervals were produced with***

248   ***less accurate timing***

249   Next, we aimed to establish whether preparation time and the temporal interval

250   structure of sequences modulated the observed relative timing accuracy across

251   presses (Figure 2c, middle). In Experiment 1, the mean relative temporal error did not

252   differ across the three delay conditions (one-way repeated measures ANOVA: $F(2, 36)$

253    $= .105$, $p = .901$, $\eta p^2 = .006$). This indicates that time to prepare the sequence did not

254   affect the degree of relative temporal accuracy. Here, sequence accuracy in conditions

255   with a shorter preparation time might have been compensated by slower initiation RT

256   (cf. above). In Experiment 2, there was a significant effect of Timing (one-way repeated

257   measures ANOVA: $F(2, 34) = 28.226$, $p < .001$, $\eta p^2 = .624$). Pairwise comparisons

258   (Bonferroni-corrected for three tests) revealed that participants performed at a higher

259   relative temporal accuracy when producing a slow regular sequence compared to an

260   irregular ($p < .001$) and a fast regular compared to an irregular sequence ($p < .001$),

261   while there was no difference between the slow and fast regular conditions ($p = 1.000$).

262   Experiment 3 replicated the main effect of Timing (one-way repeated measures

263   ANOVA: $F(1.454, 24.723) = 7.060$, $p = .007$, $\eta p^2 = .293$, Greenhouse-Geisser

264   corrected, $\chi_2(2) = 7.527$, $p = .023$). In line with the findings of Experiment 2, there

265   were smaller temporal errors in the slow sequence condition compared to the irregular

266   condition (p = .049) and in the fast compared to the irregular sequence (p =. 008).

267   There was no significant difference in temporal performance between the two regular

268   conditions (p = 1.000). These results suggest that the production of sequences which

269   consist of several different IPIs (irregular sequence) as opposed to only one interval

270   length (isochronous/regular sequence) is associated with decreases in temporal

271   accuracy of the sequence.

272   ***Action probes show graded activation of sequence elements at the end of***

273   ***preparation and are modulated by preparation duration, not sequence timing***

274   In half of the trials in the test phase on Day 3, instead of the *Go* cue that

275   prompted the production of the prepared finger sequence, participants encountered a

276   visual *Probe* cue which instructed them to respond with the corresponding finger press

277   as quickly and accurately as possible (Figure 1b). This allowed us to obtain two

278   behavioural measures related to the competitive state of each constituent press at the

279   end of the preparation period – the relative action activation and the probability of

280   correct action selection – for each action in the sequence, respectively. Specifically,

281   lower RT would suggest higher activation of the correctly selected action and lower

282   press error rate a higher probability of selection, and thus availability of the associated

283   action.

284   *Reaction times.* To evaluate the relative activation state of the probed actions

285   associated with different sequence positions (Figure 3a), we normalized the RT of

286   each probe position relative to the RT of the first position of the prepared sequence

287   (RT increase in % relative to 1_{st} position; cf. Supplementary Figure 1a for raw RT

288   values). In Experiment 1, results showed a main effect of Position (F (1,615, 29.062)

289   = 45.958, p < .001, ηp^2 = .719, Greenhouse-Geisser corrected, $\chi 2$ (5) = 22.621, p

290   < .001). Planned contrasts to detect differences between adjacent positions revealed

291   a significant RT increase with each position compared to its preceding one (2_{nd} *vs* 1_{st}

292   position, F (1, 18) = 63.360, p < .001, ηp^2 = .779; 3_{rd} *vs* 2_{nd} position, F (1, 18) = 54.534,

293   p < .001, ηp^2 = .752; 4_{th} *vs* 3_{rd} position, F (1, 18) = 24.900, p < .001, ηp^2 = .580). In line

294   with our hypothesis, these differences indicate a graded activation of actions according

295   to their serial position in the sequence, with the first action being the most activated.

296   We also found a significant Position × Delay interaction (F (6, 108) = 2.980, p = .010,

297   ηp^2 = .142). Planned contrasts using the long preparation duration as the reference

298   condition for the Delay factor, showed a significantly greater increase of the 2_{nd}

299   position relative to the 1st position at the long *vs* the short delay (F (1, 18) = 7.349, *p*

300   = .014, ηp^2 = .290). These results suggest that a longer preparation time prior to

301   sequence execution boosted the competitive activation of actions.

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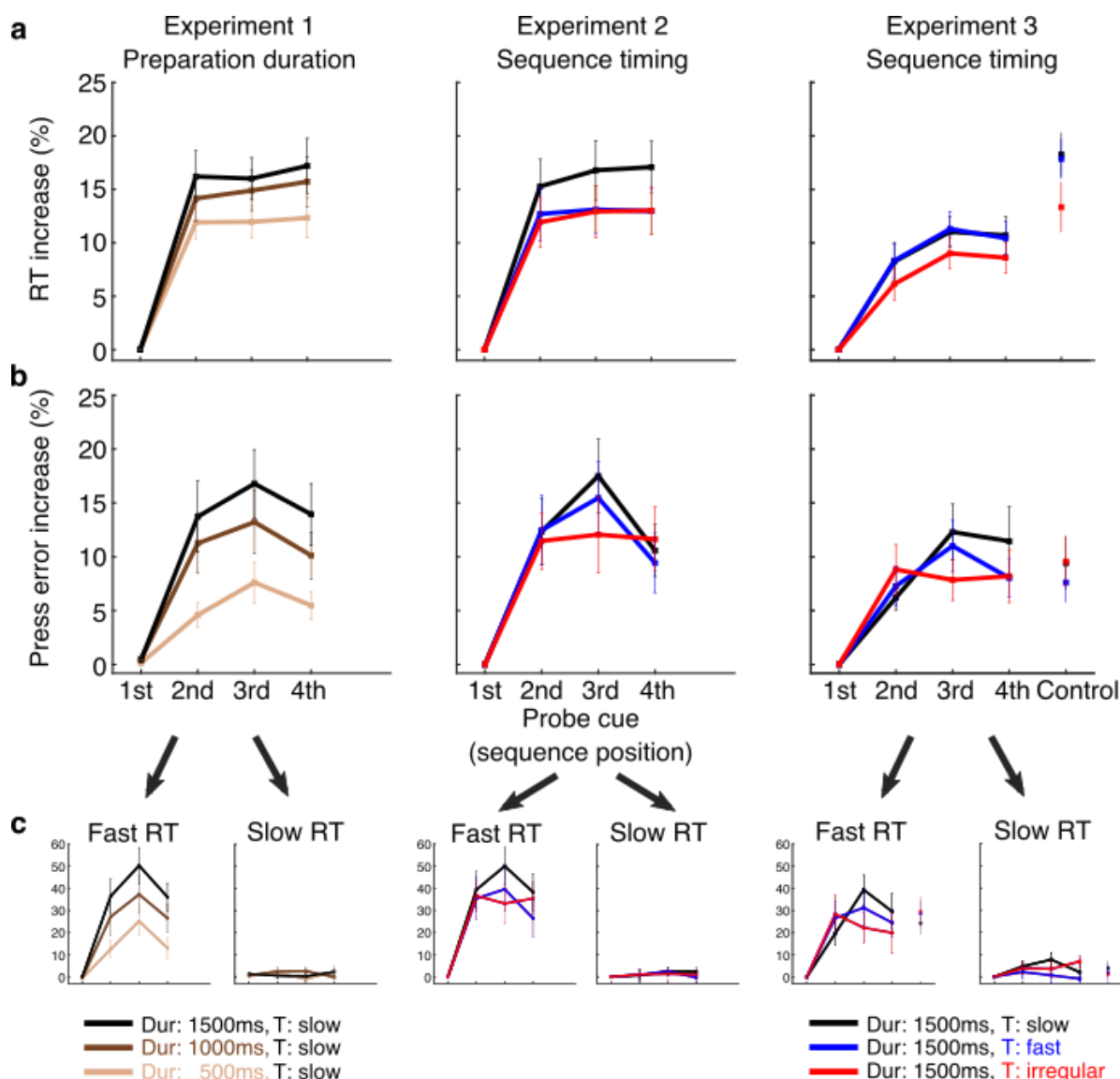
Figure 3 | Competitive state of actions during sequence preparation. *Probe* trials prompting the production of an action associated with the 1st-4th press position of the prepared sequence or a control action not present in any sequence (Experiment 3). **a.** Reaction time (RT) gradually increased for later sequence positions relative to the first position and became more pronounced with longer preparation duration, with responses to actions in later sequence positions becoming slower on average, when participants had more time to prepare the sequence (Experiment 1). No significant changes to RT increase were observed between conditions in which participants prepared sequences performed with different timing (Experiment 2 and 3). The RT increase was most pronounced for the action not featuring in the planned sequence (control action was a thumb press; Experiment 3), cf. raw RT graphs in Supplementary Figure 1. **b.** Press error rate also increased gradually for later sequence positions relative to the first position, with the exception of the last position, thus approaching an inverted U-shape. The press error gradient became more pronounced with longer preparation duration, i.e. responses to probes associated with later positions became less accurate when participants had more time to prepare the cued sequence. **c.** This pronounced effect on error increase was driven by trials where the response to action probes was short (lower RT quartile). When participants slowed down

their response allowing more time for deliberation and correction (upper RT quartile), the characteristic error increase was absent or less pronounced. Error bars represent standard errors.

303

304   In Experiment 2, we replicated the main effect of Position ($F_{(2.230, 37.904)}$ = 305   25.131, $p < .001$, $\eta p^2 = .596$, Greenhouse-Geisser corrected, $\chi^2 (5) = 15.333$, p 306   = .009). Planned contrasts showed significant differences when contrasting all pairs of 307   adjacent probe positions replicating the findings of Experiment 1. Specifically, RT 308   increase of the 2_{nd} position was larger compared to the 1_{st} ($F_{(1, 17)} = 48.072$, $p < .001$, 309 $\eta p^2 = .739$). Similarly, there was a significantly greater RT increase for the 3_{rd} position 310   vs the 2_{nd} ($F_{(1, 17)} = 32.040$, $p = .001$, $\eta p^2 = .653$) and the 4_{th} vs the 3_{rd} ($F_{(1, 17)}$ = 311   28.873, $p < .001$, $\eta p^2 = .629$). Crucially, there was no interaction between Position and 312   Timing ($F_{(2.430, 41.318)} = 2.823$, $p = .061$, $\eta p^2 = .142$, Greenhouse-Geisser 313   corrected, $\chi^2 (20) = 59.308$, $p < .001$). This suggests that preparing a sequence with a 314   different temporal structure did not impact the competitively cued activations at the 315   end of preparation.

316   Experiment 3 once more replicated a main effect of Position ($F_{(3, 51)}$ = 317   29.852, $p < .001$, $\eta p^2 = .637$). Planned contrasts, similarly, revealed a significantly 318   greater RT increase for the 2_{nd}, 3_{rd} and 4_{th} positions over their preceding 1_{st}, 2_{nd} and 319 3_{rd} positions, respectively (2_{nd} vs 1_{st}, $F_{(1, 17)} = 61.485$, $p < .001$, $\eta p^2 = .783$; 3_{rd} vs 320 2_{nd}, $F_{(1, 17)} = 69.762$, $p < .001$, $\eta p^2 = .804$; $F_{(1, 17)} = 14.180$, $p = .002$, $\eta p^2 = .455$). 321   In addition, the finger press which did not feature in any of the planned sequences 322   (control action: thumb) showed a further RT increase relative to the last (4_{th} position) 323   item of the sequence (paired samples t-test: $t (17) = 3.062$, $p = .007$, $d = .840$, two- 324   tailed). Timing did not interact with Position ($F_{(3.743, 63.632)} = 1.089$, $p = .367$, 325 $\eta p^2 = .060$, Greenhouse-Geisser corrected, $\chi^2 (20) = 36.727$, $p = .014$). This result 326   replicates Experiment 2. Thus, CQ during sequence preparation was not dependent 327   upon the speed or temporal structure of the planned sequences, and suggests that 328   fine grained competitive activation gradient of constituent actions of a sequence is 329   activated above the level of an unrelated effector.

330   *Error rate.* To evaluate the relative probability of selection of the probed actions 331   associated with different sequence positions (Figure 3b), in each experiment the finger 332   error rate for each probe action was calculated and normalized to that of the first 333   position (Error rate increase in % relative to 1_{st} position; cf. Supplementary Figure 1b 334   for raw error rate values). Equally, we assessed the same factors, predicting an

335   ascending error rate increase by position. Experiment 1 showed a main effect of

336   Position (4 × 3 repeated measures ANOVA: $F_{(1.948, 35.073)}$ =

337   18.017, $p < .001$, $\eta p^2 = .500$, Greenhouse-Geisser corrected, $\chi_2 (5) = 13.595$, $p = .019$).

338   Planned contrasts revealed a significantly increased error rate for the 2nd position

339   compared to the 1st position ($F_{(1, 18)} = 29.675$, $p < .001$, $\eta p^2 = .622$) and for the 3rd

340   position compared to the 2nd position ($F_{(1, 18)} = 25.937$, $p < .001$, $\eta p^2 = .590$), whilst

341   the last, 4th position showed a lower error increase than the 3rd position ($F_{(1, 18)} =$

342   5.092, $p = .037$, $\eta p^2 = .220$). This error rate pattern during preparation shows an

343   inverted U-shape, similar to serial position curves during production[23] and suggests

344   the presence of a ranked probability across sequence positions for action selection.

345   The Position × Delay interaction ($F_{(4.137, 74.466)} = 3.813$, $p = .007$, $\eta p^2 = .175$,

346   Greenhouse-Geisser corrected, $\chi_2 (20) = 34.036$, $p = .028$) was driven by a significant

347   increase of the 2nd position compared to 1st position at the long *vs* the short delay (F

348    $_{(1, 18)} = 10.877$, $p = .004$, $\eta p^2 = .377$) as revealed by planned contrasts. No other

349   pairs showed a significant difference. In accordance with the RT results, these findings

350   suggest that accuracy of probe elements during sequence planning is modulated by

351   preparation, in that a longer preparation time is associated with more pronounced error

352   increases for the 2nd position when compared to a short preparation period, suggesting

353   less availability for selection of actions in later positions the more sequence planning

354   advances.

355   Experiment 2 showed a significant main effect of Position ($F_{(3, 51)} =$

356   14.397, $p < .001$, $\eta p^2 = .459$). Planned contrasts revealed that this effect was driven

357   by a significant error rate increase for the 2nd position *vs* the 1st position ($F_{(1, 17)} =$

358   24.070, $p < .001$, $\eta p^2 = .586$). The 3rd position performed at a greater error increase

359   than the 2nd position ($F_{(1, 17)} = 15.510$, $p = .001$, $\eta p^2 = .477$), whilst the 4th position

360   was not significantly different from the 3rd position ($F_{(1, 17)} = 1.284$, $p = .273$,

361    $\eta p^2 = .070$). These results replicate the CQ effect of serial actions during preparation,

362   found in Experiment 1, with a graded increase in error rates for later elements up to

363   the 3rd position. We did not find a significant Position × Timing interaction ($F_{(6, 102)}$

364    $= 1.583$, $p = .160$, $\eta p^2 = .085$).

365   Similarly in Experiment 3, there was a main effect of Position ($F_{(3, 51)} =$

366   13.725, $p < .001$, $\eta p^2 = .447$), with the 2nd position showing a greater error increase

367   than the 1st position ($F_{(1, 17)} = 29.074$, $p < .001$, $\eta p^2 = .631$), and the 3rd position

368   performing with more errors than the 2nd position (F (1, 17) = 17.903, p = .001,

369   ηp^2 = .513). Error rates of the 4th position did not differ from the 3rd position (F (1, 17)

370   = 3.791, p = .068, ηp^2 = .182). Our prediction that the control action would not be part

371   of this queuing pattern, implying a much weaker probability to be selected for

372   execution, was refuted by a non-significant difference from the 4th position (paired

373   samples t-test: t (17) = -.323, p = .751, d = .111, two-tailed). As in Experiment 2,

374   Position did not interact with Timing (F (3.803, 64.654) = 1.869, p = .130, ηp^2 = .099,

375   Greenhouse-Geisser corrected, χ_2 (20) = 42.899, p = .002). Together, this indicates

376   that the competitive error rate for probed actions during preparation was not modulated

377   by the speed or temporal structure of the planned sequence.

378   Whilst there was no significant interaction of Timing and Position for action

379   probes during preparation (neither for RT, nor for error rate), we observed a non-

380   significant, but consistent flattening of the CQ curve for the temporally irregular

381   sequence across Experiments 2 and 3. However, this patterns of results cannot be

382   attributed to changes in temporal grouping of actions per se, but may be driven by

383   accuracy: The irregularly (non-isochronously) timed sequence was characterized by a

384   highly significant increase in relative temporal error when compared to both the slow

385   and fast regularly (isochronously) timed sequences (Figure 2b, Experiments 2 and 3)

386   due to the increased temporal complexity. This lends support to the alternative

387   hypothesis, namely that the precision of the sequence plan is driving the CQ state of

388   actions during the preparation period.

389   ***A steeper CQ error gradient is bound to fast responses***

390   Next, we sought to determine whether the characteristic error rate gradients were the

391   result of automatic responses, or deliberated action selection after the *Probe* cue. To

392   test this hypothesis, we assessed the error rate gradient for fast *vs* slow responses

393   following the *Probe* cue. We extracted the relative error rate increases for action

394   probes in the first and third RT quartiles for each experiment (Figure 3c). Only for the

395   fast responses, we found a main effect of Position (Experiment 1, F (1.758, 31.650) =

396   19.731, p < .001, ηp^2 = .523, Greenhouse-Geisser corrected, χ_2 (5) = 17.279, p = .004;

397   Experiment 2, F (2.033, 34.559) = 16.325, p < .001, ηp^2 = .490, Greenhouse-Geisser

398   corrected, χ_2 (5) = 19.928, p = .001; Experiment 3, F (3, 51) =

399   12.749, p < .001, ηp^2 = .429). Planned contrasts for adjacent positions confirmed a

400   graded increase in finger errors up to the 3rd position (Experiment 1, 2nd position *vs* 1st

401   position, $F_{(1, 18)}$ = 26.954, $p < .001$, $\eta p^2 = .600$; 3rd position vs 2nd position, $F_{(1, 18)}$

402   = 35.745, $p < .001$, $\eta p^2 = .665$; 4th position vs 3rd position, $F_{(1, 18)}$ = 2.347, $p = .143$,

403    $\eta p^2 = .115$; Experiment 2, 2nd position vs 1st position, $F_{(1, 17)}$ = 27.138, $p < .001$,

404    $\eta p^2 = .615$; 3rd position vs 2nd position, $F_{(1, 17)}$ = 15.222, $p = .001$, $\eta p^2 = .472$; 4th

405   position vs 3rd position, $F_{(1, 17)}$ = 4.982, $p = .039$, $\eta p^2 = .227$; Experiment 3, 2nd

406   position vs 1st position, $F_{(1, 17)}$ = 21.580, $p < .001$, $\eta p^2 = .559$; 3rd position vs 2nd

407   position, $F_{(1, 17)}$ = 13.888, $p = .002$, $\eta p^2 = .450$; 4th position vs 3rd position, $F_{(1, 17)}$

408   = 1.845, $p = .192$, $\eta p^2 = .098$). We also found a significant Position × Delay interaction

409   (Experiment 1, $F_{(6, 108)}$ = 4.003, $p = .001$, $\eta p^2 = .182$), driven by a significant increase

410   of the 2nd position 1st position at the long vs the short delay ($F_{(1, 18)}$ = 18.132, p

411    $< .001$, $\eta p^2 = .502$) and at the long vs the intermediate delay ($F_{(1, 18)}$ = 10.370, p

412    $= .005$, $\eta p^2 = .366$). Error rate increases did not change by sequence position number

413   in the slow responses (Experiment 1, $F_{(3, 54)}$ = .313, $p = .816$, $\eta p^2 = .017$; Experiment

414   2, $F_{(3, 51)}$ = .552, $p = .649$, $\eta p^2 = .031$; Experiment 3, $F_{(3, 51)}$ =

415   1.672, $p = .185$, $\eta p^2 = .090$), accompanied by an absent Position × Delay interaction

416   (Experiment 1, $F_{(3.559, 64.058)}$ = 1.302, $p = .280$, $\eta p^2 = .067$, Greenhouse-Geisser

417   corrected, $\chi^2_{(20)}$ = 37.340, $p = .012$). The control action was not different from the 4th

418   position in either RT pole (fast RTs, $t_{(17)}$ = 1.654, $p = .117$, $d = .473$, two-tailed; slow

419   RTs, $t_{(17)}$ = .203, $p = .842$, $d = .050$, two-tailed). These results suggest that the CQ

420   gradient at the end of a preparation period of 500 to 1500 ms was driven by automatic

421   responses rather than by cognitive action selection and replanning, and constitute a

422   readout for the state of actions during sequence planning.

423   ***Preparatory CQ gradient correlates with temporal accuracy and initiation***

424   ***speed***

425   Neurally derived CQ of sequence actions during planning predicts the

426   participants' subsequent performance accuracy as shown previously[11]. In line with this

427   finding, we found that more time to prepare a sequence is associated with a more

428   pronounced competitive RT and error rate increase for action probes. To test the

429   association directly, we predicted that a more pronounced (steeper) CQ gradient of

430   RTs and error rates would correlate with a better performance in sequence production,

431   specifically with faster correct sequence initiation, and less temporal and finger press

432   errors. Correlation analyses were performed on group data obtained from trials in the

433   slow timing condition and long preparation duration (1500 ms) present across all three

434   experiments (N = 55). The magnitude of the CQ gradient during preparation was

435   calculated based on RT and error rate increase data in *Probe* trials (difference

436   between adjacent positions; Figure 4a and 4b). Results showed that participants with

437   a more pronounced CQ based on relative RT and error rate increase initiated correct

438   sequences faster (CQ RT increase: *r* = -.393, *p* = .002, one-tailed; CQ error increase:

439   *r* = -.539, *p* < .001, one-tailed). Higher RT based CQ also predicted smaller relative

440   temporal error (*r* = -.345, *p* = .005, one-tailed). However, in contrast to the correlations

441   with the neural measure of CQ reported in a previous study[11], neither CQ RT increase,

442   nor CQ error increase showed negative correlations with finger error (CQ RT increase:

443   *r* = .083, *p* = .273, one-tailed; CQ error increase: *r* = .118, p = .196, one-tailed). Also,

444   contrary to the CQ RT increase, a more pronounced CQ error increase of probe

445   actions at the end of preparation was not associated with reduced temporal error

446   during execution (*r* = -.051, p = .356, one-tailed). Thus, CQ error increase may be a

447   less sensitive predictor for temporal accuracy than CQ RT increase.

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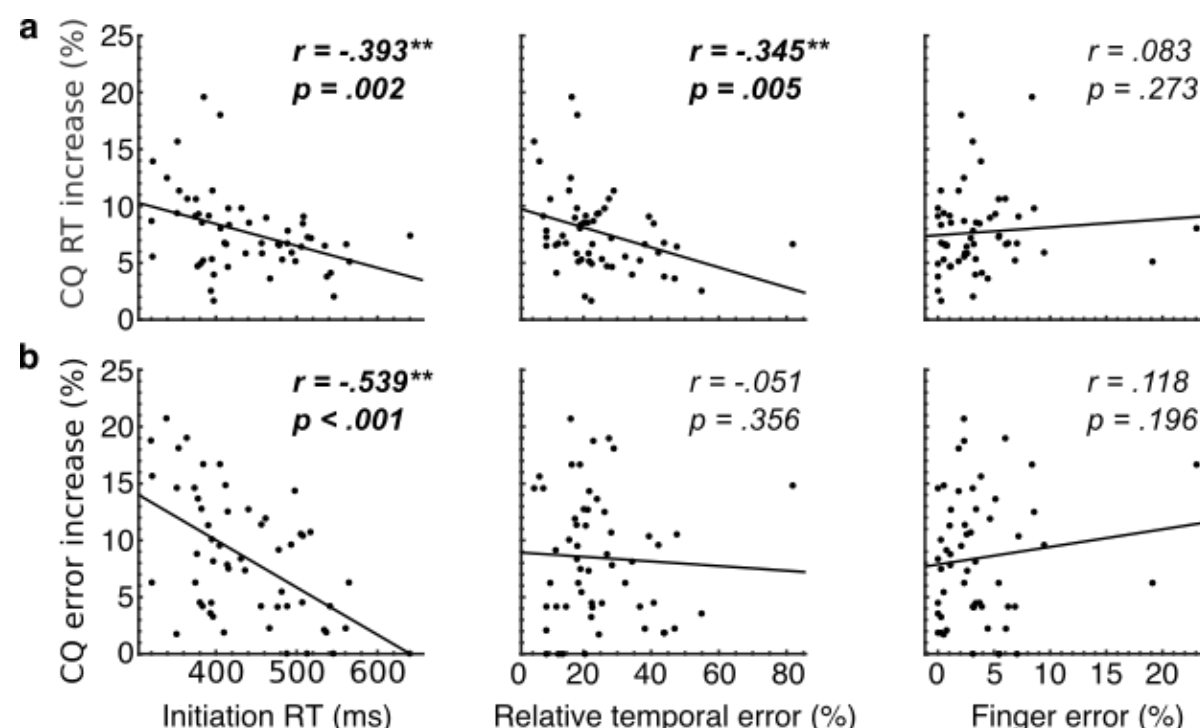
Figure 4 | Correlation between overall CQ measures during preparation and subsequent production. Average relative RT (**a**) and press error increase (**b**) between adjacent positions (1st to 2nd, 2nd to 3rd, 3rd to 4th) obtained through probe trials was taken as a proxy for CQ of actions during preparation. Larger CQ during preparation was associated with faster initiation speed of correct sequences, and smaller relative temporal errors. Larger CQ was not associated with reduced finger error rate (proportion of trials with wrong finger order, finger order repetitions, or missing presses), as predicted based on neural CQ findings (Kornysheva et al. 2019). All correlations are one-tailed, in line with one-sided predictions.

450   In sum, consistent with previous neurophysiological findings[11], our behavioural

451   results show that during sequence preparation of sequence from memory participants

452   establish a competitive activation and selection gradient of constituent actions

453   according to their serial order. This competitive gradient expands with longer

454   preparation durations and is more pronounced in participants with faster sequence

455   initiation and more precise interval timing.

456

457   **Discussion**

458   Sequence planning is central to skilled action control, however its content and

459   organisation is poorly understood[2,4]. Neurophysiological findings in humans have

460   demonstrated that a trained action sequence is pre-planned by establishing a

461   competitive activation gradient of action patterns according to their serial position, and

462   that the quality of this neural pattern during planning predicts subsequent

463   performance[11–14]. Here we have established a behavioural measure of the preparatory

464   action activation gradient and demonstrate that it reflects the skill (sequence

465   production accuracy and fluency of initiation), rather than the temporal structure

466   (sequence production speed and temporal interval pattern) of the planned sequence.

467   Both the time to respond and the probability of making a finger press mistake

468   increased progressively when participants responded to action cues during

469   preparation that were associated with later *vs* earlier positions in the respective

470   sequence. The non-linear increase was particularly pronounced for the first three out

471   of four planned actions in the sequence. This response gradient demonstrates that the

472   relative availability of each planned action in the sequence decreases with serial

473   position, as predicted by competitive queuing (CQ) models[6,7,24,25] and previous

474   neurophysiological findings[11,14].

475   The preparatory action activation gradient markedly contrasts with mechanisms

476   for non-sequential action planning involving multiple actions: A cued set of possible

477   actions triggers equal activity increase in cortical populations tuned to the respective

478   actions, and the preparatory competition is only resolved once an action cue specifies

479   the target action[26]. In contrast, sequence preparation establishes a fine-tuned gradient

480   of action activations, with the latter switching flexibly depending on the retrieved

481   sequence. Notably, actions that were part of the planned sequence were activated

482   above the level of a control action which was not part of the retrieved sequence (Figure

483   3a, right). This suggests that all constituent actions were concurrently activated above

484   a passive baseline, albeit to a different degree depending on their position in the

485   planned sequence.

486   Our study provides a behavioural measure of the competitive state of

487   constituent actions during sequence planning. This is complementary to previous

488   behavioural work which revealed CQ of actions during production, such as accuracy

489   and RT curves obtained from sequence execution[27,28], or on-the-fly action planning

490   following sequence initiation, assessed behaviourally[29] and through measures of

491   cortico-spinal excitability[10]. Gilbert and colleagues have employed a paradigm at the

492   interface between sequence preparation and production to characterize the CQ

493   profiles the respective sequential actions – silent rehearsal[30]. Here participants were

494   asked to listen to sequences of spoken digits and silently rehearse the items during a

495   retention interval. They received explicit instructions to rehearse the sequence at the

496   same pace as active production. After an unpredictable delay, a tone prompted the

497   report of an item being rehearsed at that moment and revealed graded overlapping

498   probabilities of neighbouring items, suggesting potential CQ during internal rehearsal.

499   In contrast to the latter study, our paradigm did not allow for active rehearsal during

500   preparation: First, our participants retrieved the sequence entirely from memory

501   without a sensory instruction period which might have facilitated active entrainment

502   with the sequence prior to planning. Second, the period for sequence retrieval and

503   planning was comparatively brief (ranging from 500 to 1500 ms after *Sequence* cue

504   onset) and not sufficient to cycle through the full sequence at the rate participants

505   employed for active production. In addition, if the observed CQ gradient were

506   somehow driven by silent rehearsal at the target rate, it would have been more

507   pronounced for the fast sequences, as more of the planned sequence could fit into the

508   preparation phase. However, there was no significant difference between relative

509   activation curves for fast and slow sequences.

510   Whilst active motor rehearsal at scale during the short preparation phase is

511   unlikely, an alternative serial mechanism underlying the different levels of action

512   activation may be mediated by rapid sequence replay. The latter has been observed

513   in the hippocampus during navigation tasks[31] and perceptual sequence encoding[32],

514   as well as in the motor cortex in the context of motor sequence learning tasks[33]. Replay

515   has been shown to involve fast sweeps through the neural patterns associated with

516 the sequence during wakeful rest and planning (preplay)[31,34–36], and is characterized

517 by a multifold temporal sequence compression[32,33,37,38]. How replay could translate

518 into a parallel activation of serial items described here is uncertain. One possibility is

519 that serial sweeps during motor sequence preparation involve fast repeated replay

520 fragments[37,39] of different length during planning, starting with the first elements – e.g.

521 1_{st}-2_{nd}-3_{rd}, 1_{st}-2_{nd}, 1_{st}, 1_{st}-2_{nd}-3_{rd}-4_{th}, 1_{st}-2_{nd} etc. This would produce an overall bias

522 towards the activation of earlier rather than later parts of the planned sequence, which

523 may be translated into a cumulative ramping activity for each constituent action by a

524 separate neuronal mechanism during the preparation period[26,40]. Future analysis of

525 the 'sequenceness'[32,33] of the corresponding neural patterns during preparation should

526 shed light on the presence of preplay and its hypothesized relationship to parallel CQ

527 of actions[11].

528 The CQ gradient was established after a brief retrieval and preparation period,

529 and revealed through faster rather than slower responses to probes (Figure 3c). This

530 suggests that out behavioural measure of CQ during sequence planning reflects a

531 rapid and automatic process involved in the execution of well-trained motor sequences

532 from memory, and is not a result of slow deliberation or higher-level decision making.

533 Contrary to a prominent account of motor control of skill learning[41,42], this data implies

534 that discrete motor sequence production incorporates automatic planning

535 mechanisms which are associated with fluent and accurate execution of sequential

536 actions.

537 Remarkably, longer preparation times reinforced the competitive activation

538 gradient making responses to action probes for later sequence positions even slower

539 and more inaccurate relative to those for earlier positions. Whilst counterintuitive in the

540 context of single action performance gains from longer foreperiod durations[21], the

541 gradient expansion with time suggests a dynamic refinement of the plan for sequence

542 production during the retrieval and preparation phase. This refinement involves the

543 graded suppression of later actions in the sequence, making them less available for

544 production, even more so with time. Crucially, the gradient increase with preparation

545 duration was not accompanied by substantial expansion or compression of sequence

546 production. Instead, the CQ gradient was associated with a faster initiation of correctly

547 performed sequences whilst retaining the same level of press and timing accuracy,

548 suggesting increased sequence fluency. This demonstrates that the action activation

549 gradient established during planning reflects the preparedness for correct and fluent
550 production, rather than the planned temporal structure of the sequence.

551 Furthermore, participants who had a more pronounced competitive activation
552 during planning exhibited both faster initiation times and a more accurate temporal
553 execution of the sequence after the "Go" cue, particularly when looking at the RT
554 based CQ gradient. These findings strengthen the interpretation that an ordered
555 competitive activation of actions during planning preempts subsequent fluency and
556 temporal accuracy of the sequence[11]. Yet, we did not replicate the association of the
557 planning gradient with finger error probability found in the latter study. This may be due
558 to a smaller pool of timing and finger order sequences that the participants had to learn
559 relative to the previous paradigm, and the presence of only one finger order (but
560 different sequence timing) in Experiments 2 and 3. This likely facilitated finger
561 accuracy to reach ceiling levels in a substantial number of participants. Future
562 experiments should resolve an association with finger accuracy through the inclusion
563 of a larger pool of trained sequences to provoke more frequent finger errors.
564 Alternatively, reaching or drawing tasks would allow to make the spatial in addition to
565 temporal feature of the sequential behaviour continuous and capture fine-grained
566 spatial errors at overall high accuracy levels of sequence production.

567 In contrast, doubling the speed of sequence production did not change the
568 relative activation between sequential actions at the end of the preparation period.
569 This suggests invariance of the gradient in the competitive planning layer across
570 sequences produced at different time scales. This transfer across speed profiles is in
571 line with the presence of flexible motor timing and temporal scaling in dynamic
572 neuronal populations[43,44], and a separate neural process controlling the speed of an
573 action or action sequence during execution, e.g. through the strength of an external
574 input to the network involved in the generation of timed behavior.[43] Preparing a
575 sequence of the same length with an irregular compared to isochronous interval
576 structure was associated with a tendency for a dampened CQ gradient during
577 sequence planning. However, this non-significant trend on CQ is unlikely to be the
578 effect of temporal grouping, as the irregular interval sequence was characterized by a
579 significant increase in temporal interval production error (Figure 2c, middle panel).
580 Instead, we hypothesize that longer preparation time (above 1500 ms) would have
581 benefitted the participants and enhanced the relative activation gradient in line with

582   Experiment 1 in order to form a more accurate plan for the complex sequencing of two

583   different (non-isochronous) rather than just one constituent IPI (isochronous).

584   Our results show that CQ of actions during sequence planning reflects the

585   overall action order and temporal accuracy of the sequence, but not its temporal

586   structure – neither its speed, nor its temporal grouping. This dissociation is

587   counterintuitive, however, we propose that temporal accuracy can be dissociated from

588   timing in CQ models. In our model (Figure 5 and Methods), we assume that positional

589   associations of the items in the sequence (positional context and parallel planning

590   layer) are determined by the respective sequence cue, and the corresponding start-

591   state of the cued sequence becomes gradually activated. Crucially, we show that

592   changing the width of the receptive field for each position (Figure 5a) affects the

593   activation gradient of action items during sequence planning (Figure 5b). Specifically,

594   our model demonstrates that narrowing this positional tuning will cause a steeper

595   relative activation gradient at the end of sequence preparation, with actions in later

596   positions being progressively less activated. Conversely, wider tuning, would broaden

597   the excitation from the positional context to parallel planning layer and lead to smaller

598   relative activation differences between actions at the end of the planning period.

599   Notably, while the positional tuning in CQ models is hypothesized to be acquired

600   through exposure (Hebbian learning)[45], we assume that it is dynamically established

601   throughout the preparation period (cf. Methods section). Thus, the width of the

602   positional tuning of individual actions in the parallel planning layer may underly the

603   accuracy of actions, independently of the overall speed and temporal structure of

604   sequences.

605
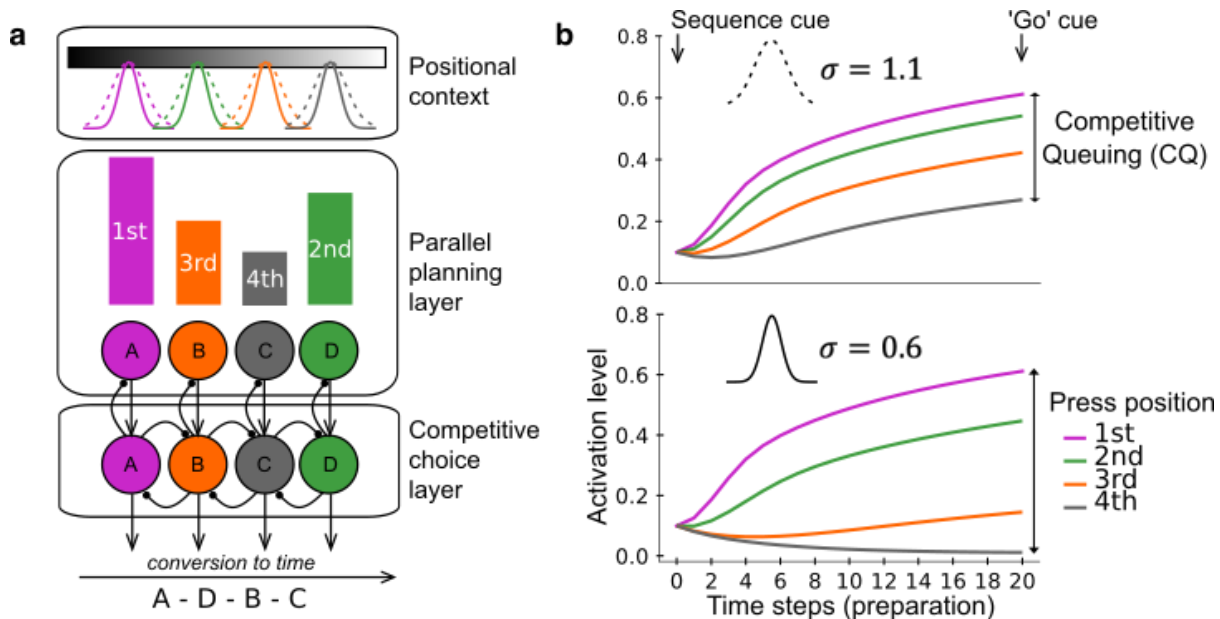
Figure 5 | Competitive queuing (CQ) model and the role of positional tuning in sequence preparation. a. The Parallel planning and Competitive choice layers of the CQ model contain nodes representing possible sequence items, such as finger presses A, B, C and D. When learning a sequence, connections are formed from sequentially activated nodes in the Positional context layer to item nodes in the Parallel planning layer as each is activated in turn. Crucially, the current model incorporates a positional tuning of the nodes. The receptive field of this positional tuning has a tuning (variance) parameter σ, controlling the model's sensitivity to positional differences. This tuning curve may be acquired though training (variability of instructive stimulus and training exposure), as well as reflect an intrinsic variability of each participant (sensory or motor variability). **b.** The tuning width of the receptive field determines, inversely, the spread of the competitive activations of corresponding action items following the *Sequence* cue, with a narrow or sharper tuning producing more pronounced CQ during preparation. Time steps represent linear arbitrary values.

606

607 Although our empirical data and CQ model do not support the integration of the

608 timing signal with action order before sequence execution, they do not exclude the

609 presence of a separate preparation process for the speed and timing of the respective

610 sequence, which may take place concurrently or at different time points during

611 preparation[46–48]. In previous work, we proposed a drift-diffusion based model which

612 contains input from separate modules that activate action order and timing.[49] This

613 model was based on behavioural sequence learning data demonstrating that

614 sequence timing is encoded independently of the action order, but requires

615 multiplicative, rather than additive integration with each action. This enables previously

616 learnt sequence timing to be transferred to new sequences, but only after the action

617 order has been acquired, reconciling previous experimental findings[50–54]. Most

618 recently Zeid and Bullock proposed how such plans might be generated in the context

619 of CQ models[51], proposing that two CQ modules could operate in parallel - one

620 controlling the item order and the other controlling the sequence of inter-onset-
621 intervals that define a rhythmic pattern, including separate parallel planning and
622 competitive choice layers. While this model is in line with neurophysiological and
623 imaging evidence for a separate control of timing for sequence generation[50,55–59],
624 empirical data for a dedicated CQ process for temporal intervals is lacking.

Conclusions

626 In sum, our findings indicate that the graded relative activation state during a
627 brief period of retrieval and planning reflects the subsequent action order and
628 correlates with the individual's sequence fluency and accuracy. It appears to be
629 invariant to the exact timing of the sequence, but is instead bound to the precision of
630 the positional tuning. In contrast to neurophysiological approaches involving advanced
631 neural pattern analysis[11,14], a simple behavioural paradigm could provide a
632 straightforward and cost-effective proxy to assess the state of action preparation
633 across trials in individual participants. This behavioural readout may help advance our
634 understanding of the neural processes associated with disorders affecting the fluent
635 production motor sequences, such as stuttering, dyspraxia, and task-dependent
636 dystonia[60–64].

637

Methods

Participants

640 Data were collected from a total of 55 right-handed University students
641 (Experiment 1: *N* = 19, 11 females; *M* = 24.2 years, *SD* = 4.1; Experiment 2: *N*=18, 11
642 females; *M* = 24.2 years, *SD* = 4.5; Experiment 3: *N* = 18, 9 females; *M* = 20.8 years,
643 *SD* = 2.4). Four additional participants were tested, but excluded from analysis based
644 on their sequence production error rate (cf. Participant exclusion criteria). They were
645 hypothesis-naive and had no previous exposure in performing a similar experimental
646 task. All participants had normal or corrected-to-normal vision and reported no history
647 of neurological or psychiatric disorders or hearing problems. Handedness was
648 evaluated through the online Handedness Questionnaire
649 (http://www.brainmapping.org/shared/Edinburgh.php) adapted from the Edinburgh
650 Handedness Inventory [65] (Experiment 1, *M* = 88.4, *SD* = 9.4; Experiment 2, *M* = 90.6,
651 *SD* = 9.7; Experiment 3, *M* = 90, *SD* = 11.8). All participants provided written informed
652 consent before participation and were debriefed after completing the study. They were

653   compensated either monetarily or with course credits at the end of the experiment. All
654   procedures were approved by the Bangor University School of Psychology Research
655   Ethics Committee (Ethics Review Board Approval Code 2017-16100-A14320).

656   ***Participant exclusion criteria***

657   Mean finger and temporal interval error rate during sequence production in the
658   test phase (Day 3) above three standard deviations of the group mean performance
659   was considered as outlier performance, in each experiment separately. This was to
660   ensure that participants reached a comparable skill level in sequence performance
661   from memory and to have sufficient number of trials for RT analysis per participant,
662   which included correct trials only. We set this blindly to the individual *Probe* trial
663   performance to ensure that data exclusion was independent of the data analysed to
664   to test our main hypotheses. This resulted in the exclusion of data from one participant
665   in Experiment 1 who showed 53.1% finger error in the short delay, 54.7% in the
666   intermediate delay and 53.9% in the long preparation duration conditions. Two
667   participants' data sets were removed from Experiment 2, one with 25% finger error in
668   the slow timing and 18.8% in the irregular timing conditions, and the other with 44.5%
669   in the fast timing conditions. The data of one participant was excluded from Experiment
670   3 due to 12.5% finger error in the fast timing condition. No outlier performance was
671   found for temporal interval production in any condition of each experiment according
672   to the above criteria. Overall, the data of 19 participants were analyzed for Experiment
673   1, 18 participants for Experiment 2, and 18 participants for Experiment 3.

674   ***Apparatus***

675   For all three experiments participants were seated in a quiet room in front of a
676   19-inch LCD monitor (LG Flatron L1953HR, 1280 x 1024 pixels, refresh rate 60Hz),
677   wearing headphones for noise isolation. All instructions about when each block began,
678   visual stimuli and feedback were controlled by Cogent 2000 (v1.29)
679   (http://www.vislab.ucl.ac.uk/cogent.php) through a custom-written MATLAB program
680   (v9.2 R2017a, The MathWorks, Inc., Natick, Massachusetts, United States) and
681   projected on to the LCD screen with inter-stimulus-intervals calculated in refresh rates
682   to ensure precise stimulus timing. In Experiments 1 and 2, a customized foam channel
683   was attached to the outer-half surface of the table to stabilize the cable of a Pyka 5-
684   button fiber optic response device (Current Designs). A thin anti-slip black mat was
685   placed underneath the response device to prevent sliding during the task. The

686   response device was positioned horizontally and adjusted accordingly for each

687   participant to ensure good control over the target buttons as well as arm and wrist

688   comfort. Participants were instructed to place the right index, middle, ring and little

689   fingers on the respective target buttons of the device. Experiment 3 used an identical

690   experimental set-up with the exception that responses were recorded using a

691   computer keyboard and participants were instructed to place their right thumb in

692   addition to the rest of the right-hand fingers on the designated keyboard keys. For

693   hand stabilization and comfort their wrist was positioned on a wrist rest.

694   ***Behavioural task and design***

695   In Experiments 1 and 2, the task involved the recording of sequential and single

696   button presses produced with the four fingers (index, middle, ring and little) of the right

697   hand on a response device while performing a visually cued motor learning task

698   adapted from Kornysheva et *al*.[11]. Experiment 3 additionally required single presses

699   with the thumb. Participants were trained to associate a visual cue (an abstract fractal

700   shape, henceforth *Sequence* cue) with a specific a four-element finger sequence

701   produced with a specific timing. In all experiments, the paradigm employed two main

702   trial types: sequence and single-press (*Probe*) trials. *Sequence* trials were further

703   divided into visually instructed and memory-guided trials. Instructed trials involved the

704   presentation of four visual digit cues (index, middle, ring and little) at specified intervals

705   comprising a unique target sequence. These were only used during training in the first

706   two days, and during two refresher blocks on the third day. The test phase on the third

707   day only involved sequence production without visual guidance (memory-guided trials,

708   Supplementary Figure 3). *Probe* trials involved the production of only one visual digit

709   cue (*Probe* cue) corresponding to one of the serial positions in the target sequence

710   (Figure 1b).

711   *Experiment 1.* All participants were trained in producing two four-element target

712   sequences comprising two different finger order types (F1, F2) with isochronous

713   temporal intervals of 800 ms between presses (T1). Two additional finger order types

714   (F3, F4) of the same temporal sequence (T1) served as practice sequences to impose

715   familiarization with the task. Four additional finger order types (F5, F6, F7, F8) with

716   isochronous intervals of 800 ms (T1) were used to evaluate sequence-specific learning

717   in a visually cued task alongside the target sequences, immediately before and after

718   the training phase. The data from this control task is not presented here, as the current

719   work evaluates the preparation and performance during trials involving production
720   from memory. As a result, the experiment employed a total of eight unique *Sequence*
721   cues associated with eight finger sequences. The sequences were randomly
722   generated offline through a custom-written MATLAB code for each participant.
723   Specifically, the sequence generation process produced sequences for each
724   participant randomly excluding sequences with ascending and descending digit triplets.
725   The trained sequences started with different digits.

726   All trial types started with a *Sequence* cue. The *Sequence* cue had a fixed
727   duration of 400ms followed by a fixation cross, the latency of which varied depending
728   on the delay period from *Sequence* cue onset to *Go* cue. The resultant short (500 ms),
729   intermediate (1000 ms), and long (1500 ms) delay periods following the *Sequence* cue
730   comprised the three preparation duration conditions employed in the task. After the
731   delay period, a black hand stimulus appeared as the *Go* cue. In an instructed trial, the
732   *Go* cue was presented on a grey background for 2400 ms, guiding the participants
733   throughout the execution of the sequence by sequentially displaying a small white
734   circle on the digits of the hand stimulus. This acted as a visual digit cue appearing
735   sequentially on each of the four digits, with the time intervals between the digit cues
736   forming the target temporal structure of the sequence (T1) and defining its duration of
737   2400 ms. To achieve finger and temporal accuracy during training, participants were
738   asked to press the correct target buttons in synchrony with the digit cues until the
739   completion of the sequence, with the aim to progress towards synchronization with the
740   target timing. As the first digit cue of a sequence appeared at the same time as the *Go*
741   cue, immediate initiation of the sequence was emphasized in the instructions.

742   In memory-guided trials, a green rectangle was used as a background for the
743   *Go* cue, remaining on the screen for 2400 ms. Memory-guided trials featured the *Go*
744   cue without the appearance of digit cues, requiring participants to produce the
745   upcoming target sequence from memory. In these trials, participants were instructed
746   to initiate the sequence as quickly as possible and produce the sequence according
747   to its target finger and temporal structure (i.e. F1T1, F2T1).

748   In probe trials, the *Go* cue was displayed for 1000 ms on a grey background
749   with a digit cue presented on one digit (*Probe* cue), prompting a single press of the
750   corresponding target button. Here, the instructions were to respond to the *Probe* cue

751   as fast and accurately as possible. Participants were encouraged to avoid premature
752   responses (before the *Go* cue) in all trial types.

753   Following the *Go* cue, a fixation cross (1000 ms) and, subsequently, feedback
754   (1000 ms) were presented on the screen. The duration of a sequence trial including
755   feedback was 5.4 s, while a probe trial had a duration of 4 s. The inter-trial-interval (ITI)
756   was fixed at 800 ms. The experiment consisted of two 90min long training (Days 1 and
757   2) and a test (Day 3) sessions taking place over three consecutive days. Day 1
758   commenced with a practice block which involved two instructed and two memory-
759   guided *Sequence* trials for each of the target finger sequences as well as two random
760   probe trials, all randomly combined with the three delays. Over the three days,
761   participants serially underwent a pre-training (2 blocks), a training (36 blocks), a post-
762   training (2 blocks) and a test phase (2 refresher training blocks + 16 test blocks)
763   completing a total of 58 blocks. Participants were naïve as to the structure of the
764   gradual transition from the training through to the testphase and which block type they
765   were administered. The pre- and post-training blocks consisted of 24 instructed trials
766   each; each block was 2.48 min long and contained randomized mixed repetitions of
767   the two target and four control sequences matched equally with the delay conditions.
768   The training phase was organized in three stages: 12 blocks of 288 instructed and 72
769   probe trials (stage A, 80% instructed and 20% probe trials in each block), 12 blocks of
770   144 instructed, 144 from memory and 72 probe trials (stage B, 40% for each sequence
771   type and 20% probe trials in each block), and 12 blocks of 288 memory-guided and
772   72 probe trials (stage C, 80% memory and 20% probe trials in each block). A training
773   block (3 min long) of either stage consisted of 30 trials. On each block there was a
774   stable 20% occurrence of probe trials (6 in each block) comprising a total of 216 probes
775   throughout the training blocks. Distribution of probe trials in this phase was determined
776   by the minimum number of trials possible, namely 24 (2 sequences × 3 delays × 4
777   probe digits), and the block repeats. Eventually each probe digit occurred 18 times in
778   each training stage. All 40 blocks were evenly assigned to the study sessions such
779   that from Day 1 through the end of Day 2 participants had completed the training and
780   the post-training synchronization task. The testphase (Day 3) started with two
781   refresher training blocks of mixed type and immediately progressed to 16 blocks of 48
782   trials each, in which 24 memory-guided and 24 probe trials were randomly presented.
783   Duration of a test block was 4.4 min. The two trained sequences used in the memory-

784   guided trials were matched to the three delay conditions with each combination being
785   repeated four times within the block. This gave a total of 128 memory-guided trials per
786   delay condition, across blocks. In probe trials, each probe digit was combined with the
787   three delay conditions resulting in 32 trials per digit per delay condition. The testphase
788   had a total of 768 trials (384 memory-guided sequences and 384 probes). Overall, the
789   participants underwent 2004 trials excluding the practice trials.

790   *Experiment 2*. Procedures for Experiment 2 were identical to Experiment 1
791   except that the preparation period was fixed at 1500 ms and participants were trained
792   in associating three unique *Sequence* cues with one finger sequence (F1) to be
793   performed with three target temporal structures (T1, T2, T3) or IPIs: slow (T1, 800-
794   800-800 ms), fast (T2, 400-400-400 ms) and irregular (T3, 400-1600-400 ms), forming
795   respective target sequence durations of 2400 ms, 1200 ms, and 2400ms. The trial
796   followed the same structure as in Experiment 1, but the *Go* cue remained on the
797   screen for 3000 ms in a sequence trial and for 1000 in a probe trial. This was followed
798   by a fixation cross (1000 ms) and feedback (1000 ms) with a varying ITI of 500, 900
799   and 1300 ms. As a result, a sequence trial was 6.5 min long and a probe trial 4.5 min
800   long. The participants underwent the same structure of training and testsessions as in
801   Experiment 1. Similarly, we conducted a synchronization task, in a pre-post design.
802   Here, three additional control timing conditions were used to test for temporal transfer
803   (trained timing conditions) with the target timing patterns combined with a different
804   finger sequence. Overall, in this experiment participants were exposed to 15 unique
805   temporally structured sequences associated with their respective *Sequence* cue and
806   completed 2016 trials over 58 blocks.

807   *Experiment 3*. The training/testprocedures, trial structure, and the pre/post-
808   training synchronization task in Experiment 3 were identical to those of Experiment 2,
809   except that probe trials would additionally cue the thumb. This served as a control
810   condition to obtain reaction times and error rates for unplanned responses as thumb
811   presses were not part of any learnt finger sequence. Across each training stage, there
812   were 60 probe trials, while the testphase (30 blocks × 26 trials) contained 360 memory-
813   guided *Sequence* trials (120 trials per timing condition), 360 probe trials (30 trials per
814   digit per timing condition), and 60 thumb probe trials (20 trials per timing condition).
815   Overall, participants completed 1990 trials over 72 blocks, excluding the practice block.

816   *Feedback.* In all experiments, a points system was designed to reward fast
817   initiation and accurate performance, and avoid any drift in the motor production from
818   memory. After each sequence trial, feedback was presented on the screen for 1000
819   ms in the form of points (0-10) based on three performance criteria: reaction time (RT)
820   to assess sequence initiation, percentage of deviation from the target temporal
821   intervals of the sequence, and finger press accuracy. Points gained from the RT
822   component of the sequence, i.e. response from *Go* cue to the first press, were defined
823   by tolerance RT windows of 0-200, 200-360, 360-480, 480-560, 560-600 ms resulting
824   in 5, 4, 3, 2 and 1 points, respectively. For late (> 600) responses, 0 points were given.
825   A schematic feedback provided information on both finger accuracy and temporal
826   sequence accuracy performance. An '*x*' or a '*-*' symbol was shown for every correct or
827   incorrect press, respectively. Temporal errors were calculated after each trial as
828   deviations of press from target timing in percent of the target interval to account for the
829   scalar variability of timing[66,67]. Thresholds for mean absolute percentage deviation
830   across all correct presses were set at 10, 20, 30, 40 and 50 percent assigning 5, 4, 3,
831   2 and 1 points, respectively. Timing interval deviation > 50% resulted in 0 points. If a
832   press was performed too early the respective symbol was displayed below the midline,
833   while for a late response it was displayed above. This applied only to the second, third
834   and fourth presses of the sequence, whilst the first symbol reflecting the first press
835   was always positioned on the midline, representing the starting point of the sequence.
836   Deviation from target onset (presented or assumed) rather than interval timing
837   encouraged participants to synchronize with the visually cued sequences during
838   training, however, may have contributed to a tendency to compress the overall
839   sequence length during trials produced from memory.

840   Participants were instructed to adjust their performance by keeping the crosses
841   as close to the midline as possible. If at least one incorrect press or an incorrect
842   number of presses was recorded (< 4 or > 4), 0 points were given on that trial. The
843   points on each trial were displayed above the schematic feedback, and were the sum
844   of the RT, interval deviation and finger accuracy points. The feedback following a probe
845   trial displayed only points (0-5) gained based on RT and finger press accuracy utilizing
846   the same tolerance windows as described above for assessing sequence initiation RT.
847   In the case of an incorrect press or incorrect number of presses (< 1 or > 1), 0 points
848   were given regardless of the RT length. To incentivize the participants to gain as many

849   points as possible on each trial, we offered an extra monetary reward (10£) to those

850   two with the highest total points.

851   ***Data analysis***

852   Data analyses were performed using custom written code in Matlab (v9.2

853   R2017a, The MathWorks, Inc., Natick, Massachusetts, United States) and SPSS

854   version 22.0 (IBM Corp., Armonk, N.Y., USA). Median reaction time (RT; correct trials

855   only) and mean error rates for each *Probe* position and condition were calculated

856   relative to the 1st position in each participant and condition (RT and error rate increase

857   in %).

858   Repeated measures ANOVAs were undertaken for RT and error rate in *Probe*

859   trials, and for inter-press-intervals (IPI), temporal error, finger error, and sequence

860   initiation RT in *Sequence* trials produced from memory. Planned contrast analyses for

861   the main and interaction terms of interest in each ANOVA model involved user-defined

862   orthogonal contrasts. To evaluate the RT and error rate increase for the control action

863   (Experiment 3), we used two-tailed paired-samples t-tests (control *vs* 4th position).

864   Mean relative increase between adjacent positions (1st to 2nd, 2nd to 3rd, 3rd

865   to 4th) for RT (CQ RT increase) and press error rate (CQ error increase) in *Probe* trials

866   were taken as a measure for the strength of the competitive action gradient during

867   preparation. Using the group data (N = 55), we conducted six planned one-tailed

868   Pearson correlations between the CQ strength derived from RT and error increase,

869   respectively, and each of the sequence production measures.

870   ***CQ model of sequence preparation***

871   To our knowledge, no CQ model has previously been applied to response

872   preparation. While models differ somewhat with respect to how sequence position is

873   represented, they all require some form of "start state", which has stronger links to

874   items or responses that should occur earlier in the sequence[5,8,68,69]. In the

875   implementation, we use the Start-End CQ model[16], but we expect that other CQ

876   models with distinct start states would behave similarly if the same assumptions

877   regarding preparation were added to them.

878   The model makes the following assumptions: Each learned sequence is

879   hierarchically organized, with a "sequence node (or nodes)" linking to, and activating,

880   the responses which make up the sequence. The sequence node activates the

881   position codes (associations) of the items in the sequence. Following the *Sequence*

cue, the start-state of the cued sequence becomes gradually activated. The start-state of the intended sequence produces an activation gradient over the planned responses based on its strength of association with them. The additions to the published CQ model of Houghton (2018)[16] consist of: (i) the gradual increase of the start state activation, (Equation 1); (ii) the damping of response activations prior to the *Go* cue (Equation 3); and inhibition of the competitive response selection process, also prior to the *Go* cue. The model's activation of planned responses during preparation is shown in Figure 5.

Sequence node activation. Following presentation of the *Sequence* cue, the associated sequence node s_j becomes gradually activated. We implement a simple linear "ramp",

$$a_j(t) = b_j + ct$$

where t is (discrete) time (since cue presentation), b_j is the baseline activation, and c is the rate of increase. The activation of the start-state S_j retrieved by the learned sequence s_j follows this activation,

$$S_j(t) = a_j(t)S_j \qquad (1)$$

S_j (without a time index) is the asymptotic (i.e., stored) value for the sequence, set here to unity. The effect of this is simply that the start-state gradually increases its activation following the cue.

Input to response nodes. Activation spreads from the start-state $S_j(t)$ to finger responses via its positional associations W_j (a matrix) with the response tokens[16]. The input from sequence s_j to its associated actions is given by,

$$Q(t) = g\big(S_j(t)W_j\big) \qquad (2)$$

Here $Q(t)$ (a matrix) represents the state of the queue of response tokens. W_j encodes the positional weights from the sequence level to the responses in s_j, and the

914   product $S_j(t)W_j$ computes the differences between the start state of the sequence

915   ($S_j(t)$) and the position codes W_j of the sequence items (represented using the phase

916   code of Houghton, 2018).

917   Finally, the function g represents a Gaussian receptive field, or positional tuning

918   curve, applied element-wise to the signals coming from the matrix W_j. The receptive

919   field is sensitive to the difference between the state of the start-signal S_j and the

920   position codes in W_j, peaking when they are identical (see Houghton, 2018, Equation

921   1). The receptive field has a tuning (variance) parameter σ, controlling the model's

922   sensitivity to positional differences (Figure 5a).

923   *Finger response activation.* Each finger response in the sequence s_j becomes

924   gradually active during preparation, due to the increasing activation of the sequence's

925   start state (Equation 1), sending an increasing degree of activation to the responses

926   in the sequence, modulated by the similarity of the response's position code to the

927   start state (Equation 2). For a finger response $F_{k,j}$ (i.e., *k*th finger in sequence *j*), its

928   activation during preparation is, in discrete time form,

929

930
$$F_{k,j}(t+1) = 1 - F_{k,j}(t) \times \left(\delta F_{k,j}(t) + Q_k(t) \right) \qquad (3)$$

931

932   In the second term on the right, δ controls the decay rate (of the current

933   activation level), and $Q_k(t)$ is the input to finger F_k given by Equation 2. Note that if the

934   latter equals 0, then response activation spontaneously decays due to the decay term,

935      $\delta < 1$.

936   The first term on the right, $1 - F_{k,j}(t)$, acts as "damping" factor; it becomes

937   smaller as the response activation increases towards a ceiling of 1. This prevents

938   activations growing without bound as the preparation interval increases (Figure 5b). It

939   is proposed that on detection of the *Go* signal, this damping term ceases to act,

940   permitting activations to rapidly increase, and initiating the competitive response

941   selection process intrinsic to CQ models.

942

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