

1 The planning horizon for movement sequences

2 Abbreviated title: Sequence planning horizon

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27

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31

32 **Abstract**

33 When performing a long chain of actions in rapid sequence, future movements need to be planned
34 concurrently with ongoing action. However, how far ahead we plan, and whether this ability improves
35 with practice, is currently unknown. Here we designed an experiment in which healthy volunteers
36 produced sequences of 14 finger presses quickly and accurately on a keyboard in response to numerical
37 stimuli. On every trial, participants were only shown a fixed number of stimuli ahead of the current
38 keypress. The size of this viewing window varied between 1 (next digit revealed with the pressing of
39 the current key) and 14 (full view of the sequence). Participants practiced the task for five days and
40 their performance was continuously assessed on random sequences. Our results indicate that
41 participants used the available visual information to plan multiple actions into the future, but that the
42 planning horizon was limited: receiving information about more than 3 movements ahead did not result
43 in faster sequence production. Over the course of practice, we found larger performance
44 improvements for larger viewing windows and an expansion of the planning horizon. These findings
45 suggest that the ability to plan future responses during ongoing movement constitutes an important
46 aspect of skillful movement. Based on the results, we propose a framework to investigate the neuronal
47 processes underlying simultaneous planning and execution.

48

49 **Key words**

50 Motor planning; Sequence production; Practice effects; Hand function; Skillful movement.

51 **Significance Statement**

52 Although skill learning has typically focused on the training of specific movement sequences, practice
53 improves performance even for random sequences. Here we hypothesize that a fundamental aspect of
54 skilled sequential behavior is the ability to plan multiple actions into the future, both before and during
55 execution. By controlling the amount of visual information available for motor planning, we show that
56 people plan at least three movements beyond current action and that this planning horizon expands
57 with practice. Our findings suggest that coordinating ongoing movement and planning of future actions
58 is an essential component of skilled sequential behavior and offer testable predictions for the neural
59 implementation of online motor planning.

60

61 Introduction

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

70 Previous studies of motor sequence learning have largely focused on the training of specific
71 movement sequences (Cohen et al., 1990; Kornysheva et al., 2019, 2013; Mantziara et al., 2020;
72 Verwey, 2001; Verwey et al., 2014; Verwey and Abrahamse, 2012; Willingham, 1999; Aaron L. Wong et
73 al., 2015). However, many sequences we execute in everyday life are not fully predictable and practice
74 improves performance even for random or untrained sequential movements (Ariani et al., 2020;
75 Waters-Metenier et al., 2014; Wiestler et al., 2014). Some of these sequence-general improvements
76 arise because participants learn to translate individual visual stimuli into motor responses and to
77 execute these responses more quickly (Ariani and Diedrichsen, 2019; Hardwick et al., 2019). Such
78 improvements in single responses benefit the production of all sequences, including random ones.

79 In the present study, we focus on a second core ability that benefits the production of
80 unpredictable sequences: the ability to plan future movements ahead of time. Planning of movements
81 before their initiation, here referred to as *preplanning*, has been studied extensively (Churchland et al.,
82 2010; Cisek and Kalaska, 2010; Haith et al., 2016; Kaufman et al., 2014; Rosenbaum, 1980; Rosenbaum
83 et al., 2007, 1987; Aaron L Wong et al., 2015). However, long or complex movement sequences are
84 unlikely to be fully preplanned, so planning of the remaining elements must continue throughout
85 sequence production – a process that we have recently named *online planning* (Ariani and Diedrichsen,
86 2019). Take the example of a basketball player dribbling up the court. The player needs to control a
87 continuous flow of movements (e.g., to keep the dribble alive) while scouting the court and planning
88 future movements depending on the actions of both teammates and opposing defenders. Some
89 evidence for online planning has been observed for a range of behaviors, such as reading (Rayner, 2014,
90 1998; Rayner and Reingold, 2015), walking (Matthis and Fajen, 2014), sequential reaching (Säfström
91 et al., 2014, 2013) and path tracking (Bashford et al., 2018). However, to what extent the motor system
92 plans upcoming movements during sequence production (i.e., the horizon of online planning) remains
93 poorly understood.

94 Here we asked 1) how far the benefit of planning ahead extends beyond current execution, and
95 2) whether this planning horizon can be improved with practice. To answer these questions, we used a
96 discrete sequence production (DSP) task, in which participants performed random sequences of 14
97 keypresses with their right hand in response to numerical cues. We manipulated how many digits
98 participants could see ahead of the current keypress. Viewing window size ranged from 1 (only the next
99 movement is cued, as in the serial reaction time task, SRTT) to 14 (the entire sequence shown at once,
100 as in the DSP task). Participants practiced producing varying sequences over 5 days. This design allowed
101 us to examine the horizon of both pre- and online planning in sequence production, as well as the
102 influence of practice on the planning horizon.
103

104 **Methods**

105 *Participants*

106 Seventeen right-handed neurologically healthy volunteers (8 women, 9 men; age 18–36 years, mean
107 25.81 years, SD 5.09 years) were recruited for this study. Handedness was assessed with the Edinburgh
108 Handedness Inventory (mean 82.81, SD 18.07). Individuals participated in 5 sessions of practice (2 hours
109 each, on 5 separate days). All participants provided written informed consent and were naive to the
110 purposes of the study. Two participants abandoned the study after the first session of practice. One
111 participant had an unusually high error rate (> 30%, while every other participant managed to keep the
112 error rate < 20%, as per instructions). These 3 participants were excluded from successive analyses
113 (final N = 14). For one of the remaining 14 participants, age and handedness data was missing, and for
114 another participant eye tracking data was missing. All experimental methods were approved by the
115 Research Ethics Board at Western University.

116

117 *Apparatus*

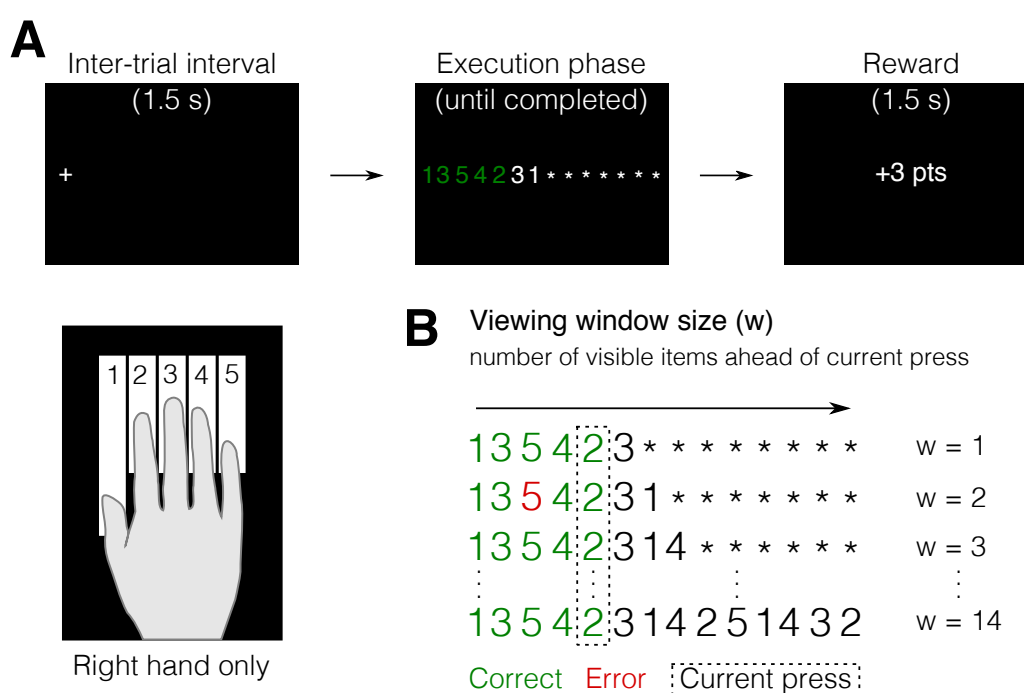
118 Participants placed their right hand on a custom-made keyboard (Fig. 1A), with a force transducer
119 (Honeywell FS series) mounted underneath each key. The keys were immobile and measured isometric
120 finger force production. The dynamic range of the force transducers was 0-16 N and the resolution 0.02
121 N. A finger press/release was detected when the force crossed a threshold of 1 N. The forces measured
122 from the keyboard were low pass filtered, amplified, and sent to PC for online task control and data
123 recording. Additionally, we recorded monocular left eye movements using an SR Research EyeLink 1000
124 desk-mounted eye tracker. Eye movements were recorded at a rate of 500 Hz. Participants sat
125 approximately 40 cm away from a 20" (50.8 cm) screen. Numerical stimuli were shown in white against
126 a black background, horizontally aligned in a single line, and spanned 13.5cm for an entire sequence
127 (~19° of visual angle). Individual digits were about 1 cm tall, 0.5 cm wide, and spaced 1 cm apart (from
128 center to center, ~1.43° of visual angle).

129

130 *Procedure*

131 In each of the five practice sessions, participants sat in front of a computer screen with their right hand
132 on the keyboard, and their chin placed on the eye tracker chinrest. The task required participants to
133 produce sequences of keypresses in response to numerical cues appearing on the screen (numbers 1
134 to 5, corresponding to fingers of their right hand, thumb to little finger, respectively) as quickly and
135 accurately as possible (Fig. 1A). On every trial, only a fixed number of digits (viewing window size, w)
136 were revealed to the participants, while the rest were masked with asterisks (Fig. 1B). The masked digits
137 were revealed to the participant as they proceeded, from left to right, with the presses in each

138 sequence. The window size varied within the domain of $w = \{1, 2, 3, 4, 5, 6, 7, 8, 14\}$, and was
 139 randomized across trials within every block. As an attentional pre-cue, at the beginning and at the end
 140 of every trial, during the inter-trial interval (ITI, 1.5 seconds), participants were presented with a fixation
 141 cross on the location of the first digit in the sequence. This fixation was used to account for possible
 142 drifts in trial-by-trial calibration of eye-to-digit location mapping. Within every block of trials,
 143 participants were instructed to keep their chin on the eye tracker chinrest at all times and to minimize
 144 head movements. With every press, subjects received feedback about the correctness of their action:
 145 the white numbers turned either green or red and were accompanied by either a high-pitch or a low-
 146 pitch sound for correct and incorrect presses, respectively.
 147



148
 149 **Figure 1 | Varying viewing window in a discrete sequence production (DSP) task.** **A.** Example
 150 trial in a DSP task with viewing 2 items ahead of the current keypress, while the remaining
 151 items are masked by asterisks. **B.** Viewing window size (w) manipulation, from $w = 1$
 152 (equivalent to a simple reaction time task), to $w = 14$ (display of the entire sequence at once).
 153 The arrow indicates the from-left-to-right direction of response order. Participants could start
 154 each sequence whenever they felt ready and were rewarded on the basis of their movement
 155 time (MT, the time from the first keypress to the release of the last key in the sequence).
 156

157 To motivate participants to improve in the task, they were rewarded with points based on their
 158 performance after each trial. Points were awarded on the basis of sequence movement time (MT) and
 159 execution accuracy. MT corresponded to the time interval between making the first press in the
 160 sequence to releasing the last press in the sequence. Accuracy was calculated as $1 - \text{error rate}$
 161 (proportion of error trials in a block) in percentage. Specifically, a trial was considered an error if it

162 contained one or more incorrect presses, for which participants received 0 points. Correct sequences
163 were rewarded with at least 1 point. Finally, participants were awarded 3 points if 1) a sequence was
164 correct and 2) MT 5% or more faster than a specific time threshold. This time threshold was designed
165 to get increasingly difficult adjusting to every subject's speed throughout training. It would decrease by
166 5% from one block to the next if two performance criteria were met: median MT in the current block
167 faster than best median MT recorded hitherto, and mean error rate in the last block \leq 15%. If either
168 one of these criteria was not met, the thresholds remained unchanged. At the end of each block,
169 participants received feedback on their error rate, median sequence MT, total points obtained during
170 the block, and total points obtained during the session. Subjects were asked to try to maintain an error
171 rate below 15%.

172 In the original design, we intended to compare also how the ability to plan ahead might affect
173 partially familiar (structured) sequences. Therefore, each one of the 5 practice sessions consisted of 8
174 blocks (27 trials each) of 14-item sequences and 3 blocks (60 trials each) of specific short 3-/4-item
175 segments that composed the structured sequences. One-third of the trials in the sequence blocks were
176 randomly generated by random shuffles of the digits 1 to 5. The remaining two-thirds of the trials were
177 structured sequences. As the results from the structured sequences turned out to be hard to interpret,
178 the present paper focuses only on the completely unfamiliar, random sequences.

179

180 *Control experiment to measure the limits imposed by visual acuity and crowding effects*

181 To determine how far out from the fovea the digit stimuli could be recognized, we ran a short control
182 experiment. In a modified version of the task, we asked an independent sample of participants ($N = 3$)
183 to fixate on the first digit of a random series of 14 digits and report all digits with finger presses, while
184 maintaining fixation on the first digit. The task was non-speeded, as we wanted to determine how many
185 digits could be recognized, given human limits in visual acuity (Rayner, 1975) and the limits imposed by
186 attentional crowding effects (Levi, 2008). Participants were instructed to press the fingers
187 corresponding to the digits they could see, and guess when they were not sure anymore. Each
188 participant repeated this task for 6 blocks with 27 trials each. We calculated the probability of making
189 the correct keypress as a function of distance from the fixated digit. Chance performance was $p = 0.2$
190 (1 out of 5 fingers).

191

192 *Data analysis*

193 Data were analyzed with custom code written in Matlab (The MathWorks, Inc., Natick, MA). To evaluate
194 the speed of sequence production, we inspected the time intervals between different keypresses.
195 Reaction times (RT) were defined as the time from stimulus onset to first press (i.e., the first crossing

196 of the 1 N force threshold). Note that participants were not instructed to react particularly fast. Instead,
197 they could take as much time as they wanted until they felt ready to start. MTs were defined as the
198 time between the first press and the release of the last press in the sequence (i.e., the time between
199 the first and the last crossing of the force threshold). Finally, we calculated inter-press intervals (IPI)
200 between subsequent pairs of presses in the sequence (i.e., the time interval between every two
201 consecutive crossings of the force threshold). Unless otherwise noted, we used within-subject repeated
202 measures ANOVAs and 2-sided paired samples *t*-tests for statistical inference in assessing the effects
203 of viewing window or practice on RT, MT, and IPI. Error trials were excluded from data analysis. To
204 provide meaningful error bars for within-subject comparison, the standard error for each condition was
205 calculated on the residuals after subtracting the mean across conditions for each participant. This way,
206 the error bars visualized the size of the relevant error term in a repeated-measures ANOVA.

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

209

$$210 \quad MT' = a \times e^{(-b(w-1))} + c,$$

211

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

219

$$220 \quad w^* = \frac{-\log(0.01)}{b+1},$$

221

222 where the 0.01 arises from the criterion of the 99% drop (i.e., 1% above the MT' asymptote). The
223 improvement in effective planning horizon with practice was then assessed by fitting the model to the
224 data of each participant on each day and comparing w^* between day 1 and day 5 with a within-subject
225 2-sided paired samples *t*-test. While the use of a 99% criterion is arbitrary, changes in this criterion only
226 scale the effect planning horizon by a specific value but do not change the outcome of the statistical
227 analysis.

228

229

230 *Analysis of eye movements*

231 To assess changes in fixation strategies, we estimated the eye position with respect to each finger press
232 in the sequence as follows. For each trial in each block, we mapped the calibrated eye position (in eye
233 tracker units) to the digits on the screen to calculate the digit (D_t) on which the eye was currently fixated
234 at the time of each keypress:

235

$$236 \quad D_t = 1 + \frac{(x_t - x_0)}{p_x}$$

237

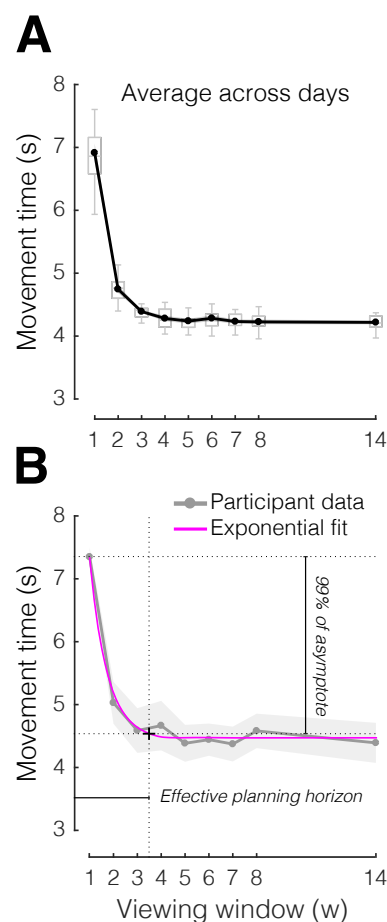
238 Where x_t is the eye's current horizontal position at the time of press (median position within a 25 ms
239 time window around the keypress) in eye tracker units, x_0 is the median horizontal position of the eye
240 at the beginning of the trial (i.e., the position of the fixation cross / first digit), and p_x is a normalizing
241 unit constant throughout a block of trials, used to convert eye tracker units to digit positions. Finally,
242 we computed the estimated eye position at the time of each keypress by subtracting the position
243 corresponding to the keypress (1 to 14) from D_t and plotted this estimate against each keypress position
244 in the sequence (Fig. 7). In other words, a value of 0 means that the eye was exactly on the digit at was
245 currently pressed, and a value of +1 would indicate that the eyes were a full digit ahead the currently
246 pressed digit.

247

248 Results

249 *Preplanning of future movements speeds up sequence production*

250 First, we assessed the benefit of being able to plan future finger movements on sequence production.
251 To determine this, we varied the amount of available information and tested how this window size
252 affected the speed of performance. On average, across all days of practice, larger window sizes
253 produced shorter MTs (Fig. 2A), as confirmed by the highly significant main effect of window size on
254 MT in a repeated measures ANOVA ($F_{8,104} = 176.980, p < 10e-10$). This finding suggests that the
255 availability of visual information allows for preplanning of sequential actions into the future, which in
256 turn reduces MT. Interestingly, this benefit appeared to plateau around a window size of 3 or 4. Indeed,
257 when we compared the MT of each viewing window to the average MT for larger window sizes, we
258 found a significant difference for $w = 3$ vs $w > 3$ ($t_{13} = 4.644, p = 4.591e-04$), but not for $w = 4$ vs $w > 4$
259 ($t_{13} = 2.083, p = 0.058$). To obtain an individual measure of the planning horizon, we fit an exponential
260 model to the MT curve of each participant (Fig. 2B, see Methods).
261



262

263 **Figure 2 | The benefit of planning ahead on sequential performance. A.**
264 *Average movement time as a function of viewing window, across the 5 days of*
265 *practice. B. Method used to estimate the effective planning horizon. Example*
266 *data from one participant (gray) is fit to an exponential model (magenta). The*

267 *intersection between performance at 99% of asymptote and the exponential fit*
268 *was chosen as criterion to determine the effective planning horizon. Box plots*
269 *show the median and whole range of individual data points (one per*
270 *participant). Shaded areas reflect standard error of the mean.*
271

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

276 Was this limitation in planning horizon simply due to a perceptual limitation? Obviously, the
277 drop-off of visual acuity from the fovea to the periphery (Rayner, 1975) could limit the ability of the
278 participants to identify more visually presented letters simultaneously. Moreover, even if acuity is
279 sufficient, the presentation of multiple digits can lead to “crowding”, an ubiquitous attentional effect
280 that impairs the ability to recognize visual objects in clutter (Levi, 2008). To test both of these possible
281 limitations for our display, we conducted a control experiment (see Methods) and found that
282 participants were able to accurately identify up to 6 items to the right of fixation (~6 cm) with more
283 than 95% accuracy (mean accuracy for 7th item = $97.67\% \pm 0.78$ 95% CI). Thus, given that eye position
284 was on average only slightly to the right of the currently pressed digit (see analysis of eye movement
285 strategies below), it seems very unlikely that peripheral visual acuity and crowding can explain the
286 limitation in planning horizon.

287

288 ***Practice expands the planning horizon***

289 We then asked whether practicing sequences would affect the ability to plan future movements by
290 comparing performance at the beginning (day 1) and at the end (day 5) of practice (Fig. 3A). We
291 observed that MT improved across all window sizes (main effect of day: $F_{1,13} = 18.004$, $p = 0.001$).
292 Significant improvements were found even for a window size of 1 (MT difference day 1 vs. day 5: 586
293 ± 262 ms; $t_{13} = 2.234$, $p = 0.022$). This condition was, in essence, a serial reaction time task, where each
294 cue was only presented after the preceding key was pressed, meaning that participants were forced to
295 serially cycle through the planning and execution of every press, with no possibility for planning ahead.
296 Therefore, MT improvements for a window size of 1 must be a consequence of 1) better stimulus
297 identification, 2) better stimulus-response (S-R) mapping, or 3) better execution (i.e., motor
298 implementation) of single responses.

299 If learning was restricted to improvement in any of these three processes, we would predict
300 equal MT improvement across all window sizes, given that stimulus identification, S-R mapping, and
301 execution are necessary steps across all viewing windows. Contrary to prediction, we found a significant
302 interaction between window size and stage of practice (day 1 vs. day 5; $F_{8,104} = 3.220$, $p = 0.003$).

303 Furthermore, when we directly inspected the MT improvement (percentage change relative to average
304 MT for each w , Fig. 3B), we found significantly larger gains for larger viewing windows ($w = 2$ vs. $w = 1$:
305 $t_{13} = 3.338$, $p = 0.005$; $w = 3$ vs. $w = 2$: $t_{13} = 2.722$, $p = 0.017$), until again the gains plateau for $w = 4$ or
306 larger ($w = 4$ vs. $w = 3$: $t_{13} = 0.113$, $p = 0.912$). Thus, although responses to single items improved with
307 practice, this improvement cannot explain why performance benefits were more pronounced for larger
308 window sizes. Instead, the additional performance benefit must arise because participants became
309 more efficient at using the advance information provided by larger viewing windows.

310 Part of this increased efficiency may be due to expansion of the planning horizon (i.e., how far
311 ahead participants were able to plan). Indeed, we also found evidence that with practice, participants
312 planned further into the future. When we determined the effective planning horizon for each
313 participant and day (Fig. 2B) using an exponential fit (see Methods), we found that the planning horizon
314 expanded from 3.20 to 3.88 digits ahead of current action between day 1 and day 5 (paired-samples t -
315 test, $t_{13} = 2.840$, $p = 0.014$, Fig. 3C). Despite the high inter-subject variability, out of 14 participants, only
316 2 show a negative slope when regressing the effective planning horizon onto the day of practice.
317 Furthermore, there was no relationship between the average planning horizon and the slope (i.e., the
318 rate of change) across days ($r = 0.28$, $p = 0.3376$), suggesting that participants with small and large
319 horizons improved similarly.

320 While significant, the increase of planning horizon by less than a digit appears to be quite small.
321 How important is a larger planning horizon for faster performance with practice? To obtain insight into
322 this question, we looked at the inter-subject variability within each training day: We correlated our
323 measure of planning horizon for each participant with their mean movement time for larger viewing
324 windows ($w > 5$) for each day of practice. To avoid any statistical dependency between these
325 parameters induced by measurement noise, the effective planning horizon was estimated on data from
326 odd blocks and the mean movement time was estimated on data from even blocks. This analysis (Fig.
327 3D) revealed a clear negative correlation between the two measures for each day of practice (all $r < -$
328 0.54 , all $p < 0.05$). Roughly speaking, from this analysis, we would expect that the observed increase in
329 effective planning horizon by 0.68 items should lead, on average, to a decrease in movement time of
330 about 435 ms, which corresponds to ~82% of the improvement from day 1 to day 5 for $w = 14$ (~1110
331 ms) that was not explained by improvements in single responses (i.e., ~580 ms for $w = 1$). Thus,
332 participants became better at planning future movements in advance, and this improvement could
333 potentially be explained by the increased ability to plan more actions into the future.

334

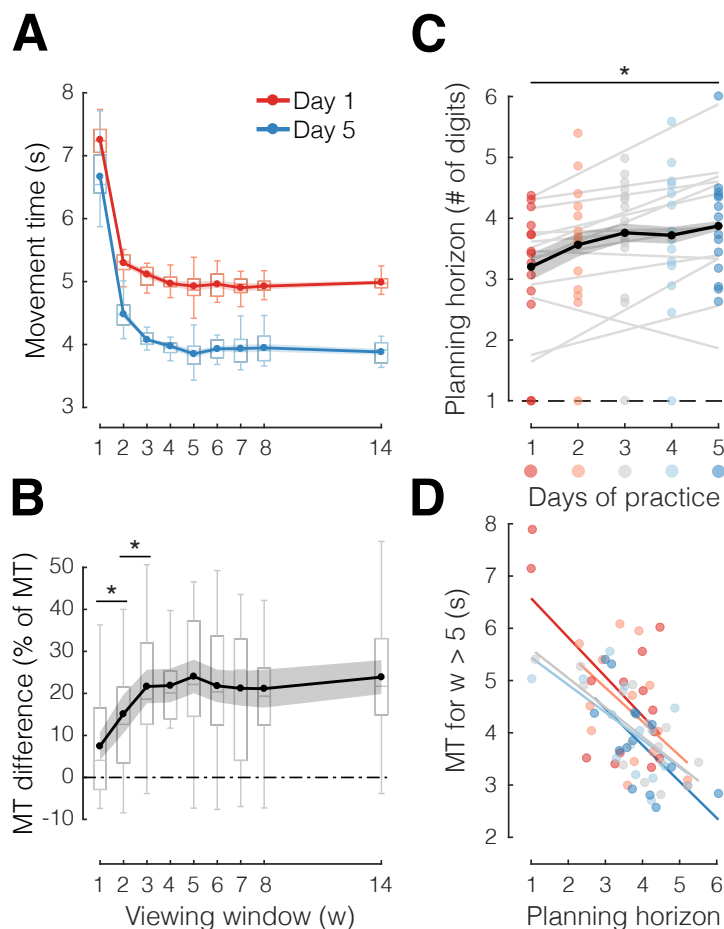


Figure 3 | The effective planning horizon increases with practice. **A.** Average movement time (MT) as a function of viewing window (w), separately for early (day 1, red) and late (day 5, blue) stages of sequence practice. **B.** Difference in performance (sequence MT) between early and late practice (data in A), normalized by average MT for each w , as a function of w . **C.** Mean effective planning horizon (estimated as shown in Fig. 2B) for each day of practice. **D.** Correlation between mean MT for $w > 5$ (which enabled planning ahead) and mean effective planning horizon, separately for different days (days 1 to 5 in gradient red to blue). For this analysis, planning horizon was estimated on odd blocks and MT on even blocks. Dots reflect individual data points (one per participant). Box plots show the median and quartiles of group data. Shaded areas reflect standard error of the mean. * $p < 0.05$, two-tailed paired-samples t -tests.

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Note that faster MTs for larger window sizes did not occur at the expense of reduced accuracy in performance. On average, the percent accuracy of presses remained roughly constant around 85-90% across all viewing window conditions. We found no significant main effect of window size ($F_{8,104} = 1.182$, $p = 0.317$), practice stage ($F_{1,13} = 0.325$, $p = 0.578$), or interaction between the two factors ($F_{8,104} = 0.548$, $p = 0.818$).

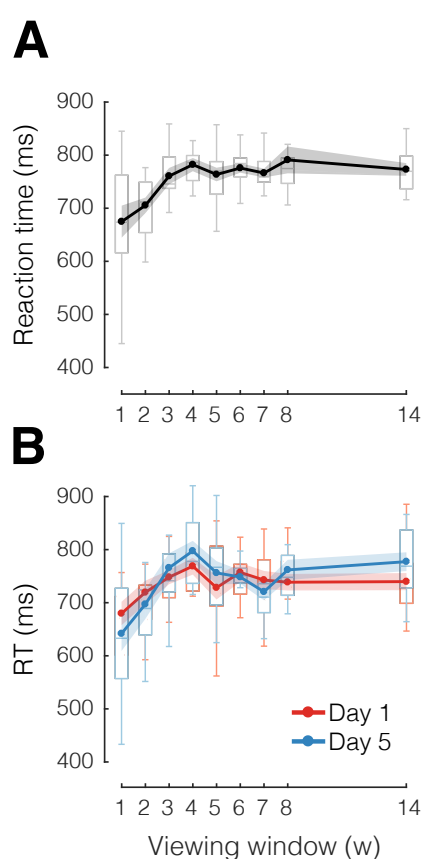
Taken together, these results show that participants became faster in sequence production by getting better at 1) making single responses (involving stimulus identification, S-R mapping, or execution) and 2) exploiting available information to plan more upcoming movements in advance.

358

359 **Reaction times increase with the amount of preplanning**

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

367



368

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

374

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

378 Did this relationship between RTs and the amount of available information change with
379 practice? When we compared RTs across early and late stages of practice (Fig. 4B) we found no
380 indication that, late in practice, participants waited longer to initiate a sequence ($F_{1,13} = 0.012$, $p =$
381 0.913), or that their strategy changed over time (no interaction between practice stage and window
382 size: $F_{8,104} = 1.187$, $p = 0.314$).

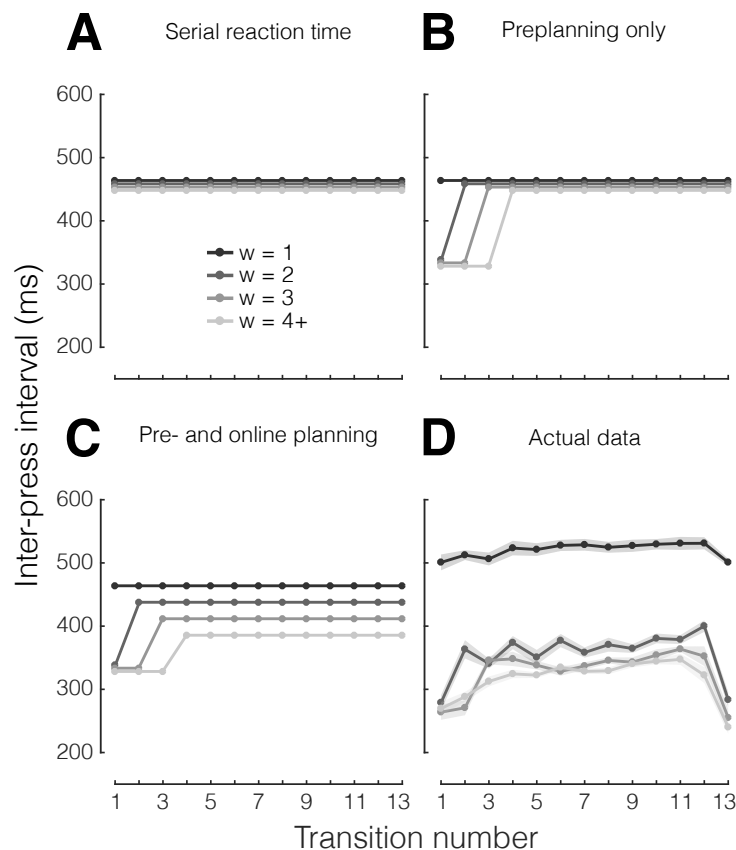
383

384 *Planning ahead continues during sequence production*

385 So far, our results have indicated that participants improve their ability to perform random sequences
386 of finger movements by becoming more efficient in using the information provided by larger window
387 sizes. However, it remains unclear whether participants got better at planning movements before
388 sequence production (preplanning), during sequence production (online planning), or both. To
389 distinguish the contributions of preplanning and online planning to performance improvements, we
390 examined the time intervals between individual presses in a sequence (i.e., the IPIs). The rationale
391 behind this analysis is that short IPIs reflect an increased readiness to press (i.e., better planning) than
392 long IPIs. If all keypresses were equally well prepared (e.g., as in the case of $w = 1$, which does not allow
393 participants to plan ahead), then all IPIs within a sequence should roughly have the same duration
394 depending on the serial RT (null hypothesis, Fig. 5A). Alternatively, if only early presses in a sequence
395 can be fully preplanned, then only these IPIs should be significantly shorter, and later IPIs revert to
396 serial RT speed (Fig. 5B). Finally, if online planning continues in parallel with execution, we should expect
397 an effect of window size also on mid to late IPIs (Fig. 5C).

398 In light of these predictions, we first inspected the IPIs averaging across practice stages (Fig.
399 5D). For a window size of 1, all IPIs had approximately the same duration (~500 ms), reinforcing the
400 idea that for $w = 1$, each keypress is selected, planned, and executed independently. In contrast, for
401 window sizes larger than 1, we found a clear effect of IPI placement (i.e., finger transition number within
402 the sequence) on IPI duration ($F_{12,156} = 33.111$, $p < 10e-10$). Specifically, the first and last IPIs were
403 consistently performed much faster than the middle IPIs, regardless of the size of the viewing window
404 ($W > 1$). For $w = 2$, the first IPI (first 2 finger presses) was faster than subsequent IPIs; for $w = 3$, the first
405 two IPIs (first 3 finger presses) were faster than subsequent IPIs. For $w > 3$, this preplanning advantage
406 appeared to be spread over the first 3 finger transitions. This pattern of results indicates that the initial
407 speed up reflects the fact the visible digits can be preplanned during the reaction time, and hence are
408 executed faster.

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

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

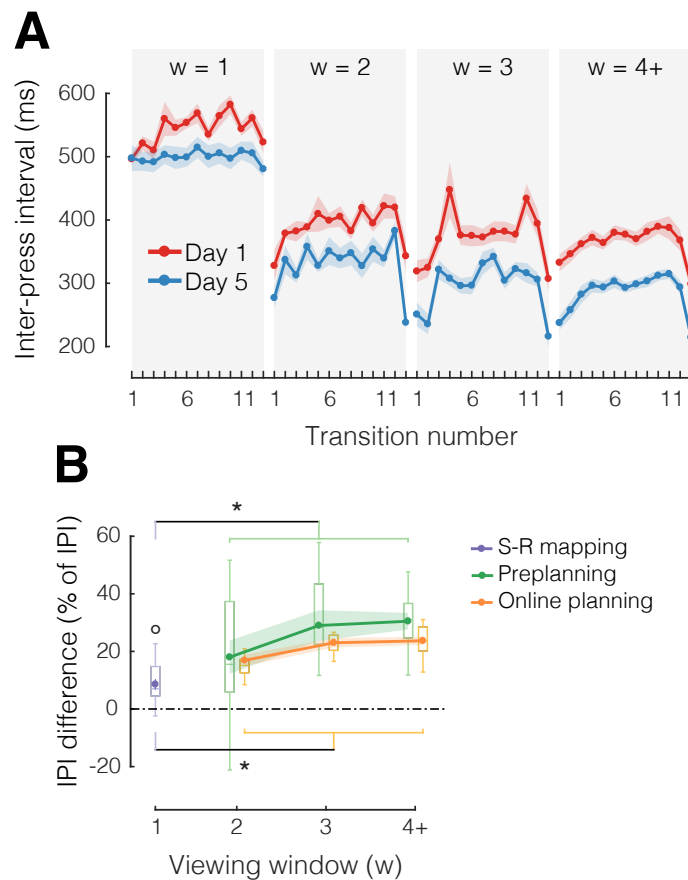
432 We also observed that, consistent across all window sizes greater than 1, the last IPI was
433 executed much more quickly than preceding IPIs. Currently, we do not have a definitive answer about
434 the reasons for this result. One idea is that participants tend to select and plan the last 2 presses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

441

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

443 Finally, we asked whether practice effects on MT are more likely related to improvements in
444 preplanning, online planning, or both. From day 1 to day 5 (Fig. 6A), we observed significant main
445 effects of practice stage on IPI duration on both early (IPI 1-3: $F_{1,13} = 17.623$, $p = 0.001$) and middle IPIs
446 (IPI 5-12: $F_{1,13} = 15.988$, $p = 0.002$). To quantify the relative contributions of preplanning and online
447 planning, we carried a separate analysis (Fig. 6B) averaging across IPIs that were more likely preplanned
448 (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
449 window condition, which had to be planned online). For $w = 1$, only the first press, but not the first IPI,
450 can be preplanned. Therefore, we cannot attribute any of the observed improvements to either
451 sequence preplanning or online planning. Instead, eventual improvements need to arise from improved
452 visual identification, S-R mapping, or execution. We computed the IPI difference between day 1 and
453 day 5 for these three categories, normalized it by the average IPI duration across days (separately for
454 each category), and plotted it against viewing window size (Fig. 6B). This analysis confirmed that IPIs
455 became faster with practice even for $w = 1$ (one-sample t -test vs zero difference: $t_{13} = 2.305$, $p = 0.038$).
456 Additionally, we found clear further improvements in IPI duration for $w > 1$: compared to $w = 1$, these
457 effects were present both for the IPIs that were likely preplanned ($t_{13} = 4.028$, $p = 0.001$), and for those
458 that relied on online planning ($t_{13} = 6.009$, $p = 4.379e-05$). There was no significant difference between
459 preplanning and online planning in terms of learning improvements ($F_{1,13} = 1.141$, $p = 0.305$), nor was
460 there an interaction between planning process and viewing window ($F_{2,26} = 1.000$, $p = 0.382$). Thus,
461 preplanning and online planning appear to have similar capacity limits and to benefit similarly from
462 practice in sequence production. Moreover, given that on day 5 participants did not spend more time
463 preplanning than they did on day 1 (Fig. 4B), improvements in IPI with practice (Fig. 6A) reinforce the
464 idea that participants could make use of more visual information in roughly the same amount of
465 preparation time (i.e., with comparable RTs).

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

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Increases in planning horizon are not explained by changes in eye movement strategies

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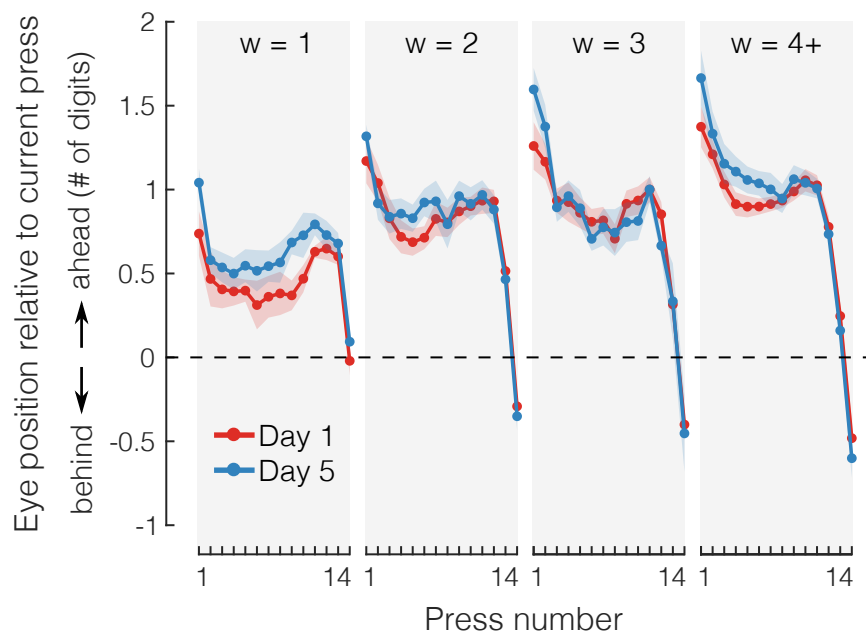
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To determine to what degree changes in fixation strategies could cause improvements in the planning horizon, we analyzed eye tracking data. To assess potential learning effects in fixation strategies, we estimated eye position at the time of each keypress in the sequence (see Methods). We then plotted this estimated eye position at the time of each press relative to the digit that was produced (Fig. 7). A value of 0 in means that the eye was exactly on the digit at was currently pressed, and a value of +1 would indicate that the eyes were a full digit ahead the currently pressed digit. For statistical comparison across days, we selected the keypresses in the middle of a sequence (presses 3-10) given that those are most likely to be influenced by fixation strategies. A 2-by-4 repeated measures ANOVA

487 revealed a significant main effect of viewing window size ($F_{3,36} = 17.815$, $p < 0.0001$), indicating that
488 subjects tended to look further ahead when more information was available. However, no main effect
489 of day ($F_{1,12} = 0.624$, $p = 0.445$) or interaction between day and window size was found ($F_{3,36} = 2.739$, p
490 $= 0.058$), indicating that fixation strategies were not the cause of improvements in the effective
491 planning horizon. The results were similar even when including all of the keypresses (1-14): significant
492 main effect of window size ($F_{3,36} = 10.691$, $p < 0.0001$), but no main effect of day ($F_{1,12} = 0.730$, $p =$
493 0.410), or interaction between the two ($F_{3,36} = 1.779$, $p = 0.169$). Together with our data showing that
494 perceptual limitations cannot account for the limited planning horizon (see above), these results argue
495 that participants increased their ability to preplan more actions by overcoming a central (cognitive-
496 motor) bottleneck, rather than a purely perceptual bottleneck.
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Figure 7 | Eye movement strategies do not change with practice. Mean eye position relative to current press at the time of press as a function of press number, for different days of practice (Day 1, red; Day 5, blue) and for different viewing windows (w , gray shaded areas). Viewing windows of size of 4 or larger were grouped together as 4+. Shaded areas reflect standard error of the mean. Dashed line indicates eye position that would be equivalent to looking directly at the digit corresponding to the current finger press. Positive numbers indicate that the eyes are further ahead than the current press, and negative numbers indicate that the eyes are lagging behind.

509 Discussion

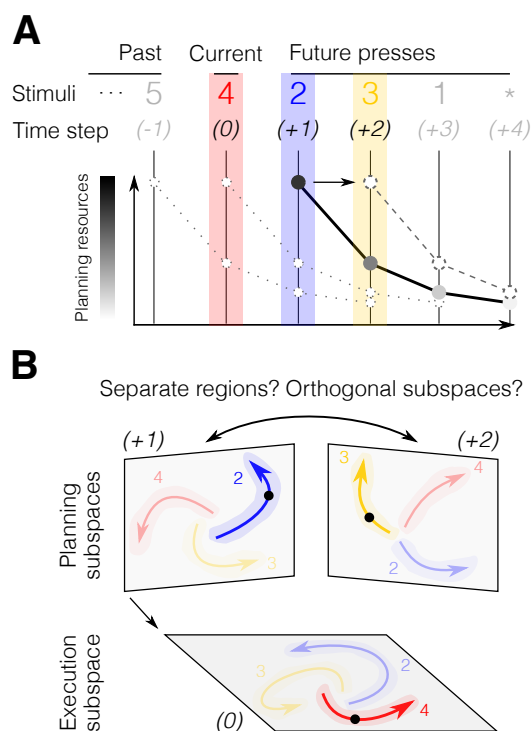
510 The ability to move and simultaneously plan future movements is a fundamental yet underappreciated
511 faculty of the human brain. By manipulating the amount of visual information available for motor
512 planning in a discrete sequence production task, we show that participants planned multiple actions
513 (at least 3) into the future (Fig. 2-4). Practice led to larger gains in speed for larger window sizes (MT
514 difference, Fig. 3B), as well as increases in the horizon of sequence planning (exponential fit, Fig. 3C).
515 In-depth analysis of the inter-press intervals (Fig. 5-6) revealed that enhanced planning of future actions
516 was present both before (preplanning) and during (online planning) sequence production.

517

518 *Fast sequence production relies on the speed of online planning*

519 Before voluntary movements can be performed, they need to be planned (Bock and Arnold, 1992; Cisek
520 and Kalaska, 2004, 2002; Crammond and Kalaska, 2000, 1994; Keele, 1968; Keele and Summers, 1976;
521 Kerr, 1978; Rosenbaum, 1980), at least to some degree (Ames et al., 2014; Cisek and Kalaska, 2010).
522 However, many real-life motor skills require quick sequences of movements that are not always
523 predictable. Proficiency in such skills depends on our ability to select and plan future movements both
524 before and during sequence production. To investigate this ability, we used a viewing window paradigm
525 that varied the amount of information available for planning the next movements. We replicate
526 previous findings of anticipatory planning in the context of random sequences (Herbort and Butz, 2009;
527 Rhodes et al., 2004; Rosenbaum et al., 1987), and longer reaction times when more information for
528 planning is available (Henry and Rogers, 1960). Critically, once such preplanning reaches capacity, the
529 execution of later elements in the sequence slows down, which we interpret as evidence that
530 successive movements need to be planned online. By varying the available time for preplanning, in a
531 previous paper (Ariani and Diedrichsen, 2019) we showed that this was the case even for relatively
532 short (e.g., 5-item) and well-known (e.g., trained) sequences – only the first 3 elements were fully
533 planned prior to execution. Further evidence for online planning comes from a wide range of activities
534 in which visual information is used for planning. For example, when participants make anticipatory eye
535 movements to future targets in reading (Rayner, 1978), sequential reaching (Säfström et al., 2014), and
536 object manipulation (Johansson et al., 2001). More directly, a recent unpublished study tackled the
537 horizon of online planning by restricting the viewing window in a continuous manual tracking task
538 (Bashford et al., 2018). Together, these studies support our view that the ability of the motor system
539 to deal with a stream of incoming stimuli while producing motor responses (i.e., online planning)
540 enables skillful performance of movement sequences.

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Figure 8 | Planning capacity and hypothetical neural implementation of sequential behavior. **A.** The “soft” horizon of sequence planning depends on the amount of resource available. In this illustrative example, most resources are invested in the planning of the immediately upcoming press (+1, 2, blue). The further in time a press is from the current press (0, 4, red), the smaller the corresponding planning investment. Once a press has been initiated, the resources are redistributed by shifting the planning curve one step ahead, thus allowing for continuous online planning of future presses (e.g., +2, 3, yellow). **B.** Hypothetical neuronal population activity in brain regions involved in planning and execution processes. Each plane refers to an independent subspace of the multidimensional population activity with possible neural trajectories for the current action (0), and future actions (+1, +2), color-coded as in A. Shaded areas reflect single trial variability. The current neural state is indicated by a black dot. Planning of the next (+1) and future actions (+2) may evolve in separate regions or in orthogonal subspaces within the same region.

559 **Motor planning has a limited capacity**

560 We found that the span of the planning horizon (~3-4 movements) was smaller than the typical amount
 561 of information that can be stored in short-term memory (Cowan, 2010; Miller, 1956). However, more
 562 recent theories of short-term memory posit that capacity is not limited by a fixed number of items, but
 563 rather by finite attentional resources that can be flexibly allocated across multiple items (Bays and
 564 Husain, 2008; Luck and Vogel, 1997). Similarly, characterizing the planning horizon as having a hard,
 565 discrete limit (i.e., a specific number of movements) may not be the best description. A more realistic
 566 model would assert that cognitive resources of a central bottleneck (Pashler, 1994) are mainly allocated
 567 to the next upcoming movement, with a decaying distribution for elements further into the future (Fig.
 568 8A). Such soft distribution of central resources to multiple tasks is consistent with classical models of

569 the Psychological Refractory Period (McLeod, 1977; Smith, 1967; Welford, 1952). In the context of
570 sequence preplanning, this idea is also consistent with the Competitive Queueing (CQ) hypothesis
571 (Averbeck et al., 2006, 2002; Kornysheva et al., 2019; Mantziara et al., 2020; Rhodes et al., 2004): the
572 first element would be preplanned the most, with subsequent elements being prepared to a decreasing
573 degree. Eventually, subjects run out of resources and start executing responses. Completing preceding
574 movements frees up new resources that can be allocated to plan successive movements online. The
575 discrepancy between the short-term memory span and the planning horizon may reflect the fact that
576 planning a movement takes up more central resources than remembering a digit.

577 Importantly, the limits in planning horizon appear to be of central (cognitive) origin, rather than
578 strictly perceptual or motor. As shown by the first (and last) IPI in a sequence, participants are in
579 principle capable of executing key presses faster than the asymptote reached even for large window
580 sizes. Additionally, perceptually, participants are able to identify 6 digits to the right of their eye fixation,
581 which is at least a full digit more than their average planning horizon.

582

583 *The horizon of motor planning expands with practice*

584 If the capacity of motor planning depends on a soft, flexible horizon, we can ask whether this limit can
585 be improved with practice. In agreement with a previous study (Bashford et al., 2018), we found that
586 practice had expanded the span of the planning horizon. Our conclusion was based on two key
587 observations: 1) the benefit of seeing further ahead was greater later in practice (significant interaction
588 between w and day on MT); 2) the influence of window size on MT can be described with an exponential
589 function whose decay rate decreased with practice (change in the slope of the exponential). Speed
590 improvements that are independent of the amount of available information can be attributed to
591 improved stimulus identification, S-R mapping, or implementation of single responses (Ariani and
592 Diedrichsen, 2019; Haith et al., 2016; Hardwick et al., 2019). As participants become more fluent at
593 translating numbers on the screen into finger movements, each individual press is executed more
594 quickly, thus contributing to faster sequence production across all window sizes. The greater
595 performance benefits for larger window sizes together with the expansion of the effective planning
596 horizon indicate that participants improved their ability to make better use of advance information.
597 Given the nature of the exponential fit, it is hard to separate the relative contributions of planning
598 efficiency (i.e., benefitting more from a specific window size) and larger horizons to such improvements.
599 Unlike previous studies that examined sequence-specific effects in sequence production (Ariani and
600 Diedrichsen, 2019; Berlot et al., 2020; Verwey, 2001; Verwey and Wright, 2004; Wiestler and
601 Diedrichsen, 2013), here we focused on random sequences. Note that, because of this, the observed
602 practice effects cannot be explained by the formation of specific chunking structures previously

603 proposed as a way to deal with the complexity of planning long movement sequences (Popp et al.,
604 2020; Ramkumar et al., 2016). Instead, we found that even without prior experience with a specific
605 sequence, people can improve in the motor planning processes that underlie sequence production. In
606 other words, practice effects are not only about learning *what* sequence to produce, but also about
607 learning *how* to coordinate execution and planning efficiently.

608

609 *Implications for the neural control of sequential movements*

610 The present study provides behavioral evidence that online planning constitutes a central component
611 of motor skill. More speculatively, it raises the question of how planning and execution processes can
612 simultaneously occur in the brain without interfering with each other. One possibility is that planning
613 and execution processes take place in separate but communicating anatomical areas (Fig. 8B), such as
614 the dorsal premotor cortex (PMd) for planning and the primary motor cortex (M1) for execution.
615 However, several studies have reported signals related to movement planning also in brain structures
616 responsible for movement (Ames et al., 2019, 2014; Ariani et al., 2018; Crammond and Kalaska, 2000;
617 Elsayed et al., 2016), with signals often mixed even within single neurons (Alexander and Crutcher,
618 1990; Evars and Tanji, 1976; Prut and Fetz, 1999; Riehle and Requin, 1989). Therefore, a more likely
619 scenario is that planning and execution occur in overlapping neuronal populations, but occupy
620 orthogonal subspaces of the multidimensional neuronal code (Fig. 8B), such that planning activity does
621 not trigger motor output (Kaufman et al., 2014; Lara et al., 2018; Zimnik and Churchland, 2020). Finally,
622 an intriguing possibility that should be investigated in future studies is that multiple future movements
623 could be planned as an integrated packet (i.e., as a movement chunk), such that there is only one,
624 shared, planning subspace, with specialized code for specific transitions (i.e., 2-3) in movement
625 sequences. Namely, for random sequences, and provided a large enough viewing window, one could
626 imagine that participants plan ahead until they can see and execute that chunk before moving on to
627 the planning of what has since been revealed in a discontinuous fashion (which is revealed by longer
628 and non-homogeneous inter-press intervals). Likewise, in the context of known (i.e., learned) or
629 predictable sequences, it is possible that participants could recall and anticipate an upcoming chunk of
630 information by only seeing part of it, thus planning and executing that chunk before moving on to the
631 next. Some evidence compatible with such an integrated code has been reported in studies of the SMA
632 (Hoshi and Tanji, 2004; Tanji and Shima, 1994), which found neurons sensitive to specific sequences of
633 actions. However, most neurophysiological studies have focused on planning-related signals before
634 movement onset (preplanning). Therefore, it remains an open question how the neural substrates for
635 planning change when the same neuronal population has to concurrently control an ongoing
636 movement (i.e., online planning). Our behavioral results highlight notable similarities between

637 preplanning and online planning: both processes led to faster performance when participants had a
638 chance to plan up to 3 upcoming sequence elements, with diminishing gains for larger window sizes.
639 Additionally, practice-related improvements were comparable between early IPIs (mostly preplanning)
640 and late IPIs (online planning). These similarities suggest that preplanning and online planning may rely
641 on the same neural process (i.e., motor planning) happening in different contexts, either in isolation
642 before movement initiation or in parallel with execution.

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