

The planning horizon for movement sequences

Running title: The horizon of sequence planning

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27 **Abstract**

28 When performing a long chain of actions in rapid sequence, future movements need to be planned
29 concurrently with ongoing action. However, how far ahead we plan, and whether this ability improves
30 with practice, is currently unknown. Here we designed an experiment in which healthy volunteers were
31 asked to produce 14-item sequences of finger movements quickly and accurately on a keyboard in
32 response to numerical stimuli. On every trial, participants were only shown a fixed number of stimuli
33 ahead of the current keypress. The size of this viewing window varied between 1 (next digit revealed
34 with the pressing of the current key) and 14 (full view of the sequence). Participants practiced the task
35 for five days and their performance was continuously assessed on random sequences. Our results
36 indicate that participants used the available visual information to plan multiple actions into the future,
37 but that the planning horizon was limited: receiving more information than 3 movements ahead did
38 not result in faster sequence production. Over the course of practice, we found larger performance
39 improvements for larger viewing windows. Additionally, we show that improved planning was
40 accompanied by an expansion of the planning horizon with practice. Together, these findings show that
41 one important aspect of sequential motor skills is the ability of the motor system to exploit visual
42 information for planning multiple responses into the future.

43

44 **Key words**

45 Motor planning; Sequence production; Practice effects; Hand function.

46 Introduction

47 Humans exhibit a wide range of behaviors on a daily basis, from whole-body activities like running or
48 riding a bike, to fine dexterous skills like writing or typing on a keyboard. Many of such skills share one
49 common feature: they are comprised of a series of separate motor elements that are strung together
50 in quick succession to form longer and more complex sequences of movements (Lashley, 1951). When
51 learning a new skill, people usually need many hours of practice to achieve fluidity in performance
52 (Ericsson et al., 1993). With practice, sequence production becomes quicker, more accurate, and less
53 effortful (Verwey, 1994; Rhodes et al., 2004; Diedrichsen and Kornysheva, 2015; Krakauer et al., 2019),
54 leading in the long run to the skillful behaviors typically observed in elite athletes (Yarrow et al., 2009).

55 Many studies of motor sequence learning have focused on the training of specific movement
56 sequences (Cohen et al., 1990; Willingham, 1999; Verwey, 2001; Verwey and Abrahamse, 2012;
57 Kornysheva et al., 2013, 2019; Verwey et al., 2014; Wong et al., 2015b; Mantziara et al., 2020).
58 However, many sequences we execute in everyday life are not fully predictable. Yet, practice improves
59 performance even for random or untrained sequential movements (Waters-Metenier et al., 2014;
60 Wiestler et al., 2014; Ariani et al., 2020). Some of these sequence-general improvements are due to
61 the fact that participants learn to translate individual visual stimuli into motor responses and to execute
62 these responses more quickly (Ariani and Diedrichsen, 2019; Hardwick et al., 2019). Such improvements
63 in single responses benefit the production of all sequences, including random ones.

64 In the present study, we focus on a second core ability that enables fast execution of
65 unpredictable sequences: the ability to plan future movements ahead of time. Planning of movements
66 before their initiation, here referred to as preplanning, has been studied extensively (Rosenbaum, 1980;
67 Rosenbaum et al., 1987, 2007; Churchland et al., 2010; Cisek and Kalaska, 2010; Kaufman et al., 2014;
68 Wong et al., 2015a; Haith et al., 2016). However, long or complex movement sequences are unlikely to
69 be fully preplanned, so planning of the remaining elements must continue throughout sequence
70 production – a process that we have recently named online planning (Ariani and Diedrichsen, 2019).
71 Take the example of a basketball player dribbling up the court. The player needs to control a continuous
72 flow of movements (e.g., to keep the dribbling alive) while scouting the court and planning future
73 movements depending on the actions of both teammates and opposing defenders. Some evidence for
74 online planning has been observed for a range of behaviors, such as reading (Rayner, 1998, 2014;
75 Rayner and Reingold, 2015), sequential reaching (Säfström et al., 2013, 2014) and path tracking
76 (Bashford et al., 2018). However, to what extent the motor system plans upcoming movements during
77 sequence production (i.e., the horizon of motor planning) remains poorly understood.

78 Here we asked 1) how far the benefit of planning ahead extends beyond current execution, and
79 2) whether this planning horizon can be improved with practice. To answer these questions, we used a

80 discrete sequence production (DSP) task, in which participants performed random sequences of 14
81 keypresses with their right hand in response to numerical cues. We manipulated how many digits
82 participants could see ahead of the current keypress. Viewing window size ranged from 1 (only the next
83 movement is cued, as in the serial reaction time task, SRTT) to 14 (the entire sequence shown at once,
84 as in the DSP task). Participants practiced producing varying sequences over 5 days. This design allowed
85 us to examine both the horizon of motor planning in sequence production and the influence of practice
86 on the planning horizon.

87 **Methods**

88 *Participants*

89 Seventeen right-handed neurologically healthy volunteers (8 women, 9 men; age 18–36 years, mean
90 25.81 years, SD 5.09 years) were recruited for this study. Handedness was assessed with the Edinburgh
91 Handedness Inventory (mean 82.81, SD 18.07). Individuals participated in 5 sessions of practice (2 hours
92 each, on 5 separate days). All participants provided written informed consent and were naive to the
93 purposes of the study. Experimental methods were approved by the Research Ethics Board at Western
94 University. Two participants abandoned the study after the first session of practice. One participant
95 had an unusually high error rate (> 30%, while every other participant managed to keep the error rate
96 < 20%, as per instructions). These 3 participants were excluded from successive analyses (final N = 14).
97 For one of the remaining 14 participants, age and handedness data was missing.

98

99 *Apparatus*

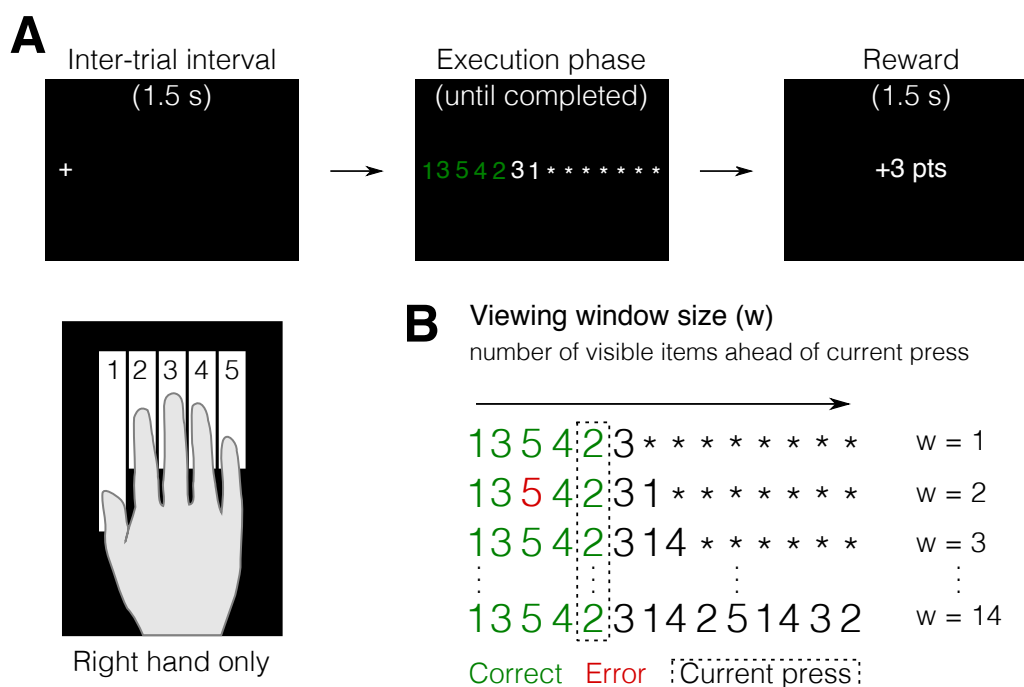
100 Participants placed their right hand on a custom-made keyboard (Fig. 1A), with a force transducer
101 (Honeywell FS series) mounted underneath each key. The keys were immobile and measured isometric
102 finger force production. The dynamic range of the force transducers was 0-16 N and the resolution 0.02
103 N. A finger press/release was detected when the force crossed a threshold of 1 N. The forces measured
104 from the keyboard were low pass filtered, amplified, and sent to PC for online task control and data
105 recording. Numerical stimuli were shown in white against a black background, horizontally aligned in a
106 single line, and spanned ~36° of visual angle for an entire sequence.

107

108 *Procedure*

109 In each of the five practice sessions, participants sat in front of a computer screen with their right hand
110 on the keyboard. The task required participants to produce sequences of keypresses in response to
111 numerical cues appearing on the screen (numbers 1 to 5, corresponding to fingers of their right hand,
112 thumb to little finger, respectively) as quickly and accurately as possible (Fig. 1A). On every trial, only a
113 fixed number of digits ahead of the current press position (viewing window size, w) were revealed to
114 the participants, while the rest were masked with asterisks (Fig. 1B). The masked digits were revealed
115 to the participant as they proceeded, from left to right, with the presses in each sequence. The window
116 size varied within the domain of $w = \{1, 2, 3, 4, 5, 6, 7, 8, 14\}$, and was randomized across trials within
117 every block. As an attentional pre-cue, during the inter-trial interval (ITI, 1.5 seconds) participants were
118 presented with a fixation cross on the location of the first digit in the sequence. With every press,
119 subjects received feedback about the correctness of their action: the white numbers turned either

120 green or red and were accompanied by a corresponding sound for correct and incorrect presses,
 121 respectively.
 122
 123



124
 125 **Figure 1 | Varying viewing window in a discrete sequence production (DSP) task.** **A.** Example
 126 trial in a DSP task with viewing 2 items ahead of the current keypress, while the remaining
 127 items are masked by asterisks. **B.** Viewing window size (w) manipulation, from $w = 1$
 128 (equivalent to a simple reaction time task), to $w = 14$ (display of the entire sequence at once).
 129 The arrow indicates the from-left-to-right direction of response order. Participants could start
 130 each sequence whenever they felt ready and were rewarded on the basis of their movement
 131 time (MT, the time from the first keypress to the release of the last key in the sequence).
 132

133
 134 To motivate participants to improve in the task, they were rewarded with points based on their
 135 performance after each trial. Points were awarded on the basis of sequence movement time (MT) and
 136 execution accuracy. MT corresponded to the time interval between making the first press in the
 137 sequence to releasing the last press in the sequence. Accuracy was calculated as $1 - \text{error rate}$
 138 (proportion of error trials in a block) in percentage. Specifically, a trial was considered an error if it
 139 contained one or more incorrect presses, for which participants received 0 points. Correct sequences
 140 were rewarded with at least 1 point. Finally, participants were awarded 3 points if 1) a sequence was
 141 correct and 2) MT 5% or more faster than a specific time threshold. This time threshold was designed
 142 to get increasingly difficult adjusting to every subject's speed throughout training. It would decrease by
 143 5% from one block to the next if two performance criteria were met: median MT in the current block

144 faster than best median MT recorded hitherto, and mean error rate in the last block $\leq 15\%$. If either
145 one of these criteria was not met, the thresholds remained unchanged. At the end of each block,
146 participants received feedback on their error rate, median sequence MT, total points obtained during
147 the block, and total points obtained during the session. Subjects were asked to try to maintain an error
148 rate below 15%.

149 In the original design, we intended to compare also how the ability to plan ahead might affect
150 partially familiar (structured) sequences. Therefore, each one of the 5 practice sessions consisted of 8
151 blocks (27 trials each) of 14-item sequences and 3 blocks (60 trials each) of specific short 3-/4-item
152 segments that composed the structured sequences. One-third of the trials in the sequence blocks were
153 randomly generated by random shuffles of the digits 1 to 5. The remaining two-thirds of the trials were
154 structured sequences. As the results from the structured sequences turned out to be hard to interpret,
155 the present paper will only focus on the completely unfamiliar, random sequences. The examination of
156 partially familiar sequences is intended for discussion in future publications.

157

158 *Data analysis*

159 Data were analyzed with custom code written in Matlab (The MathWorks, Inc., Natick, MA). To evaluate
160 the speed of sequence production, we inspected the time intervals between different keypresses.
161 Reaction times (RT) were defined as the time from stimulus onset to first press (i.e., the first crossing
162 of the 1 N force threshold). Note that participants were not instructed to react particularly fast. Instead,
163 they could take as much time as they wanted until they felt ready to start. MTs were defined as the
164 time between the first press and the release of the last press in the sequence (i.e., the time between
165 the first and the last crossing of the force threshold). Finally, we calculated inter-press intervals (IPI)
166 between subsequent pairs of presses in the sequence (i.e., the time interval between every two
167 consecutive crossings of the force threshold). Unless otherwise noted, we used within-subject repeated
168 measures ANOVAs and 2-sided paired samples *t*-tests for statistical inference in assessing the effects
169 of viewing window or practice on RT, MT, and IPI. Error trials were excluded from data analysis. To
170 provide meaningful error bars for within-subject comparison, the standard error for each condition was
171 calculated on the residuals after subtracting the mean across conditions for each participant. This way,
172 the error bars visualized the size of the relevant error term in a repeated-measures ANOVA.

173 To describe the relationship between MT and the viewing window size, we used the following
174 exponential model:

175

$$176 \quad MT' = a * \exp(-b * (w - 1)) + c,$$

177

178 where MT' is the predicted MT for a given viewing window size w . Note that for $w = 1$, the function
179 reduces to the initial value of the exponential, $MT' = a + c$. The asymptote is given by c and the slope
180 by b . This model was then fit to the MT data of each participant using Matlab's `nlinfit()` function,
181 which implements the Levenberg-Marquardt nonlinear least-squares algorithm. We determined the
182 effective planning horizon (w^*), by finding the window size for which the predicted MT of the
183 participant had dropped 99% of the difference between $w = 1$ and the asymptote, i.e., by solving the
184 equation for w :

185

186

$$w^* = -\log(0.01)/b + 1,$$

187

188 where the 0.01 arises from the criterion of the 99% drop (i.e., 1% above the MT' asymptote). The
189 improvement in effective planning horizon with practice was then assessed by fitting the model to the
190 data of each participant on each day and comparing w^* between day 1 and day 5 with a within-subject
191 2-sided paired samples t -test. While the use of a 99% criterion is somewhat arbitrary, changes in this
192 criterion only scale the effect planning horizon by a specific value but do not change the outcome of
193 the statistical analysis.

194

195 Results

196 *Preplanning of future movements speeds up sequence production*

197 First, we assessed the benefit of being able to plan future finger movements on sequence production.

198 To determine this, we varied the amount of available information and tested how this window size

199 affected the speed of performance. On average, across all days of practice, larger window sizes

200 produced shorter MTs (Fig. 2A), as confirmed by the highly significant main effect of window size on

201 MT in a repeated measures ANOVA ($F_{8,104} = 176.980, p < 10e-10$). This suggests that the availability of

202 visual information allows for preplanning of sequential actions into the future, which in turn reduces

203 MT. Interestingly, this benefit appeared to plateau around a window size of 3 or 4. Indeed, when we

204 compared the MT of each viewing window to the average MT for larger window sizes, we found a

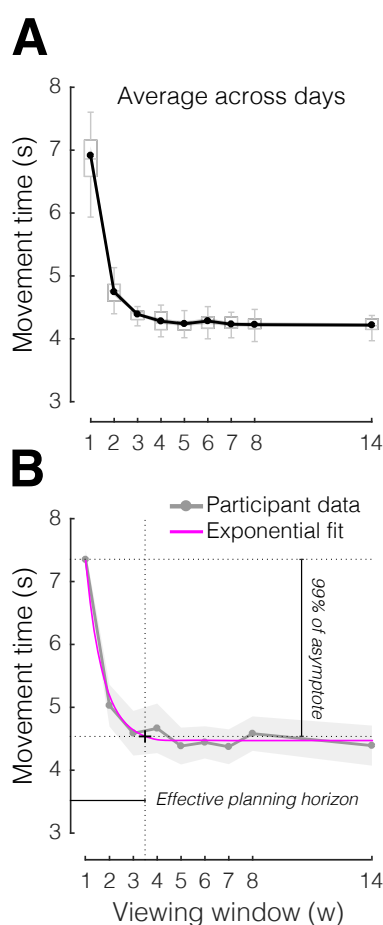
205 significant difference for $w = 3$ vs. $w > 3$ ($t_{13} = 4.644, p = 4.591e-04$), but not for $w = 4$ vs. $w > 4$ ($t_{13} =$

206 $2.083, p = 0.058$). To obtain an individual measure of the planning horizon, we fit an exponential model

207 to the MT curve of each participant (Fig. 2B, see Methods).

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Figure 2 | The benefit of planning ahead on sequential performance. A.
Average movement time as a function of viewing window, across the 5 days of

213 *practice. B. Method used to estimate the effective planning horizon. Example*
214 *data from one participant (gray) is fit to an exponential model (magenta). The*
215 *intersection between performance at 99% of asymptote and the exponential fit*
216 *was chosen as criterion to determine the effective planning horizon. Box plots*
217 *show the median and whole range of individual data points (one per*
218 *participant). Shaded areas reflect standard error of the mean.*
219

220

221 Next, we decided on an arbitrary criterion on the exponential (99% of the MT drop to the asymptote)
222 to establish the individual effective horizon of each participant. This analysis revealed a mean effective
223 planning horizon of 3.58 ± 0.28 items ahead of the current item, confirming that, on average,
224 participants were able to plan at least 3 keypresses into the future.

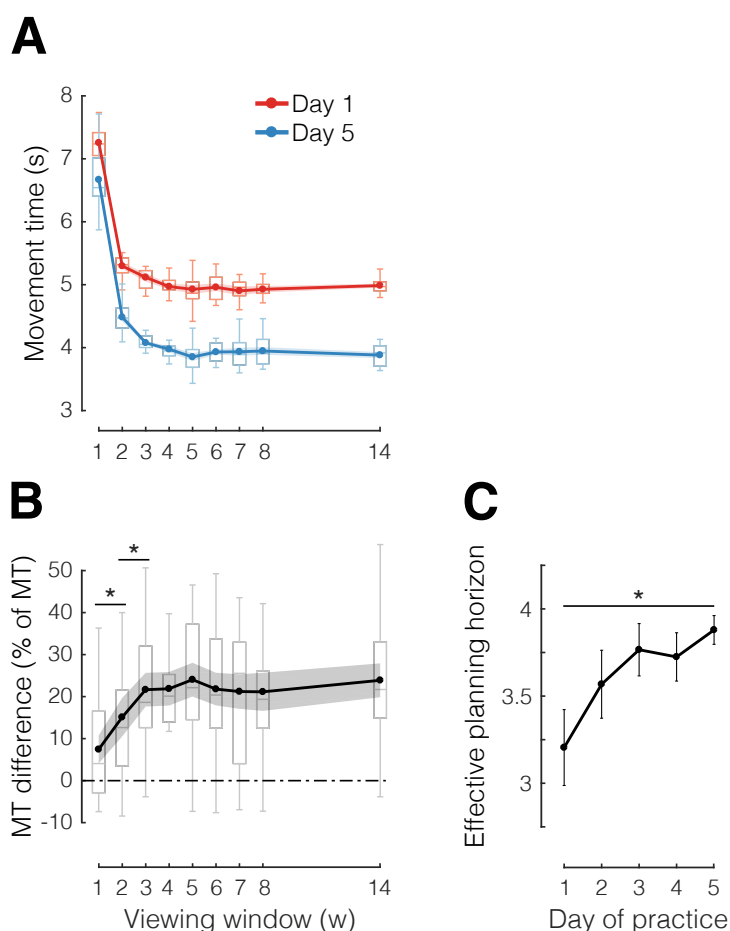
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226 ***Practice expands the planning horizon***

227 We then asked whether practicing sequences would affect the ability to plan future movements by
228 comparing performance at the beginning (day 1) and at the end (day 5) of practice (Fig. 3A). We
229 observed that MT improved across all window sizes (main effect of day: $F_{1,13} = 18.004$, $p = 0.001$).
230 Significant improvements were found even for a window size of 1 (MT difference day 1 vs. day 5: 586
231 ± 262 ms; $t_{13} = 2.234$, $p = 0.022$). This condition was, in essence, a serial reaction time task, where each
232 cue was only presented after the preceding key was pressed. Therefore, participants were forced to
233 serially cycle through the planning and execution of every press, with no possibility for planning ahead.
234 Thus, MT improvements for a window size of 1 must be a consequence of 1) better stimulus
235 identification, 2) better stimulus-response (S-R) mapping, or 3) better execution (i.e., motor
236 implementation) of single responses.

237 Importantly, if learning was restricted to improvement in any of these three processes, we
238 would predict equal MT improvement across all window sizes, given that stimulus identification, S-R
239 mapping, and execution are necessary steps across all viewing windows. Contrary to prediction,
240 however, we found a significant interaction between window size and stage of practice (day 1 vs. day
241 5; $F_{8,104} = 3.220$, $p = 0.003$). Furthermore, when we directly inspected the MT improvement (percentage
242 change relative to average MT for each horizon, Fig. 3B), we found significantly larger gains for larger
243 viewing windows ($w = 2$ vs. $w = 1$: $t_{13} = 3.338$, $p = 0.005$; $w = 3$ vs. $w = 2$: $t_{13} = 2.722$, $p = 0.017$), until
244 again the gains plateau for $w = 4$ or larger ($w = 4$ vs. $w = 3$: $t_{13} = 0.113$, $p = 0.912$). Thus, although
245 responses to single items improved with practice, this improvement cannot explain why performance
246 benefits were more pronounced for larger window sizes. Instead, the additional performance benefit
247 must be due to the fact that participants became more efficient at using the advance information
248 provided by larger viewing windows. In addition to the evidence for more efficient planning of future
249 elements, we also found evidence that participants planned further into the future. When we

250 determined the effective planning horizon for each participant and day (Fig. 2B) using an exponential
 251 fit (see Methods), we found that the planning horizon expanded from 3.20 to 3.88 digits ahead of
 252 current action between day 1 and day 5 (paired-samples t -test, $t_{13} = 2.840$, $p = 0.014$, Fig. 3C). Thus,
 253 participants not only became more efficient in planning but planned sequential actions further into the
 254 future.
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 256



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 258 **Figure 3 | The effective planning horizon increases with practice.** **A.** Average
 259 movement time (MT) as a function of viewing window (w), separately for early
 260 (day 1, red) and late (day 5, blue) stages of sequence practice. **B.** Difference in
 261 performance (sequence MT) between early and late practice (data in A),
 262 normalized by average MT, as a function of w . **C.** Mean effective planning
 263 horizon (estimated as shown in Fig. 2B) for each day of practice. Box plots show
 264 the median and whole range of individual data points (one per participant).
 265 Shaded areas (or error bars) reflect standard error of the mean. * $p < 0.05$, two-
 266 tailed paired-samples t -tests.
 267

268
 269 Note that faster MTs for larger window sizes did not occur at the expense of reduced accuracy in
 270 performance. On average, the percent accuracy of presses remained roughly constant around 85-90%

271 across all viewing window conditions. We found no significant main effect of window size ($F_{8,104} = 1.182$,
272 $p = 0.317$), practice stage ($F_{1,13} = 0.325$, $p = 0.578$), or interaction between the two factors ($F_{8,104} = 0.548$,
273 $p = 0.818$).

274 Taken together, these results show that participants became faster in sequence production by
275 getting better at 1) making single responses (involving stimulus identification, S-R mapping, or
276 execution) and 2) exploiting available information to plan more upcoming movements in advance.

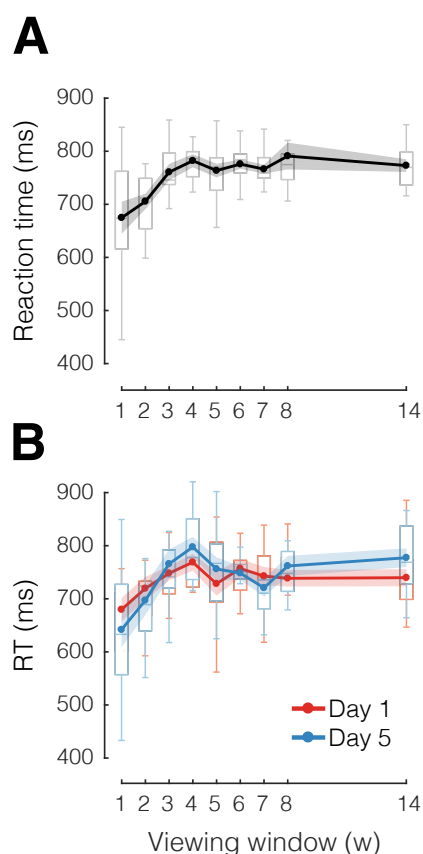
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278 *Reaction times increase with the amount of preplanning*

279 If participants invested time in preplanning the first few elements of each sequence, then we would
280 expect this to be reflected in the reaction times: namely, participants should start a sequence earlier
281 when presented with a smaller window size, and later for larger window sizes, since they would be
282 preparing more of the upcoming keypresses. Even though fast RTs were not required by the task,
283 participants likely tried to balance the benefit of getting more points with the benefit of finishing the
284 experiment more quickly. On average across all days (Fig. 4A), larger viewing windows resulted in slower
285 RTs. A repeated-measures ANOVA substantiated this effect ($F_{8,104} = 4.563$, $p = 8.726e-05$).

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289 *Figure 4 | Longer reaction times for larger viewing windows. A. Average*
290 *reaction time as a function of viewing window. B. Subset of data in A,*
291 *separating between early (day 1, red) and late (day 5, blue) stages of practice.*
292 *Box plots show the median and whole range of individual data points (one per*
293 *participant). Shaded areas reflect standard error of the mean.*
294

295

296 However, as observed for MTs, RTs appeared to plateau for window sizes larger than 3. Thus, even
297 though participants could see more than 3 elements on the screen and had virtually unlimited time to
298 preplan, they initiated the sequence in approximately 700-800 ms from cue onset.

299 Did this dependence of RTs on the amount of available information change with practice?
300 When we compared RTs across early and late stages of practice (Fig. 4B) we found no indication that,
301 late in practice, participants waited longer to initiate a sequence ($F_{1,13} = 0.012$, $p = 0.913$), or that their
302 strategy changed over time (no interaction between practice stage and window size: $F_{8,104} = 1.187$, $p =$
303 0.314). Thus, even though over time participants did not spend more time preplanning, the MT results
304 indicate that motor planning improved, as participants could make use of more visual information in
305 roughly the same amount of preparation time (i.e., with comparable RTs).

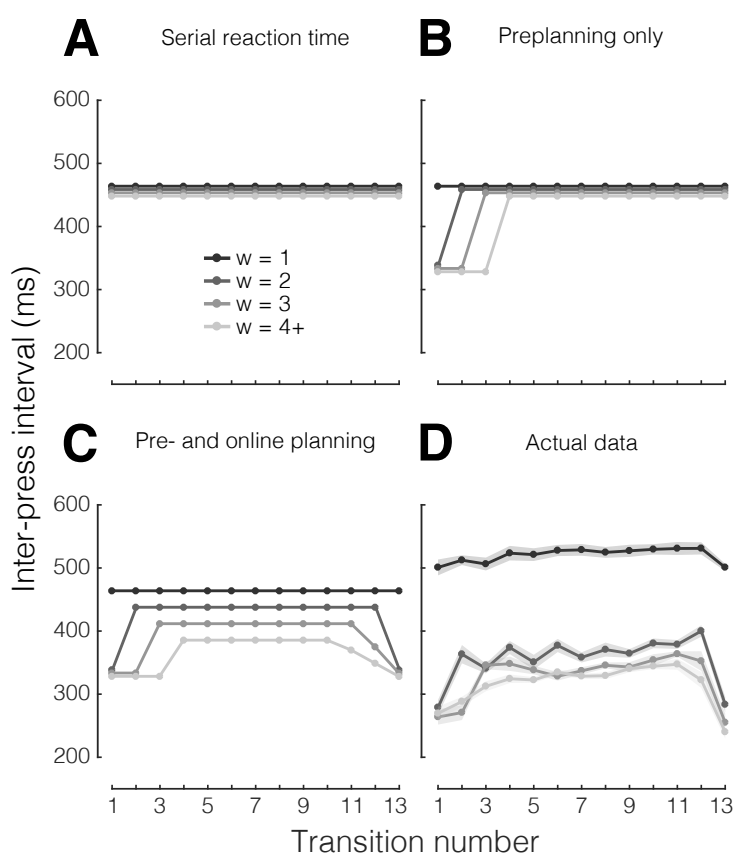
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307 *Planning ahead continues during sequence production*

308 So far, our results have indicated that participants improve their ability to perform random sequences
309 of finger movements by becoming more efficient in using the information provided by larger window
310 sizes. However, it remains unclear whether participants got better at planning movements before
311 sequence production (preplanning), during sequence production (online planning), or both. To
312 distinguish the contributions of preplanning and online planning to performance improvements, we
313 examined the intervals between individual presses in a sequence (i.e., the IPIs). The rationale behind
314 this analysis is that short IPIs reflect an increased readiness to press (i.e., better planning) than long
315 IPIs. If all keypresses were equally well prepared (e.g., as in the case of $w = 1$, which does not allow
316 participants to plan ahead), then all IPIs within a sequence should roughly have the same duration
317 depending on the serial RT (null hypothesis, Fig. 5A). Alternatively, if only early presses in a sequence
318 can be fully preplanned, while later presses can only be minimally planned, or are completely
319 unplanned, then early IPIs should be significantly shorter than later IPIs, which will revert to serial RT
320 speed (Fig. 5B). Finally, if online planning continues in parallel with execution, we should expect an
321 effect of window size also on mid to late IPIs (Fig. 5C).

322 In light of these predictions, we first inspected the IPIs averaging across practice stages (Fig.
323 5D). For a window size of 1, all IPIs had approximately the same duration (~500 ms), reinforcing the
324 idea that for $W = 1$, each keypress is selected, planned, and executed independently. In contrast, for

325 window sizes larger than 1, we found a clear effect of IPI placement (i.e., finger transition number within
 326 the sequence) on IPI duration ($F_{12,156} = 33.111, p < 10e-10$). Specifically, the first and last IPIs were
 327 consistently performed much faster than the middle IPIs, regardless of the size of the viewing window
 328 ($W > 1$). For $W = 2$, the first IPI (first 2 finger presses) was faster than subsequent IPIs; for $W = 3$, the
 329 first two IPIs (first 3 finger presses) were faster than subsequent IPIs. For $W > 3$, this preplanning
 330 advantage appeared to be spread over the first 3 finger transitions. This pattern of results clearly
 331 indicates that the initial speed up reflects the fact the visible digits can be preplanned during the
 332 reaction time, and hence are executed faster.
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 334



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 336 **Figure 5 | Predictions and analysis of inter-press intervals (IPIs).** Average inter-
 337 press interval (IPI) as a function of transition number within each sequence,
 338 separately for viewing window size (w , different shades of gray). 4+ indicates
 339 $w \geq 4$. **A.** Prediction 1 (null hypothesis): no effect of w , all IPIs roughly in the
 340 same range. **B.** Prediction 2: Fast early IPIs reflect the benefit of preplanning,
 341 but for unplanned keypresses the benefit of viewing ahead is minimal. **C.**
 342 Prediction 3: even mid to late IPIs benefit from larger w , indicating that both
 343 pre- and online planning are contributing to fast sequence production. **D.**
 344 Actual group data of mean IPIs for each keypress transition, separately for each
 345 viewing window.
 346

347

348 Consistent with RT and MT data, preplanning does not seem to improve further beyond a window size
349 of 3 or larger. Again, this reinforces the idea that participants preplanned at least the first three
350 movements of each finger sequence. Once all preplanned keypresses are executed, planning must
351 continue online, slowing down later IPIs. Thus, the slower IPIs in the middle of the sequence mostly
352 reflect limits in the speed of online planning. When we restricted our analysis to these middle IPIs
353 (transitions 5 to 12), the differences between $w = 1$ and $w = 2$ ($t_{13} = 19.557$, $p = 5.037e-11$), between w
354 $= 2$ and $w = 3$ ($t_{13} = 5.013$, $p = 2.374e-04$), and between $w = 3$ and $w = 4$ remained significant ($t_{13} =$
355 2.182 , $p = 0.048$). This indicates that, just like preplanning, online planning benefits from having visual
356 information about up to 3 presses into the future, thus highlighting clear parallels between the two
357 processes.

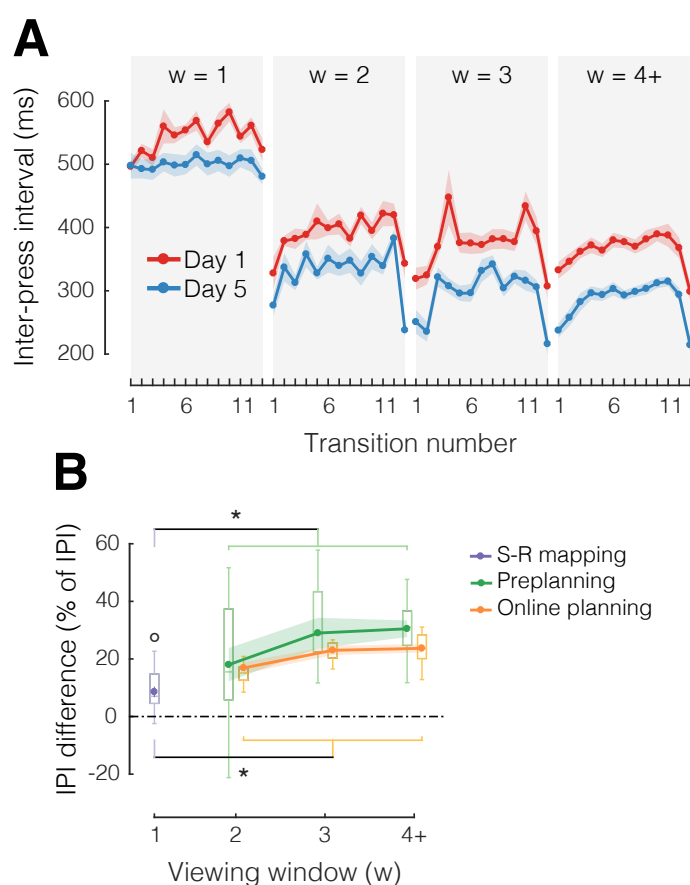
358 We also observed that, consistently across all window sizes greater than 1, the last IPI was
359 executed much more quickly than preceding IPIs. Currently, we can only speculate about the reasons
360 for this result. One idea is that participants tend to select and plan the last 2 presses as a unit. These
361 presses can then be executed very quickly, as no more movements need to be planned after those two
362 (which frees up planning capacity). Alternatively, participants could optimize the last two presses from
363 an execution biomechanics perspective. Given that no subsequent movements are needed,
364 participants do not have to maintain a specific hand posture that would be required for fast execution
365 of successive movements. Instead, they are free to optimize their hand posture for comfort and speed
366 only in regard to making the last two presses.

367

368 ***Both pre- and online planning improve with practice***

369 Finally, we asked whether practice effects on MT are more likely related to improvements in
370 preplanning, online planning, or both. From day 1 to day 5 (Fig. 6A), we observed significant main
371 effects of practice stage on IPI duration on both early (IPI 1-3: $F_{1,13} = 17.623$, $p = 0.001$) and middle IPIs
372 (IPI 5-12: $F_{1,13} = 15.988$, $p = 0.002$). To quantify the relative contributions of preplanning and online
373 planning, we carried a separate analysis (Fig. 6B) averaging across IPIs that were more likely preplanned
374 (IPI 1 for $w = 2$, IPI 1-2 for $w = 3$, and IPI 1-3 for $w \geq 4$), or not (the remaining IPIs for each viewing
375 window condition, which had to be planned online). For $w = 1$, only the first press, but not the first IPI,
376 can be preplanned. Therefore, we cannot attribute any of the observed improvements to either
377 sequence preplanning or online planning. Instead, eventual improvements need to arise from improved
378 visual identification, S-R mapping, or execution. We computed the IPI difference between day 1 and
379 day 5 for these three categories, normalized it by the average IPI duration across days (separately for
380 each category), and plotted it against viewing window size (Fig. 6B). This analysis confirmed that IPIs

381 got faster with practice even for $w = 1$ (one-sample t -test vs zero difference: $t_{13} = 2.305$, $p = 0.038$).
 382 Additionally, we found clear further improvements in IPI duration for $w > 1$: compared to $w = 1$, these
 383 effects were present both for the IPIs that were likely preplanned ($t_{13} = 4.028$, $p = 0.001$), and for those
 384 that relied on online planning ($t_{13} = 6.009$, $p = 4.379e-05$). There was no significant difference between
 385 preplanning and online planning in terms of learning improvements ($F_{1,13} = 1.141$, $p = 0.305$), nor was
 386 there an interaction between planning process and viewing window ($F_{2,26} = 1.000$, $p = 0.382$). Thus,
 387 preplanning and online planning appear to have similar capacity limits and to benefit similarly from
 388 practice in sequence production.
 389
 390



391
 392 **Figure 6 | Improvements in pre- and online planning with practice. A.** Mean IPI
 393 as a function of transition number, separately for practice stage (day 1, red;
 394 day 5, blue) and viewing window size ($w = 1, 2, 3, 4+$ in separate plots). **B.**
 395 Average IPI difference between day 1 and day 5, normalized by average IPI for
 396 each day, separately for each w and planning process (S-R mapping, purple;
 397 Preplanning, green; Online planning, orange). Box plots show the median and
 398 whole range of individual data points (one per participant). Shaded areas
 399 reflect standard error of the mean. * $p < 0.05$, two-tailed paired-samples t -tests;
 400 $^{\circ}p < 0.05$, two-tailed one sample t -test.
 401

402 Discussion

403 The ability to plan ahead for future actions while executing current ones is a fundamental yet
404 underappreciated faculty of the human brain. In this study, we manipulated the amount of visual
405 information available for motor planning while performing a discrete sequence production task. Our
406 results provide evidence that participants planned multiple sequential actions (at least 3) into the future
407 (Fig. 2-4). Furthermore, we show larger practice-induced benefits in speed for larger window sizes (MT
408 difference, Fig. 3), as well as increases in the horizon of sequence planning (based on the exponential
409 fit, Fig. 3). In-depth analysis of the inter-press intervals (Fig. 5-6) revealed that the enhanced planning
410 of future actions was present both before (preplanning) and during (online planning) sequence
411 production.

412

413 *Fast sequence production depends on the speed of online planning*

414 Before a voluntary movement can be performed, it needs to be planned (Keele, 1968; Keele and
415 Summers, 1976; Kerr, 1978; Rosenbaum, 1980; Bock and Arnold, 1992; Crammond and Kalaska, 1994,
416 2000; Cisek and Kalaska, 2002, 2004), at least to some degree (Cisek and Kalaska, 2010; Ames et al.,
417 2014). However, many real-life motor skills require quick sequences of movements that are not always
418 predictable. Proficiency in such skills depends on our ability to select and plan future movements both
419 before sequence onset and during sequence production. To shed light on this ability, we used a viewing
420 window paradigm that varied the amount of information available for planning the next finger
421 movements. We replicate previous work showing evidence for anticipatory planning in the context of
422 movement sequences (Rosenbaum et al., 1987; Rhodes et al., 2004; Herbolt and Butz, 2009), and
423 longer reaction times when more elements are available for planning ahead (Henry and Rogers, 1960).
424 Furthermore, we show that, once preplanning reaches capacity, the execution of later elements in the
425 sequence slows down, which we interpret as evidence that successive movements need to be planned
426 online. In a previous paper (Ariani and Diedrichsen, 2019), we have reported that this is the case even
427 when participants execute relatively short (e.g., 5-item) and well-known (e.g., trained) sequences. By
428 varying the time available for preplanning a sequence, we could show that only the first 3 sequence
429 elements were planned prior to execution. Further evidence for online planning across a range of
430 activities comes from studies investigating how visual information is used for motor planning. For
431 example, it has been shown that participants move their eyes to future targets in reading (Rayner,
432 1978), sequential reaching (Säfström et al., 2014), and object manipulation (Johansson et al., 2001).
433 More directly, a recent unpublished study revealed the horizon of online planning by restricting the
434 viewing window in a continuous manual tracking task (Bashford et al., 2018). Together, these studies
435 support our view that the ability of the motor system to deal with a stream of incoming stimuli while

436 producing motor responses (i.e., the speed of online planning) enables skillful performance for
437 unpredictable movement sequences.

438

439 ***Motor planning has a limited capacity***

440 Despite its importance, our ability to plan future movements is somewhat limited. We found the span
441 of the planning horizon (~3-4 movements) to be smaller than the typical amount of information that
442 can be stored in short-term memory (Miller, 1956; Cowan, 2010). However, according to a more recent
443 theory, short-term memory capacity is not dictated by a fixed number of items, but rather should be
444 viewed as a finite resource that can be allocated flexibly across multiple items via selective attention
445 (Luck and Vogel, 1997; Bays and Husain, 2008). Similarly, characterizing the planning horizon as having
446 a hard, discrete limit (i.e., a specific number of movements) may not be the best description. A more
447 realistic model may be that planning capacity has a soft horizon that depends on the amount of
448 cognitive resources available for planning. In accordance with the competitive queueing hypothesis
449 (Averbeck et al., 2002, 2006; Rhodes et al., 2004; Kornysheva et al., 2019; Mantziara et al., 2020), this
450 idea predicts that more planning resources are allocated to the immediately upcoming actions, and
451 decreasing amount of attention is paid to future actions. Eventually, subjects run out of resources and
452 start executing responses. Completing preceding movements frees up new resources that can be
453 allocated to plan successive movements online. Thus, the discrepancy between the short-term memory
454 span and planning horizon may reflect the fact that planning a movement takes up more central
455 resources than remembering a digit.

456

457 ***The horizon of motor planning can be expanded with practice***

458 Conceptualizing the capacity of motor planning as a limited resource makes it interesting to ask
459 whether the planning horizon can be improved with practice. Indeed, in agreement with a previous,
460 unpublished study (Bashford et al., 2018), we found that practice had expanded the span of the
461 planning horizon. Our conclusion was based on two key observations: 1) the benefit of seeing further
462 ahead was greater late than early in practice (significant interaction between w and day on MT); 2) the
463 influence of window size on MT can be described with an exponential function whose decay rate
464 decreased with practice (change in the slope of the exponential). Speed improvements that are
465 independent of the amount of available information can be attributed to improved stimulus
466 identification, S-R mapping, or implementation of single responses (Haith et al., 2016; Ariani and
467 Diedrichsen, 2019; Hardwick et al., 2019). As participants become more fluent at translating numbers
468 on the screen into finger movements, each individual press is executed more quickly, thus contributing
469 to faster sequence production across all window sizes. The greater performance benefits for larger

470 window sizes, together with the expansion of the effective planning horizon, however, clearly indicate
471 that participants improved their ability to make use of advance information. Importantly, we show that
472 these improvements occur not only for preplanning (i.e., before movement onset) but also for online
473 planning (i.e., after movement onset). Unlike previous studies that examined sequence-specific effects
474 in sequence production (Verwey, 2001; Verwey and Wright, 2004; Wiestler and Diedrichsen, 2013;
475 Ariani and Diedrichsen, 2019; Berlot et al., 2020), here we focused on random sequences. Note that,
476 because of this, the observed practice effects cannot be explained by the formation of specific chunking
477 structures previously proposed as a way to deal with the complexity of planning long movement
478 sequences (Ramkumar et al., 2016; Popp et al., 2020). Instead, we found that even when people have
479 no prior experience with a sequence, they can over time improve in the motor planning processes that
480 underlie sequence production. In other words, practice effects are not only about learning *what*
481 sequence to produce, but also about learning *how* to coordinate execution and planning efficiently.

482

483 ***Do pre- and online planning rely on the same neural process?***

484 Our results revealed notable similarities between preplanning and online planning. Both processes
485 contributed to faster sequential performance when participants had a chance to see at least 3
486 upcoming sequence elements, with diminishing gains for larger window sizes. Moreover, practice-
487 related improvements on the relevant IPIs (early IPIs for preplanning, late IPIs for online planning) were
488 comparable between the two processes. These similarities suggest that preplanning and online
489 planning may rely on the same process, i.e., motor planning, either happening in isolation before
490 movement initiation, or in parallel, simultaneous with execution. This raises questions about the
491 neuronal implementation of pre- and online planning. Previous research has shown that movement
492 planning is also reflected in brain structures responsible for movement execution, such as the primary
493 motor cortex (M1), and the dorsal premotor cortex (PMd, Crammond and Kalaska, 2000; Ames et al.,
494 2014, 2019; Elsayed et al., 2016; Ariani et al., 2018; Lara et al., 2018). A recent study (Ames et al., 2019)
495 also shows that *re-planning* of an ongoing movement engages similar neuronal population dynamics as
496 preplanning it. The authors recorded M1 and PMd activity in two monkeys performing a delayed
497 reaching task with occasional target jumps (20% of trials) that could occur during the RT (before
498 movement onset) and would require mid-reach corrections. They found that neuronal population
499 activity related to the target jump played out in both the neural state-spaces defined by preparatory
500 and movement activity recorded on non-jump trials. However, it remains unclear which neuronal
501 populations are engaged when online planning is not related to the ongoing movement, but rather to
502 future and possibly different movements. Since the neuronal state of the main sensorimotor regions is
503 likely occupied by execution processes related to the ongoing movement, do online planning processes

504 shift to other structures? Or do they engage separate state-space dimensions within the same region?
505 Our study lays the behavioral foundation for this investigation, showing that humans are able to plan
506 multiple movements into the future while simultaneously controlling an ongoing movement. This ability
507 of online planning improves with practice and is a key determinant of any skilled sequence production.
508

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