

**Competitive state of actions during planning predicts sequence execution accuracy**

Mantziara, Myrto; Ivanov, Tsvetoslav; Houghton, George; Kornysheva, Katja

DOI:

[10.1101/2020.05.08.085068](https://doi.org/10.1101/2020.05.08.085068)

Published: 10/05/2020

Other version

[Cyswllt i'r cyhoeddiad / Link to publication](#)*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*

Mantziara, M., Ivanov, T., Houghton, G., & Kornysheva, K. (2020). *Competitive state of actions during planning predicts sequence execution accuracy*. (bioRxiv).
<https://doi.org/10.1101/2020.05.08.085068>

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 **Competitive state of actions during planning** 2 **predicts sequence execution accuracy.**

3
4 Myrto Mantziara^{1,2}, Tsvetoslav Ivanov¹, George Houghton¹, and Katja Kornysheva^{1,2*}

5
6 ¹ School of Psychology, Bangor University, Bangor, Wales LL57 2AS, UK

7 ² Bangor Imaging Unit, Bangor University, Bangor, Wales LL57 2AS, UK

8
9
10 ***Correspondence:** Dr Katja Kornysheva at e.kornysheva@bangor.ac.uk, School of
11 Psychology, Bangor University, Wales, LL57 2AS, United Kingdom

12
13
14 **Word count:** Abstract: 240; Introduction: 786; Discussion: 2222; Methods: 3627; 39
15 pages, 5 figures, 0 tables, 3 supplementary figures.

16
17
18 **Author contributions:** M.M. and K.K. conceived the experiments; M.M. and T.I.
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.

22
23
24 **Acknowledgements:** The authors wish to thank Tom Hartley, Ken Valyear and
25 Simon Watt for helpful comments on the study.

26
27
28 **Disclosures:** The authors declare no conflicts of interest.

Competitive queuing during sequence preparation

2

29 **Abstract**

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

51

52 **Keywords:**

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

55 Introduction

56 Producing a variety of movement sequences from memory fluently is an
57 essential capacity of primates, in particular humans. It enables a skilled and flexible
58 interaction with the world for a range of everyday activities - from tool-use, speech and
59 gestural communication, to sports and music. Key to fluent sequence production is
60 sequence planning before the initiation of the first movement^{1,2}, with longer
61 preparation time benefitting sequence execution, i.e. reducing initiation time after a
62 'Go' cue and improving accuracy³. However, the underlying nature and content of
63 sequence planning is still debated⁴.

64 Computational models of sequence control, such as competitive queuing (CQ)
65 models, suggest that preparatory activity reactivates sequence segments *concurrently*
66 by means of a parallel activation gradient in the parallel planning layers⁵. Here the
67 neural activation pattern for each sequence segment is weighted according to its
68 temporal position in the sequence^{6,7}. A rich literature indirectly supporting CQ in
69 sequence control stems from observations of serial recall including transposition of
70 neighbouring items and items occupying the same position in different chunks^{6,8,9}, and
71 excitability of forthcoming items during sequence production¹⁰. Moreover, the CQ
72 account has also been substantiated directly at the neurophysiological level in the
73 context of well-trained finger sequences^{11,12}, saccades¹³ and drawing geometrical
74 shapes¹⁴. Importantly, these results have demonstrated that the neural gradient during
75 planning is relevant to subsequent execution. In particular, response separation in the
76 competitive gradient during sequence planning is predictive of sequence production
77 accuracy^{11,14}. Together, these data suggest that skilled sequence production involves
78 the concurrent planning of several movements in advance before sequence initiation
79 to achieve fluent performance.

80 While neural CQ during planning has been shown to predict subsequent
81 production, it remains unclear which properties of the sequence this preparatory
82 pattern encapsulates – the accuracy of the sequence (fluency of initiation and
83 production quality), or the temporal structure of the sequence (speed and temporal
84 grouping). Some CQ models assume the presence of a temporal context layer and
85 that the activity gradients are learned by associations of the latter to each sequence
86 element in the parallel planning layer, e.g. through Hebbian learning⁷. The form of
87 activity in the context layer can be as simple as a decaying start signal¹⁵, a combination

Competitive queuing during sequence preparation

4

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 rhythm⁷. 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.

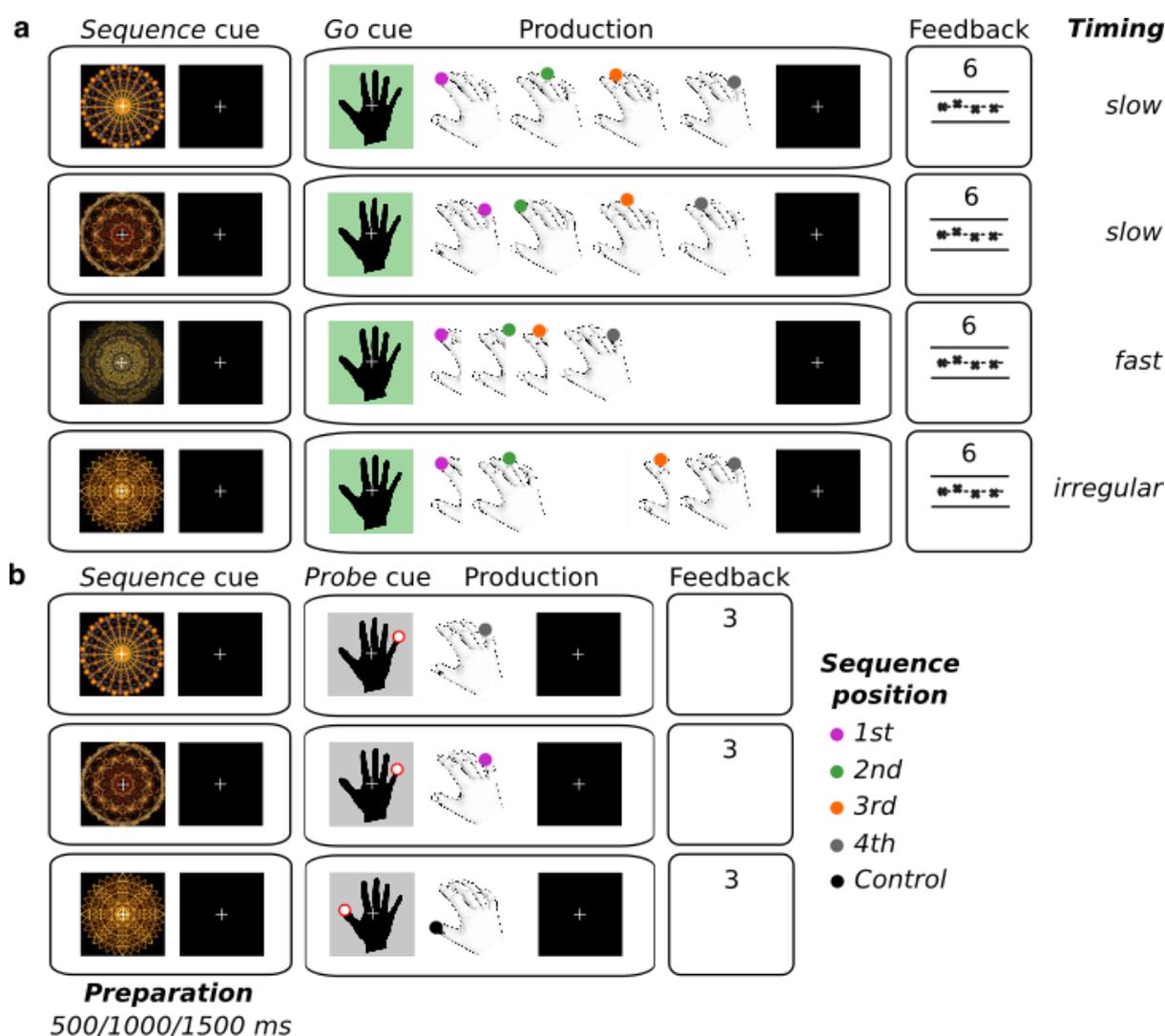
112 We find that the relative level of activation of probed actions at the end of the
113 planning period accords with their intended serial position. Contrary to the timing
114 hypothesis, we found no reliable association with speed or temporal structure of the
115 sequences. In contrast, we report 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

Competitive queuing during sequence preparation

5

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.

124



125

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.

126

127

128

Results

129

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

130

131

132

133

134

135

136

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

137

138

139

140

141

142

143

144

145

146

147

148

149

150

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

151

152

153

154

155

156

157

158

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

Competitive queuing during sequence preparation

7

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 work¹⁸. 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 Experiment 1, and three different temporal structures (slow, fast, irregular) in
172 Experiments 2 and 3 (Figure 2b).

Competitive queuing during sequence preparation

8

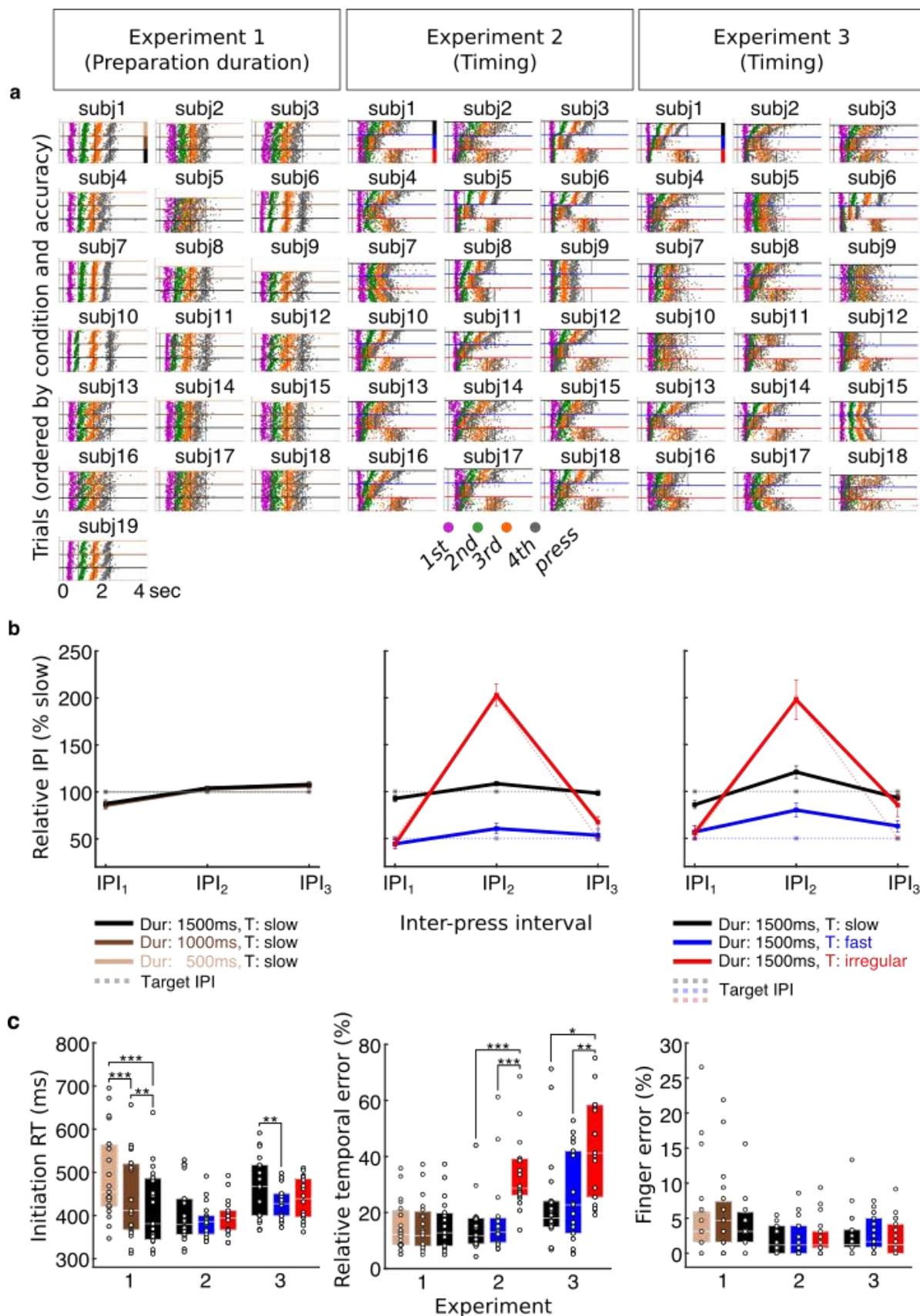


Figure 2 | Sequence production. **a.** Individual participants' raster plots show the timing of single button presses for each correct sequence trial produced from memory after the Go cue ($t = 0$) following training (target timing superimposed, grey lines). The colour code of the button presses corresponds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

Competitive queuing during sequence preparation

9

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. | * $P \leq 0.05$ | ** $P \leq 0.01$ | *** $P \leq 0.001$.

174 Despite a largely overlapping sequence timing across preparation durations in
175 Experiment 1 (Figure 2b, left), we found a small, but significant IPI \times 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 1st interval in the short ($p = .002$) and in the
179 intermediate delay ($p = .002$) compared to the long delay conditions. Additionally, the
180 3rd 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 1st interval with shorter
182 preparation time and slightly expand the 3rd 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 \times 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 1st 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 2nd 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 3rd interval exhibited a very similar profile to the 1st
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,

Competitive queuing during sequence preparation

10

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 \times Timing interaction (3 \times 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 from 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

Competitive queuing during sequence preparation

11

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

Competitive queuing during sequence preparation

12

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***

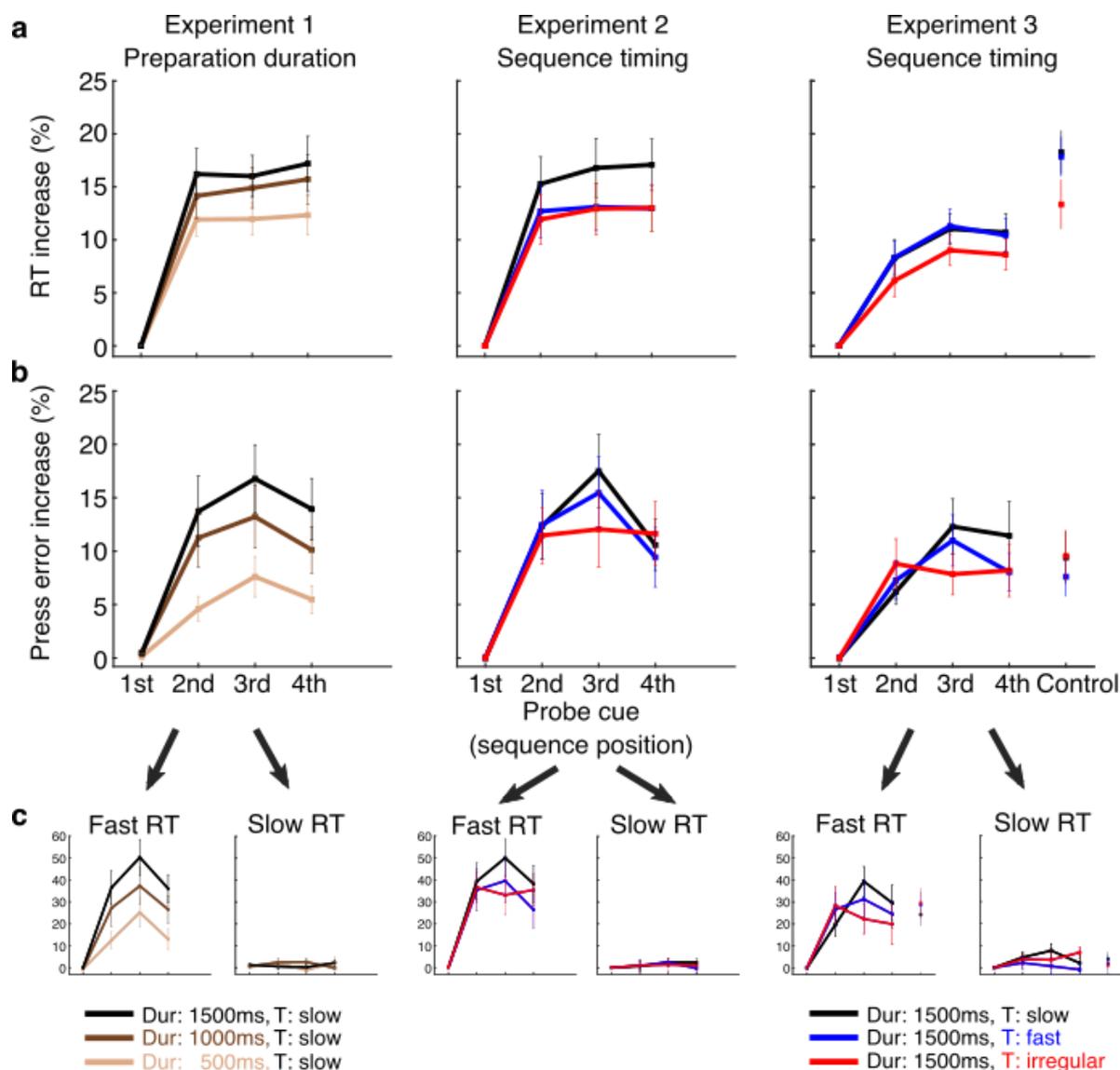
274 In half of the trials in the test phase on Day 3, instead of the *Go* cue that
275 prompted the production of the prepared finger sequence, participants encountered a
276 visual *Probe* cue which instructed them to respond with the corresponding finger press
277 as quickly and accurately as possible (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 1st 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 $= 45.958$, $p < .001$, $\eta p^2 = .719$, 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 (2nd vs 1st
292 position, $F(1, 18) = 63.360$, $p < .001$, $\eta p^2 = .779$; 3rd vs 2nd position, $F(1, 18) = 54.534$,
293 $p < .001$, $\eta p^2 = .752$; 4th vs 3rd position, $F(1, 18) = 24.900$, $p < .001$, $\eta p^2 = .580$). 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 \times Delay interaction ($F(6, 108) = 2.980$, $p = .010$,
297 $\eta p^2 = .142$). Planned contrasts using the long preparation duration as the reference
298 condition for the Delay factor, showed a significantly greater increase of the 2nd

Competitive queuing during sequence preparation

13

299 position relative to the 1st position at the long vs the short delay ($F(1, 18) = 7.349, p$
 300 $= .014, \eta p^2 = .290$). These results suggest that a longer preparation time prior to
 301 sequence execution boosted the competitive activation of actions.



302

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

Competitive queuing during sequence preparation

14

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 2nd position was larger compared to the 1st ($F(1, 17) = 48.072, p < .001,$
309 $\eta p^2 = .739$). Similarly, there was a significantly greater RT increase for the 3rd position
310 vs the 2nd ($F(1, 17) = 32.040, p = .001, \eta p^2 = .653$) and the 4th vs the 3rd ($F(1, 17) =$
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 2nd, 3rd and 4th positions over their preceding 1st, 2nd and
319 3rd positions, respectively (2nd vs 1st, $F(1, 17) = 61.485, p < .001, \eta p^2 = .783$; 3rd vs
320 2nd, $F(1, 17) = 69.762, p < .001, \eta p^2 = .804$; 4th vs 3rd, $F(1, 17) = 14.180, p = .002, \eta p^2 = .455$).
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 (4th 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 1st position; cf. Supplementary Figure 1b
334 for raw error rate values). Equally, we assessed the same factors, predicting an

Competitive queuing during sequence preparation

15

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 production²³ and suggests
344 the presence of a ranked probability across sequence positions for action selection.

345 The Position \times 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 \times 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

Competitive queuing during sequence preparation

16

368 performing with more errors than the 2nd position ($F(1, 17) = 17.903, p = .001,$
369 $\eta p^2 = .513$). Error rates of the 4th position did not differ from the 3rd position ($F(1, 17)$
370 $= 3.791, p = .068, \eta p^2 = .182$). 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 ($F(3.803, 64.654) = 1.869, p = .130, \eta p^2 = .099,$
375 Greenhouse-Geisser corrected, $\chi^2(20) = 42.899, p = .002$). 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.

A steeper CQ error gradient is bound to fast responses

389 Next, we sought to determine whether the characteristic error rate gradients were the
390 result of automatic responses, or deliberated action selection after the *Probe* cue. To
391 test this hypothesis, we assessed the error rate gradient for fast vs slow responses
392 following the *Probe* cue. We extracted the relative error rate increases for action
393 probes in the first and third RT quartiles for each experiment (Figure 3c). Only for the
394 fast responses, we found a main effect of Position (Experiment 1, $F(1.758, 31.650) =$
395 $19.731, p < .001, \eta p^2 = .523$, Greenhouse-Geisser corrected, $\chi^2(5) = 17.279, p = .004;$
396 Experiment 2, $F(2.033, 34.559) = 16.325, p < .001, \eta p^2 = .490$, Greenhouse-Geisser
397 corrected, $\chi^2(5) = 19.928, p = .001$; Experiment 3, $F(3, 51) =$
398 $12.749, p < .001, \eta p^2 = .429$). Planned contrasts for adjacent positions confirmed a
399 graded increase in finger errors up to the 3rd position (Experiment 1, 2nd position vs 1st
400

Competitive queuing during sequence preparation

17

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 \times 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 \times 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.

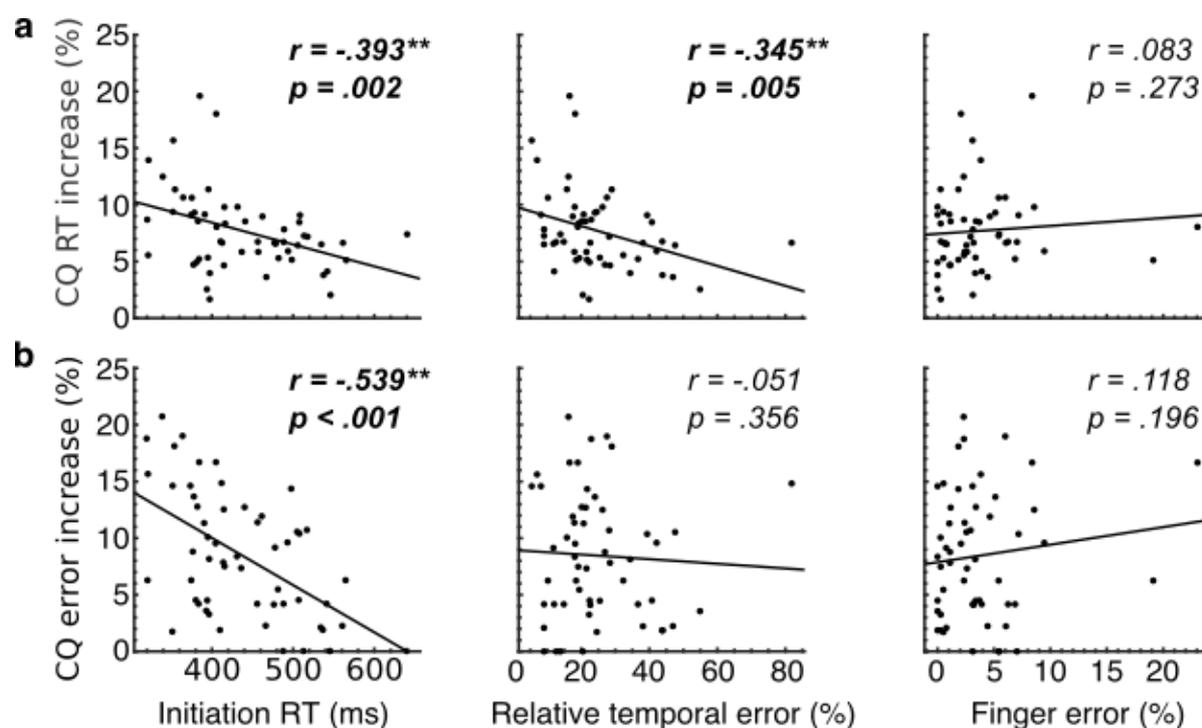
423 ***Preparatory CQ gradient correlates with temporal accuracy and initiation*** 424 ***speed***

425 Neurally derived CQ of sequence actions during planning predicts the
426 participants' subsequent performance accuracy as shown previously¹¹. 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

Competitive queuing during sequence preparation

18

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 study¹¹, 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.
448



449

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 findings¹¹, 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 action²⁶. 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

Competitive queuing during sequence preparation

20

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 behaviourally²⁹ and through measures of
491 cortico-spinal excitability¹⁰. 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 rehearsal³⁰. 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 tasks³¹ and perceptual sequence encoding³²,
514 as well as in the motor cortex in the context of motor sequence learning tasks³³. Replay
515 has been shown to involve fast sweeps through the neural patterns associated with

Competitive queuing during sequence preparation

21

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 1st-2nd-3rd, 1st-2nd, 1st, 1st-2nd-3rd-4th, 1st-2nd 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 actions¹¹.

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 our 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 durations²¹, 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

Competitive queuing during sequence preparation

22

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 sequence¹¹. 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

Competitive queuing during sequence preparation

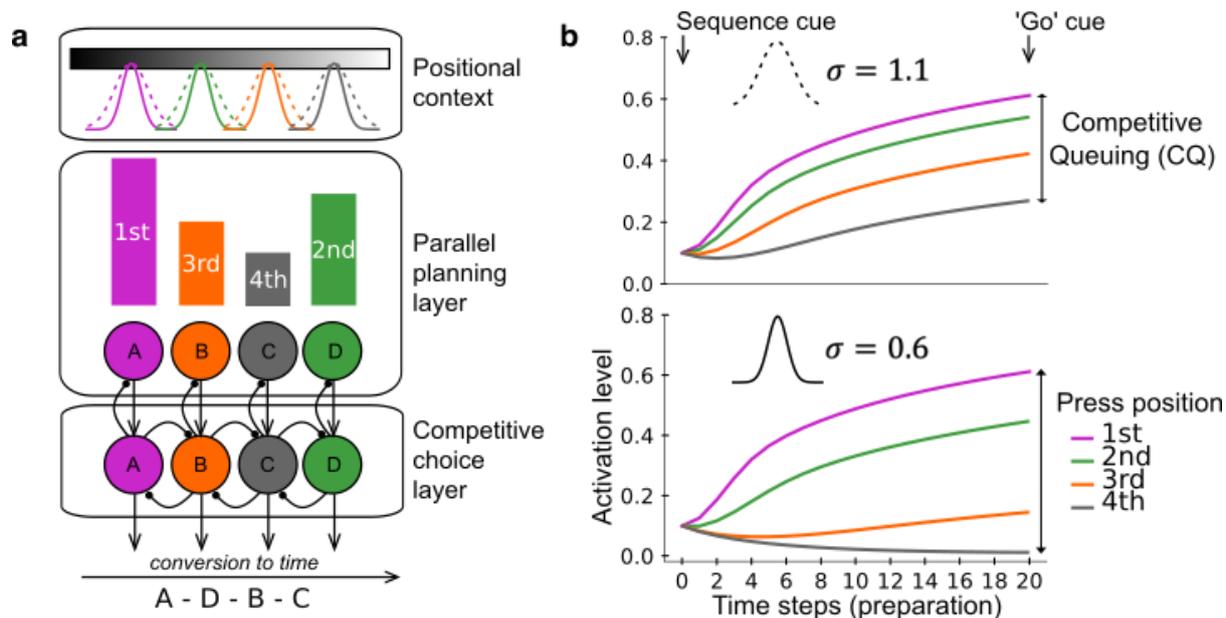
23

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.

Competitive queuing during sequence preparation

24



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 through 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 cue.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 models⁵¹, proposing that two CQ modules could operate in parallel - one

Competitive queuing during sequence preparation

25

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.

625 **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

638 **Methods**

639 **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 Inventory⁶⁵ (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

Competitive queuing during sequence preparation

26

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

Competitive queuing during sequence preparation

28

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

Competitive queuing during sequence preparation

29

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-

Competitive queuing during sequence preparation

30

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.

Competitive queuing during sequence preparation

31

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 model¹⁶, 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*

Competitive queuing during sequence preparation

33

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

890 *Sequence node activation.* Following presentation of the *Sequence* cue, the
891 associated sequence node s_j becomes gradually activated. We implement a simple
892 linear “ramp”,

893

$$894 \quad a_j(t) = b_j + ct$$

895

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

899

$$900 \quad S_j(t) = a_j(t)S_j \quad (1)$$

901

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

905

906 *Input to response nodes.* Activation spreads from the start-state $S_j(t)$ to finger
907 responses via its positional associations W_j (a matrix) with the response tokens¹⁶. The
908 input from sequence s_j to its associated actions is given by,

909

$$910 \quad Q(t) = g(S_j(t)W_j) \quad (2)$$

911

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

Competitive queuing during sequence preparation

34

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

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

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

943 References

- 944 1. Rosenbaum, D. A. Motor programming. *Massachusetts Inst. Technol. Cambridge,*
945 *MA.* (1984).

Competitive queuing during sequence preparation

35

- 946 2. Lashley, K. S. The problem of serial order in behavior. in *Cerebral mechanisms*
947 *in behavior* 112–131 (Wiley, 1951).
- 948 3. Ariani, G. & Diedrichsen, J. Sequence learning is driven by improvements in
949 motor planning. *J. Neurophysiol.* (2019). doi:10.1152/jn.00041.2019
- 950 4. Remington, E. D., Egger, S. W., Narain, D., Wang, J. & Jazayeri, M. A Dynamical
951 Systems Perspective on Flexible Motor Timing. *Trends Cogn. Sci.* **22**, 938–952
952 (2018).
- 953 5. Houghton, G. The problem of serial order: A neural network model of sequence
954 learning and recall. in *Current Research in Natural Language Generation* (1990).
- 955 6. Hartley, T. & Houghton, G. A linguistically constrained model of short-term
956 memory for nonwords. *J. Mem. Lang.* **35**, 1–31 (1996).
- 957 7. Burgess, N. & Hitch, G. J. Memory for serial order: A network model of the
958 phonological loop and its timing. *Psychol. Rev.* **106**, 551–581 (1999).
- 959 8. Henson, R. N. A. Short-Term Memory for Serial Order: The Start-End Model.
960 *Cogn. Psychol.* **36**, 73–137 (1998).
- 961 9. Glasspool, D. W. & Houghton, G. Serial order and consonant-vowel structure in
962 a graphemic output buffer model. *Brain Lang.* **94**, 304–330 (2005).
- 963 10. Behmer, L. P. *et al.* Parallel regulation of past, present, and future actions during
964 sequencing. *J. Exp. Psychol. Hum. Percept. Perform.* **44**, 1147–1152 (2018).
- 965 11. Kornysheva, K. *et al.* Neural Competitive Queuing of Ordinal Structure Underlies
966 Skilled Sequential Action. *Neuron* **101**, 1166–1180.e3 (2019).
- 967 12. Pinet, S., Dell, G. S. & Alario, F. X. Tracking keystroke sequences at the cortical
968 level reveals the dynamics of serial order production. *J. Cogn. Neurosci.* (2019).
969 doi:10.1162/jocn_a_01401
- 970 13. Basu, D. & Murthy, A. Parallel programming of saccades in the macaque frontal
971 eye field: Are sequential motor plans coactivated? *J. Neurophysiol.* (2020).
972 doi:10.1152/jn.00545.2018
- 973 14. Averbeck, B. B., Chafee, M. V., Crowe, D. A. & Georgopoulos, A. P. Parallel
974 processing of serial movements in prefrontal cortex. *Proc. Natl. Acad. Sci.* **99**,
975 13172–13177 (2002).
- 976 15. Page, M. P. A. & Norris, D. The Primacy Model: A New Model of Immediate Serial
977 Recall. *Psychol. Rev.* **105**, 761–781 (1998).
- 978 16. Houghton, G. Action and perception in literacy: A common-code for spelling and

Competitive queuing during sequence preparation

36

- 979 reading. *Psychol. Rev.* (2018). doi:10.1037/rev0000084
- 980 17. Burgess, N. & Hitch, G. J. A revised model of short-term memory and long-term
981 learning of verbal sequences. *J. Mem. Lang.* **55**, 627–652 (2006).
- 982 18. Friedman, J. & Korman, M. Offline optimization of the relative timing of
983 movements in a sequence is blocked by retroactive behavioral interference.
984 *Front. Hum. Neurosci.* **10**, 1–15 (2016).
- 985 19. Klapp, S. T. Reaction time analysis of central motor control. in *Advances in Motor*
986 *Learning and Control* (1996).
- 987 20. Sternberg, S., Monsell, S., Knoll, R. L. & Wright, C. E. The Latency and Duration
988 of Rapid Movement Sequences: Comparisons of Speech and Typewriting. in
989 *Information Processing in Motor Control and Learning* (1978).
990 doi:10.1016/b978-0-12-665960-3.50011-6
- 991 21. Niemi, P. & Naatanen, R. The foreperiod and simple reaction time. *Psychol. Bull.*
992 **89**, 133–162 (1981).
- 993 22. Vallesi, A., Shallice, T. & Walsh, V. Role of the prefrontal cortex in the foreperiod
994 effect: TMS evidence for dual mechanisms in temporal preparation. *Cereb.*
995 *Cortex* (2007). doi:10.1093/cercor/bhj163
- 996 23. Hurlstone, M. J. Functional similarities and differences between the coding of
997 positional information in verbal and spatial short-term order memory. *Memory*
998 **27**, 147–162 (2019).
- 999 24. Bullock, D. Adaptive neural models of queuing and timing in fluent action. *Trends*
1000 *Cogn. Sci.* **8**, 426–433 (2004).
- 1001 25. Hartley, T., Hurlstone, M. J. & Hitch, G. J. Effects of rhythm on memory for
1002 spoken sequences: A model and tests of its stimulus-driven mechanism. *Cogn.*
1003 *Psychol.* **87**, 135–178 (2016).
- 1004 26. Cisek, P. & Kalaska, J. F. Neural correlates of reaching decisions in dorsal
1005 premotor cortex: specification of multiple direction choices and final selection of
1006 action. *Neuron* **45**, 801–814 (2005).
- 1007 27. Verwey, W. B. & Abrahamse, E. L. Distinct modes of executing movement
1008 sequences: reacting, associating, and chunking. *Acta Psychol. (Amst)*. **140**,
1009 274–82 (2012).
- 1010 28. Rhodes, B. J., Bullock, D., Verwey, W. B., Averbach, B. B. & Page, M. P. A.
1011 Learning and production of movement sequences: Behavioral,

Competitive queuing during sequence preparation

37

- 1012 neurophysiological, and modeling perspectives. *Hum. Mov. Sci.* **23**, 699–746
1013 (2004).
- 1014 29. Behmer, L. P. & Crump, M. J. C. The dynamic range of response set activation
1015 during action sequencing. *J. Exp. Psychol. Hum. Percept. Perform.* (2017).
1016 doi:10.1037/xhp0000335
- 1017 30. Gilbert, R. A., Hitch, G. J. & Hartley, T. Temporal precision and the capacity of
1018 auditory–verbal short-term memory. *Q. J. Exp. Psychol.* (2017).
1019 doi:10.1080/17470218.2016.1239749
- 1020 31. Ólafsdóttir, H. F., Bush, D. & Barry, C. The Role of Hippocampal Replay in
1021 Memory and Planning. *Current Biology* (2018). doi:10.1016/j.cub.2017.10.073
- 1022 32. Liu, Y., Dolan, R. J., Kurth-Nelson, Z. & Behrens, T. E. J. Human Replay
1023 Spontaneously Reorganizes Experience. *Cell* **178**, 640–652.e14 (2019).
- 1024 33. Eichenlaub, J. B. *et al.* Replay of Learned Neural Firing Sequences during Rest
1025 in Human Motor Cortex. *Cell Rep.* **31**, 107581 (2020).
- 1026 34. Jafarpour, A., Fuentemilla, L., Horner, A. J., Penny, W. & Duzel, E. Replay of
1027 Very Early Encoding Representations during Recollection. *J. Neurosci.* **34**, 242–
1028 248 (2014).
- 1029 35. Drieu, C. & Zugaro, M. Hippocampal sequences during exploration:
1030 Mechanisms and functions. *Front. Cell. Neurosci.* **13**, 1–22 (2019).
- 1031 36. Dragoi, G. & Tonegawa, S. Preplay of future place cell sequences by
1032 hippocampal cellular assemblies. *Nature* (2011). doi:10.1038/nature09633
- 1033 37. Michelmann, S., Staresina, B. P., Bowman, H. & Hanslmayr, S. Speed of time-
1034 compressed forward replay flexibly changes in human episodic memory. *Nat.*
1035 *Hum. Behav.* **3**, 143–154 (2019).
- 1036 38. Kurth-Nelson, Z., Economides, M., Dolan, R. J. & Dayan, P. Fast Sequences of
1037 Non-spatial State Representations in Humans. *Neuron* (2016).
1038 doi:10.1016/j.neuron.2016.05.028
- 1039 39. Davidson, T. J., Kloosterman, F. & Wilson, M. A. Hippocampal Replay of
1040 Extended Experience. *Neuron* (2009). doi:10.1016/j.neuron.2009.07.027
- 1041 40. Li, N., Daie, K., Svoboda, K. & Druckmann, S. Robust neuronal dynamics in
1042 premotor cortex during motor planning. *Nature* **532**, 459–464 (2016).
- 1043 41. Wong, A. L. & Krakauer, J. W. Why Are Sequence Representations in Primary
1044 Motor Cortex So Elusive? *Neuron* (2019). doi:10.1016/j.neuron.2019.09.011

Competitive queuing during sequence preparation

38

- 1045 42. Krakauer, J. W. & Mazzoni, P. Human sensorimotor learning: adaptation, skill,
1046 and beyond. *Curr. Opin. Neurobiol.* **21**, 636–644 (2011).
- 1047 43. Wang, J., Narain, D., Hosseini, E. A. & Jazayeri, M. Flexible timing by temporal
1048 scaling of cortical responses. *Nat. Neurosci.* (2018). doi:10.1038/s41593-017-
1049 0028-6
- 1050 44. Goudar, V. & Buonomano, D. V. Encoding sensory and motor patterns as time-
1051 invariant trajectories in recurrent neural networks. *Elife* (2018).
1052 doi:10.7554/eLife.31134
- 1053 45. Burgess, N. & Hitch, G. Computational models of working memory: Putting long-
1054 term memory into context. *Trends Cogn. Sci.* **9**, 535–541 (2005).
- 1055 46. Bortoletto, M., Cook, A. & Cunnington, R. Motor timing and the preparation for
1056 sequential actions. *Brain Cogn.* (2011). doi:10.1016/j.bandc.2010.11.016
- 1057 47. Bortoletto, M. & Cunnington, R. Motor timing and motor sequencing contribute
1058 differently to the preparation for voluntary movement. *Neuroimage* (2010).
1059 doi:10.1016/j.neuroimage.2009.11.048
- 1060 48. Maslovat, D., Chua, R., Klapp, S. T. & Franks, I. M. Preparation of timing
1061 structure involves two independent sub-processes. *Psychological Research* **82**,
1062 981–996 (2018).
- 1063 49. Kornysheva, K., Sierk, A. & Diedrichsen, J. Interaction of temporal and ordinal
1064 representations in movement sequences. *J. Neurophysiol.* **109**, 1416–24 (2013).
- 1065 50. Kornysheva, K. & Diedrichsen, J. Human premotor areas parse sequences into
1066 their spatial and temporal features. *Elife* **3**, e03043 (2014).
- 1067 51. Zeid, O. & Bullock, D. Moving in time: Simulating how neural circuits enable
1068 rhythmic enactment of planned sequences. *Neural Networks* (2019).
1069 doi:10.1016/j.neunet.2019.08.006
- 1070 52. Ullén, F., Bengtsson, S. L. & Ullén, F. Independent Processing of the Temporal
1071 and Ordinal Structure of Movement Sequences. *J. Neurophysiol.* **90**, 3725–3735
1072 (2003).
- 1073 53. Shin, J. C. & Ivry, R. B. Spatial and Temporal Sequence Learning in Patients
1074 with Parkinson's Disease or Cerebellar Lesions. *J. Cogn. Neurosci.* **15**, 1232–
1075 1243 (2003).
- 1076 54. O'Reilly, J. X., McCarthy, K. J., Capizzi, M. & Nobre, A. C. Acquisition of the
1077 temporal and ordinal structure of movement sequences in incidental learning. *J.*

Competitive queuing during sequence preparation

39

- 1078 *Neurophysiol.* **99**, 2731–2735 (2008).
- 1079 55. Bengtsson, S. L., Ehrsson, H. H., Forssberg, H. & Ullén, F. Dissociating brain
1080 regions controlling the temporal and ordinal structure of learned movement
1081 sequences. *Eur. J. Neurosci.* **19**, 2591–2602 (2004).
- 1082 56. Bengtsson, S. L., Ehrsson, H. H., Forssberg, H. & Ullén, F. Effector-independent
1083 voluntary timing: behavioural and neuroimaging evidence. *Eur. J. Neurosci.* **22**,
1084 3255–3265 (2005).
- 1085 57. Friston, K. & Buzsáki, G. The Functional Anatomy of Time: What and When in
1086 the Brain. *Trends Cogn. Sci.* **20**, 500–511 (2016).
- 1087 58. Crowe, D. A., Zarco, W., Bartolo, R. & Merchant, H. Dynamic representation of
1088 the temporal and sequential structure of rhythmic movements in the primate
1089 medial premotor cortex. *J. Neurosci.* **34**, 11972–83 (2014).
- 1090 59. Merchant, H., Perez, O., Zarco, W. & Gamez, J. Interval Tuning in the Primate
1091 Medial Premotor Cortex as a General Timing Mechanism. *J. Neurosci.* **33**,
1092 9082–9096 (2013).
- 1093 60. Miller, N. The assessment of limb dyspraxia. *Clin. Rehabil.* **2**, 177–181 (1988).
- 1094 61. Sadnicka, A., Kornysheva, K., Rothwell, J. C. & Edwards, M. J. A unifying motor
1095 control framework for task-specific dystonia. *Nature Reviews Neurology* **14**,
1096 116–124 (2018).
- 1097 62. Howell, P. A model of serial order problems in fluent, stuttered and agrammatic
1098 speech. *Hum. Mov. Sci.* (2007). doi:10.1016/j.humov.2007.07.004
- 1099 63. Craig-McQuaide, A., Akram, H., Zrinzo, L. & Tripoliti, E. A review of brain
1100 circuitries involved in stuttering. *Front. Hum. Neurosci.* **8**, 1–20 (2014).
- 1101 64. Ingham, R. J., Ingham, J. C., Euler, H. A. & Neumann, K. Stuttering treatment
1102 and brain research in adults: A still unfolding relationship. *Journal of Fluency*
1103 *Disorders* (2018). doi:10.1016/j.jfludis.2017.02.003
- 1104 65. Oldfield, R. C. The assessment and analysis of handedness: the Edinburgh
1105 inventory. *Neuropsychologia* **9**, 97–113 (1971).
- 1106 66. Rakitin, B. C. *et al.* Scalar expectancy theory and peak-interval timing in humans.
1107 *J. Exp. Psychol. Anim. Behav. Process.* **24**, 15–33 (1998).
- 1108 67. Jazayeri, M. & Shadlen, M. N. Temporal context calibrates interval timing. *Nat.*
1109 *Neurosci.* **13**, 1020–1026 (2010).
- 1110 68. Brown, G. D. A., Hulme, C. & Preece, T. Oscillator-Based Memory for Serial

Competitive queuing during sequence preparation

40

- 1111 Order. *Psychol. Rev.* **107**, 127–181 (2000).
- 1112 69. Burgess, N. & Hitch, G. J. Toward a network model of the articulatory loop. *J.*
- 1113 *Mem. Lang.* (1992). doi:10.1016/0749-596X(92)90022-P
- 1114