

1 The planning horizon for movement sequences

2 Running title: Sequence planning horizon

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20

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27

28 **Abstract**

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

44

45 **Key words**

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

47 **Significance Statement**

48 Although skill learning has typically focused on the training of specific movement sequences, practice
49 improves performance even for random sequences. Here we hypothesize that a fundamental aspect of
50 skilled sequential behavior is the ability to plan multiple actions into the future, both before and during
51 execution. By controlling the amount of visual information available for motor planning, we show that
52 people plan at least three movements beyond current action and that this planning horizon expands
53 with practice. Our results suggest that coordinating ongoing movement and planning of future actions
54 is central to a wide range of cognitive and motor tasks, providing a new perspective on the neural
55 implementation of motor planning in the context of sequential behavior.

56

57 Introduction

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

66 Previous studies of motor sequence learning have largely focused on the training of specific
67 movement sequences (Cohen et al., 1990; Willingham, 1999; Verwey, 2001; Verwey and Abrahamse,
68 2012; Kornysheva et al., 2013, 2019; Verwey et al., 2014; Wong et al., 2015b; Mantziara et al., 2020).
69 However, many sequences we execute in everyday life are not fully predictable and practice improves
70 performance even for random or untrained sequential movements (Waters-Metenier et al., 2014;
71 Wiestler et al., 2014; Ariani et al., 2020). Some of these sequence-general improvements arise because
72 participants learn to translate individual visual stimuli into motor responses and to execute these
73 responses more quickly (Ariani and Diedrichsen, 2019; Hardwick et al., 2019). Such improvements in
74 single responses benefit the production of all sequences, including random ones.

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

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

100 **Methods**

101 *Participants*

102 Seventeen right-handed neurologically healthy volunteers (8 women, 9 men; age 18–36 years, mean
103 25.81 years, SD 5.09 years) were recruited for this study. Handedness was assessed with the Edinburgh
104 Handedness Inventory (mean 82.81, SD 18.07). Individuals participated in 5 sessions of practice (2 hours
105 each, on 5 separate days). All participants provided written informed consent and were naive to the
106 purposes of the study. Two participants abandoned the study after the first session of practice. One
107 participant had an unusually high error rate (> 30%, while every other participant managed to keep the
108 error rate < 20%, as per instructions). These 3 participants were excluded from successive analyses
109 (final N = 14). For one of the remaining 14 participants, age and handedness data was missing. All
110 experimental methods were approved by the Research Ethics Board at Western University.

111

112 *Apparatus*

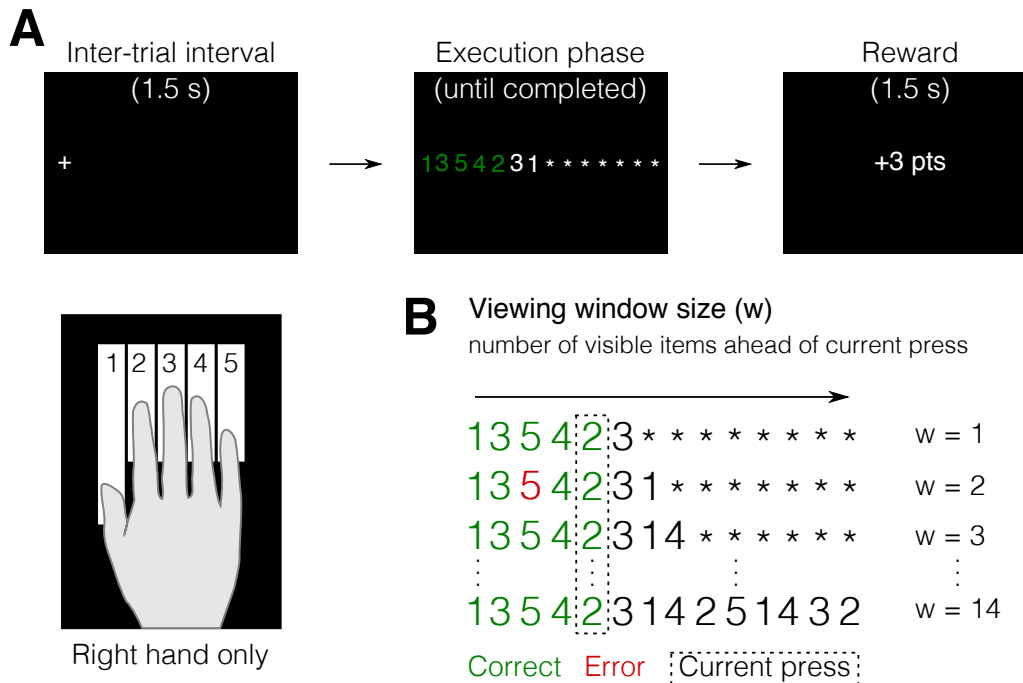
113 Participants placed their right hand on a custom-made keyboard (Fig. 1A), with a force transducer
114 (Honeywell FS series) mounted underneath each key. The keys were immobile and measured isometric
115 finger force production. The dynamic range of the force transducers was 0-16 N and the resolution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

120

121 *Procedure*

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

133 green or red and were accompanied by a corresponding sound for correct and incorrect presses,
 134 respectively.
 135
 136



137
 138 **Figure 1 | Varying viewing window in a discrete sequence production (DSP) task.** **A.** Example
 139 trial in a DSP task with viewing 2 items ahead of the current keypress, while the remaining
 140 items are masked by asterisks. **B.** Viewing window size (w) manipulation, from $w = 1$
 141 (equivalent to a simple reaction time task), to $w = 14$ (display of the entire sequence at once).
 142 The arrow indicates the from-left-to-right direction of response order. Participants could start
 143 each sequence whenever they felt ready and were rewarded on the basis of their movement
 144 time (MT, the time from the first keypress to the release of the last key in the sequence).
 145

146
 147 To motivate participants to improve in the task, they were rewarded with points based on their
 148 performance after each trial. Points were awarded on the basis of sequence movement time (MT) and
 149 execution accuracy. MT corresponded to the time interval between making the first press in the
 150 sequence to releasing the last press in the sequence. Accuracy was calculated as $1 - \text{error rate}$
 151 (proportion of error trials in a block) in percentage. Specifically, a trial was considered an error if it
 152 contained one or more incorrect presses, for which participants received 0 points. Correct sequences
 153 were rewarded with at least 1 point. Finally, participants were awarded 3 points if 1) a sequence was
 154 correct and 2) MT 5% or more faster than a specific time threshold. This time threshold was designed
 155 to get increasingly difficult adjusting to every subject's speed throughout training. It would decrease by
 156 5% from one block to the next if two performance criteria were met: median MT in the current block

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

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

169

170 *Data analysis*

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

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

187

$$188 \quad MT' = a * \exp(-b * (w - 1)) + c,$$

189

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

197

198

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

199

200 where the 0.01 arises from the criterion of the 99% drop (i.e., 1% above the MT' asymptote). The
201 improvement in effective planning horizon with practice was then assessed by fitting the model to the
202 data of each participant on each day and comparing w^* between day 1 and day 5 with a within-subject
203 2-sided paired samples t -test. While the use of a 99% criterion is arbitrary, changes in this criterion only
204 scale the effect planning horizon by a specific value but do not change the outcome of the statistical
205 analysis.

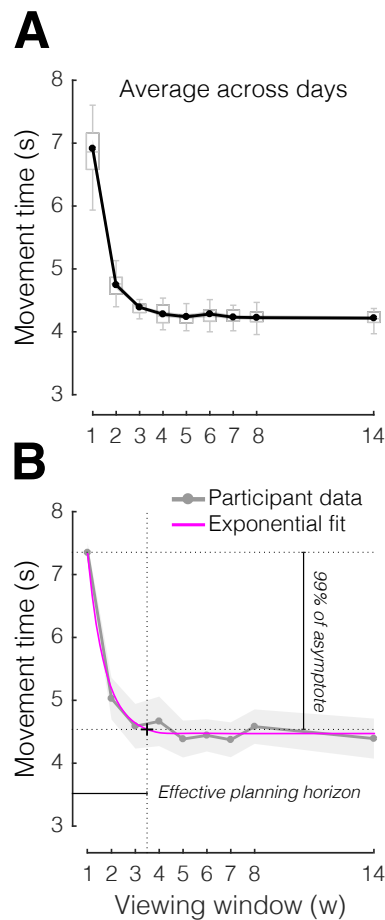
206

207 Results

208 *Preplanning of future movements speeds up sequence production*

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

225 *practice. B. Method used to estimate the effective planning horizon. Example*
226 *data from one participant (gray) is fit to an exponential model (magenta). The*
227 *intersection between performance at 99% of asymptote and the exponential fit*
228 *was chosen as criterion to determine the effective planning horizon. Box plots*
229 *show the median and whole range of individual data points (one per*
230 *participant). Shaded areas reflect standard error of the mean.*
231

232

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

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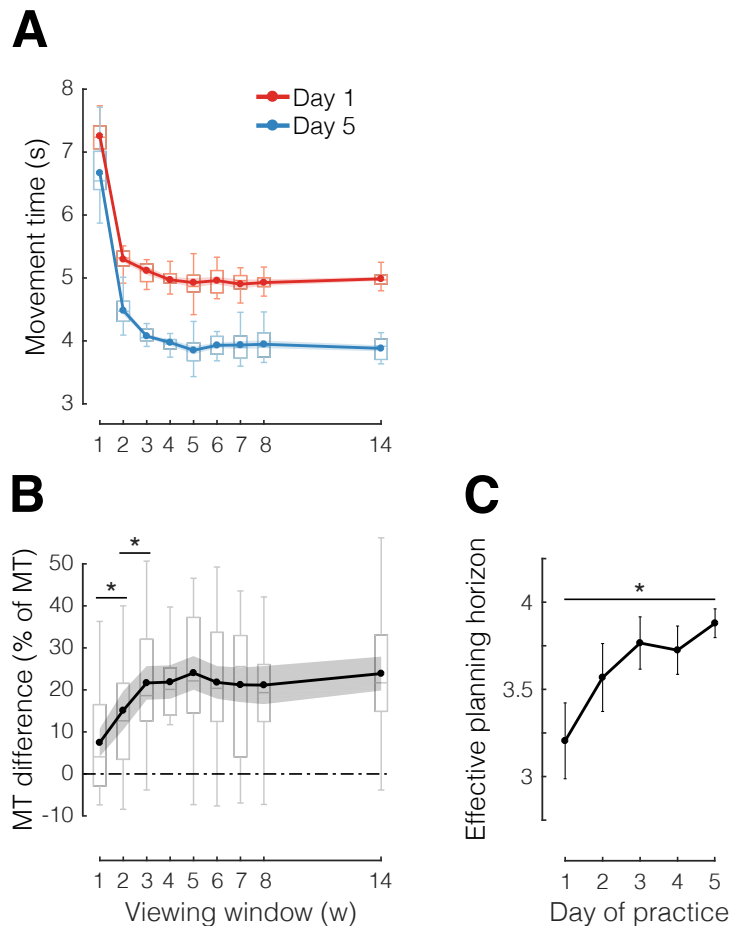
238 ***Practice expands the planning horizon***

239 We then asked whether practicing sequences would affect the ability to plan future movements by
240 comparing performance at the beginning (day 1) and at the end (day 5) of practice (Fig. 3A). We
241 observed that MT improved across all window sizes (main effect of day: $F_{1,13} = 18.004$, $p = 0.001$).
242 Significant improvements were found even for a window size of 1 (MT difference day 1 vs. day 5: 586
243 ± 262 ms; $t_{13} = 2.234$, $p = 0.022$). This condition was, in essence, a serial reaction time task, where each
244 cue was only presented after the preceding key was pressed, meaning that participants were forced to
245 serially cycle through the planning and execution of every press, with no possibility for planning ahead.
246 Therefore, MT improvements for a window size of 1 must be a consequence of 1) better stimulus
247 identification, 2) better stimulus-response (S-R) mapping, or 3) better execution (i.e., motor
248 implementation) of single responses.

249 If learning was restricted to improvement in any of these three processes, we would predict
250 equal MT improvement across all window sizes, given that stimulus identification, S-R mapping, and
251 execution are necessary steps across all viewing windows. Contrary to prediction, we found a significant
252 interaction between window size and stage of practice (day 1 vs. day 5; $F_{8,104} = 3.220$, $p = 0.003$).
253 Furthermore, when we directly inspected the MT improvement (percentage change relative to average
254 MT for each horizon, Fig. 3B), we found significantly larger gains for larger viewing windows ($w = 2$ vs.
255 $w = 1$: $t_{13} = 3.338$, $p = 0.005$; $w = 3$ vs. $w = 2$: $t_{13} = 2.722$, $p = 0.017$), until again the gains plateau for w
256 $= 4$ or larger ($w = 4$ vs. $w = 3$: $t_{13} = 0.113$, $p = 0.912$). Thus, although responses to single items improved
257 with practice, this improvement cannot explain why performance benefits were more pronounced for
258 larger window sizes. Instead, the additional performance benefit must arise because participants
259 became more efficient at using the advance information provided by larger viewing windows.

260 In addition to the evidence for more efficient planning of future elements, we also found
261 evidence that participants planned further into the future. When we determined the effective planning

262 horizon for each participant and day (Fig. 2B) using an exponential fit (see Methods), we found that the
263 planning horizon expanded from 3.20 to 3.88 digits ahead of current action between day 1 and day 5
264 (paired-samples t -test, $t_{13} = 2.840$, $p = 0.014$, Fig. 3C). Thus, participants not only became more efficient
265 in planning but planned sequential actions further into the future.
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269 **Figure 3 | The effective planning horizon increases with practice.** **A.** Average
270 movement time (MT) as a function of viewing window (w), separately for early
271 (day 1, red) and late (day 5, blue) stages of sequence practice. **B.** Difference in
272 performance (sequence MT) between early and late practice (data in A),
273 normalized by average MT, as a function of w . **C.** Mean effective planning
274 horizon (estimated as shown in Fig. 2B) for each day of practice. Box plots show
275 the median and whole range of individual data points (one per participant).
276 Shaded areas (or error bars) reflect standard error of the mean. * $p < 0.05$, two-
277 tailed paired-samples t -tests.
278

279

280 Note that faster MTs for larger window sizes did not occur at the expense of reduced accuracy in
281 performance. On average, the percent accuracy of presses remained roughly constant around 85-90%
282 across all viewing window conditions. We found no significant main effect of window size ($F_{8,104} = 1.182$,

283 $p = 0.317$), practice stage ($F_{1,13} = 0.325$, $p = 0.578$), or interaction between the two factors ($F_{8,104} = 0.548$,
284 $p = 0.818$).

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

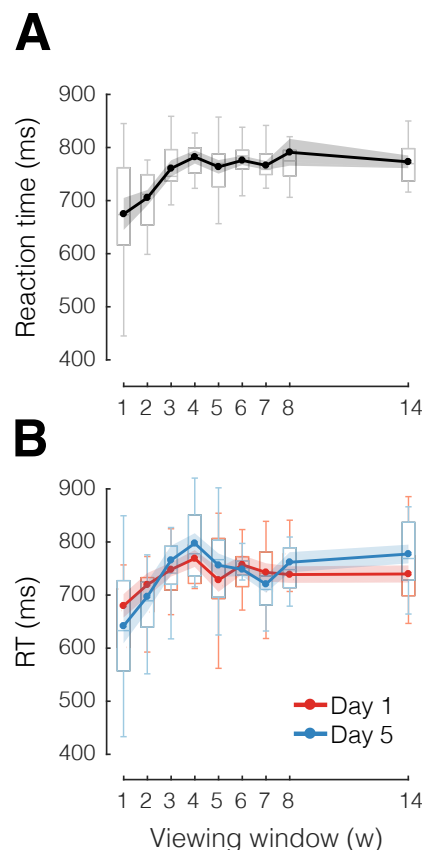
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289 *Reaction times increase with the amount of preplanning*

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

297

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299

300 *Figure 4 | Longer reaction times for larger viewing windows. A. Average*
301 *reaction time as a function of viewing window. B. Subset of data in A,*
302 *separating between early (day 1, red) and late (day 5, blue) stages of practice.*
303 *Box plots show the median and whole range of individual data points (one per*
304 *participant). Shaded areas reflect standard error of the mean.*
305

306

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

310 Did this dependence of RTs on the amount of available information change with practice?
311 When we compared RTs across early and late stages of practice (Fig. 4B) we found no indication that,
312 late in practice, participants waited longer to initiate a sequence ($F_{1,13} = 0.012$, $p = 0.913$), or that their
313 strategy changed over time (no interaction between practice stage and window size: $F_{8,104} = 1.187$, $p =$
314 0.314). Thus, even though over time participants did not spend more time preplanning, the MT results
315 indicate that motor planning improved, as participants could make use of more visual information in
316 roughly the same amount of preparation time (i.e., with comparable RTs).

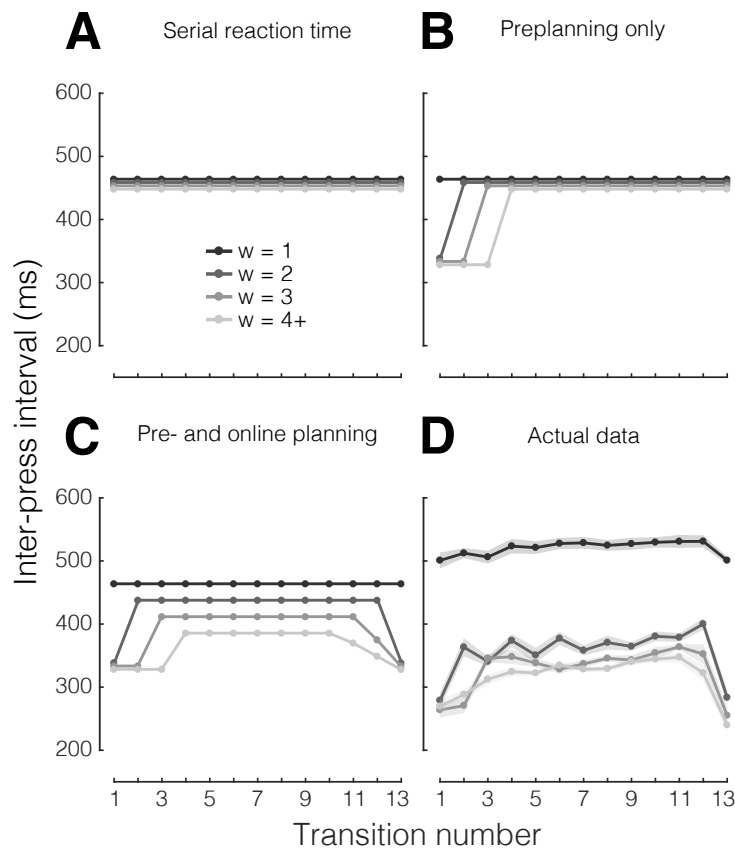
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318 *Planning ahead continues during sequence production*

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

333 In light of these predictions, we first inspected the IPIs averaging across practice stages (Fig.
334 5D). For a window size of 1, all IPIs had approximately the same duration (~500 ms), reinforcing the
335 idea that for $W = 1$, each keypress is selected, planned, and executed independently. In contrast, for

336 window sizes larger than 1, we found a clear effect of IPI placement (i.e., finger transition number within
 337 the sequence) on IPI duration ($F_{12,156} = 33.111, p < 10e-10$). Specifically, the first and last IPIs were
 338 consistently performed much faster than the middle IPIs, regardless of the size of the viewing window
 339 ($W > 1$). For $W = 2$, the first IPI (first 2 finger presses) was faster than subsequent IPIs; for $W = 3$, the
 340 first two IPIs (first 3 finger presses) were faster than subsequent IPIs. For $W > 3$, this preplanning
 341 advantage appeared to be spread over the first 3 finger transitions. This pattern of results indicates that
 342 the initial speed up reflects the fact the visible digits can be preplanned during the reaction time, and
 343 hence are executed faster.
 344
 345



346
 347 **Figure 5 | Predictions and analysis of inter-press intervals (IPIs).** Average inter-
 348 press interval (IPI) as a function of transition number within each sequence,
 349 separately for viewing window size (w , different shades of gray). 4+ indicates
 350 $w \geq 4$. **A.** Prediction 1 (null hypothesis): no effect of w , all IPIs roughly in the
 351 same range. **B.** Prediction 2: Fast early IPIs reflect the benefit of preplanning,
 352 but for unplanned keypresses the benefit of viewing ahead is minimal. **C.**
 353 Prediction 3: even mid to late IPIs benefit from larger w , indicating that both
 354 pre- and online planning are contributing to fast sequence production. **D.**
 355 Actual group data of mean IPIs for each keypress transition, separately for each
 356 viewing window.
 357

358

359 Consistent with RT and MT data, preplanning does not seem to improve further beyond a window size
360 of 3. This observation reinforces the idea that participants preplanned at least the first three
361 movements of each finger sequence. Once all preplanned keypresses are executed, planning must
362 continue online, slowing down later IPIs. Thus, the slower IPIs in the middle of the sequence mostly
363 reflect limits in the speed of online planning. When we restricted our analysis to these middle IPIs
364 (transitions 5 to 12), the differences between $w = 1$ and $w = 2$ ($t_{13} = 19.557$, $p = 5.037e-11$), between w
365 $= 2$ and $w = 3$ ($t_{13} = 5.013$, $p = 2.374e-04$), and between $w = 3$ and $w = 4$ remained significant ($t_{13} =$
366 2.182 , $p = 0.048$). This indicates that, just like preplanning, online planning benefits from having visual
367 information about up to 3 presses into the future, thus highlighting clear parallels between the two
368 processes.

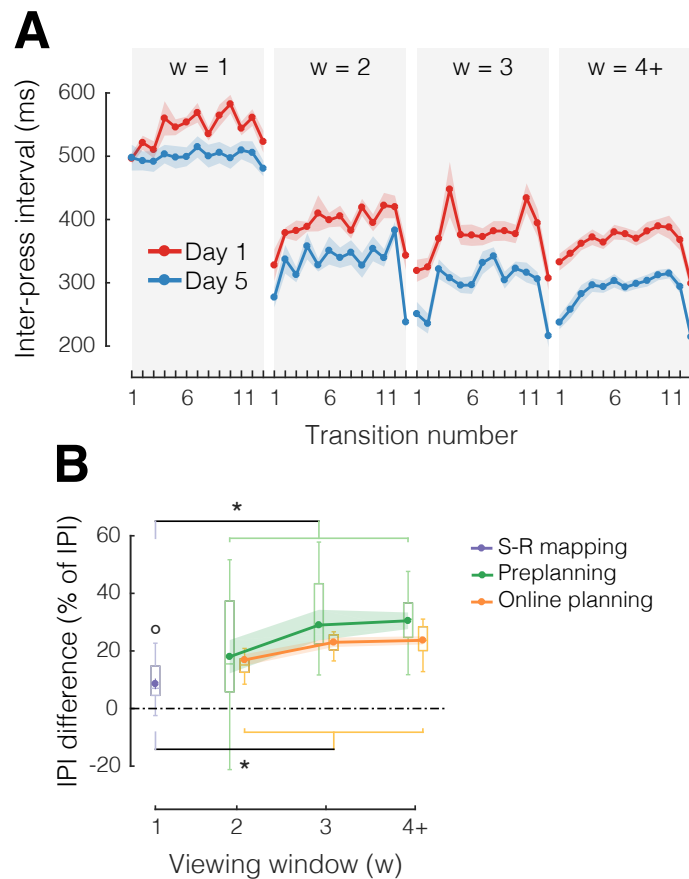
369 We also observed that, consistent across all window sizes greater than 1, the last IPI was
370 executed much more quickly than preceding IPIs. Currently, we can only speculate about the reasons
371 for this result. One idea is that participants tend to select and plan the last 2 presses as a unit.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

378

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

380 Finally, we asked whether practice effects on MT are more likely related to improvements in
381 preplanning, online planning, or both. From day 1 to day 5 (Fig. 6A), we observed significant main
382 effects of practice stage on IPI duration on both early (IPI 1-3: $F_{1,13} = 17.623$, $p = 0.001$) and middle IPIs
383 (IPI 5-12: $F_{1,13} = 15.988$, $p = 0.002$). To quantify the relative contributions of preplanning and online
384 planning, we carried a separate analysis (Fig. 6B) averaging across IPIs that were more likely preplanned
385 (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
386 window condition, which had to be planned online). For $w = 1$, only the first press, but not the first IPI,
387 can be preplanned. Therefore, we cannot attribute any of the observed improvements to either
388 sequence preplanning or online planning. Instead, eventual improvements need to arise from improved
389 visual identification, S-R mapping, or execution. We computed the IPI difference between day 1 and
390 day 5 for these three categories, normalized it by the average IPI duration across days (separately for
391 each category), and plotted it against viewing window size (Fig. 6B). This analysis confirmed that IPIs

392 got faster with practice even for $w = 1$ (one-sample t -test vs zero difference: $t_{13} = 2.305$, $p = 0.038$).
 393 Additionally, we found clear further improvements in IPI duration for $w > 1$: compared to $w = 1$, these
 394 effects were present both for the IPIs that were likely preplanned ($t_{13} = 4.028$, $p = 0.001$), and for those
 395 that relied on online planning ($t_{13} = 6.009$, $p = 4.379e-05$). There was no significant difference between
 396 preplanning and online planning in terms of learning improvements ($F_{1,13} = 1.141$, $p = 0.305$), nor was
 397 there an interaction between planning process and viewing window ($F_{2,26} = 1.000$, $p = 0.382$). Thus,
 398 preplanning and online planning appear to have similar capacity limits and to benefit similarly from
 399 practice in sequence production.
 400
 401



402
 403 **Figure 6 | Improvements in pre- and online planning with practice. A.** Mean IPI
 404 as a function of transition number, separately for practice stage (day 1, red;
 405 day 5, blue) and viewing window size ($w = 1, 2, 3, 4+$ in separate plots). **B.**
 406 Average IPI difference between day 1 and day 5, normalized by average IPI for
 407 each day, separately for each w and planning process (S-R mapping, purple;
 408 Preplanning, green; Online planning, orange). Box plots show the median and
 409 whole range of individual data points (one per participant). Shaded areas
 410 reflect standard error of the mean. * $p < 0.05$, two-tailed paired-samples t -tests;
 411 $^{\circ}p < 0.05$, two-tailed one sample t -test.
 412

413 Discussion

414

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

422

423 *Fast sequence production and the speed of online planning*

424 Before voluntary movements can be performed, they need to be planned (Keele, 1968; Keele and
425 Summers, 1976; Kerr, 1978; Rosenbaum, 1980; Bock and Arnold, 1992; Crammond and Kalaska, 1994,
426 2000; Cisek and Kalaska, 2002, 2004), at least to some degree (Cisek and Kalaska, 2010; Ames et al.,
427 2014). However, many real-life motor skills require quick sequences of movements that are not always
428 predictable. Proficiency in such skills depends on our ability to select and plan future movements both
429 before and during sequence production. To investigate this ability, we used a viewing window paradigm
430 that varied the amount of information available for planning the next movements. We replicate
431 previous findings of anticipatory planning in the context of sequences (Rosenbaum et al., 1987; Rhodes
432 et al., 2004; Herbort and Butz, 2009), and longer reaction times when more information for planning is
433 available (Henry and Rogers, 1960). Critically, once such preplanning reaches capacity, the execution of
434 later elements in the sequence slows down, which we interpret as evidence that successive movements
435 need to be planned online. By varying the available time for preplanning, in a previous paper (Ariani
436 and Diedrichsen, 2019) we showed that this was the case even for relatively short (e.g., 5-item) and
437 well-known (e.g., trained) sequences – only the first 3 elements were fully planned prior to execution.
438 Further evidence for online planning comes from a wide range of activities in which visual information
439 is used for planning. For example, when participants make anticipatory eye movements to future
440 targets in reading (Rayner, 1978), sequential reaching (Säfström et al., 2014), and object manipulation
441 (Johansson et al., 2001). More directly, a recent unpublished study tackled the horizon of online
442 planning by restricting the viewing window in a continuous manual tracking task (Bashford et al., 2018).
443 Together, these studies support our view that the ability of the motor system to deal with a stream of
444 incoming stimuli while producing motor responses (i.e., online planning) enables skillful performance
445 of movement sequences.

446

447 ***Motor planning has a limited capacity***

448 We found that the span of the planning horizon (~3-4 movements) was smaller than the typical amount
449 of information that can be stored in short-term memory (Miller, 1956; Cowan, 2010). However, more
450 recent theories of short-term memory posit that capacity is not limited by a fixed number of items, but
451 rather by finite attentional resources that can be flexibly allocated across multiple items (Luck and
452 Vogel, 1997; Bays and Husain, 2008). Similarly, characterizing the planning horizon as having a hard,
453 discrete limit (i.e., a specific number of movements) may not be the best description. A more realistic
454 model would assert that cognitive resources are mainly allocated to the next upcoming movement,
455 with a decaying distribution for elements further into the future (Fig. 7A). Such distribution is consistent
456 with the Competitive Queueing hypothesis (Averbeck et al., 2002, 2006; Rhodes et al., 2004;
457 Kornysheva et al., 2019; Mantziara et al., 2020). Eventually, subjects run out of resources and start
458 executing responses. Completing preceding movements frees up new resources that can be allocated
459 to plan successive movements online. In sum, the discrepancy between the short-term memory span
460 and the planning horizon may reflect the fact that planning a movement takes up more central
461 resources than remembering a digit.

462

463 ***The horizon of motor planning expands with practice***

464 If the capacity of motor planning depends on a soft, flexible horizon, we can ask whether this limit can
465 be improved with practice. In agreement with a previous study (Bashford et al., 2018), we found that
466 practice had expanded the span of the planning horizon. Our conclusion was based on two key
467 observations: 1) the benefit of seeing further ahead was greater later in practice (significant interaction
468 between w and day on MT); 2) the influence of window size on MT can be described with an exponential
469 function whose decay rate decreased with practice (change in the slope of the exponential). Speed
470 improvements that are independent of the amount of available information can be attributed to
471 improved stimulus identification, S-R mapping, or implementation of single responses (Haith et al.,
472 2016; Ariani and Diedrichsen, 2019; Hardwick et al., 2019). As participants become more fluent at
473 translating numbers on the screen into finger movements, each individual press is executed more
474 quickly, thus contributing to faster sequence production across all window sizes. However, the greater
475 performance benefits for larger window sizes together with the expansion of the effective planning
476 horizon indicate that participants improved their ability to make better use of advance information.
477 Unlike previous studies that examined sequence-specific effects in sequence production (Verwey,
478 2001; Verwey and Wright, 2004; Wiestler and Diedrichsen, 2013; Ariani and Diedrichsen, 2019; Berlot
479 et al., 2020), here we focused on random sequences. Note that, because of this, the observed practice
480 effects cannot be explained by the formation of specific chunking structures previously proposed as a

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

486

487 *Implications for the neural control of sequential movements*

488 The present study provides behavioral evidence that online planning constitutes a central component
489 of motor skill. It also raises the question of how planning and execution processes can simultaneously
490 occur in the brain without interfering with each other. One possibility is that planning and execution
491 take place in separate but communicating anatomical areas, such as the dorsal premotor cortex (PMd)
492 for planning and the primary motor cortex (M1) for execution. However, several studies have reported
493 signals related to movement planning also in brain structures responsible for movement (Crammond
494 and Kalaska, 2000; Ames et al., 2014, 2019; Elsayed et al., 2016; Ariani et al., 2018), with signals often
495 mixed even within single neurons (Evarts and Tanji, 1976; Riehle and Requin, 1989; Alexander and
496 Crutcher, 1990; Prut and Fetz, 1999). Therefore, a more likely scenario is that planning and execution
497 occur in overlapping neuronal populations, but occupy orthogonal subspaces of the multidimensional
498 neuronal code (Fig. 7B), such that planning activity does not trigger motor output (Kaufman et al., 2014;
499 Lara et al., 2018; Zimnik and Churchland, 2020).

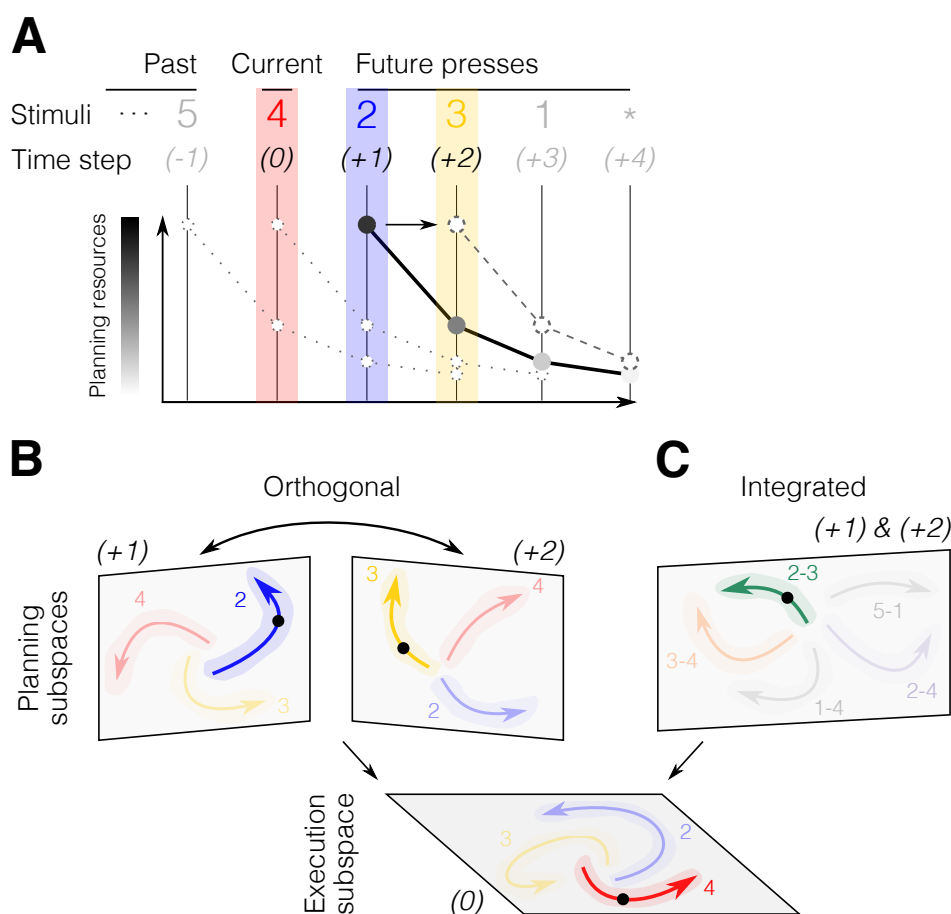
500 Although most neurophysiological studies have focused on planning-related signals before
501 movement onset (preplanning), how the neural substrates for planning change when the same
502 neuronal population has to concurrently control an ongoing movement (online planning) remains an
503 open question. Our behavioral results highlight notable similarities between preplanning and online
504 planning: both processes led to faster performance when participants had a chance to plan up to 3
505 upcoming sequence elements, with diminishing gains for larger window sizes. Additionally, practice-
506 related improvements were comparable between early IPIs (mostly preplanning) and late IPIs (online
507 planning). These similarities suggest that preplanning and online planning may rely on the same neural
508 process (i.e., motor planning) happening in different contexts, either in isolation before movement
509 initiation or in parallel with execution.

510 Finally, we showed that advanced planning does not stop at the next movement (+1) but
511 continues for subsequent movements as well (+2 and beyond). How are these parallel planning
512 processes organized at the neural level? Again, one possibility is that they are implemented in separate
513 neural populations in different brain areas, or at least orthogonal subspaces (Fig. 7B). Alternatively,
514 multiple future movements could be planned as an integrated packet (i.e., as a movement chunk), such

515 that there is only one, shared, planning subspace, with specialized code for specific transitions (i.e., 2-
 516 3) in movement sequences (Fig. 7C). Evidence for such an integrated code has been reported in studies
 517 of the SMA (Tanji and Shima, 1994; Hoshi and Tanji, 2004), which found neurons sensitive to specific
 518 sequences of actions.

519 In conclusion, our study provides a behavioral foundation for the investigation of the neural
 520 control of sequential movements, both by establishing online planning as an important element in
 521 skilled motor performance and by developing a behavioral paradigm that allows the detailed study of
 522 its neural underpinnings.

523
 524



525

526 **Figure 7 | Planning capacity and implications for neural models of sequential**
 527 **behavior.** **A.** The “soft” horizon of sequence planning depends on the amount
 528 of resources available. In this illustrative example, most resources are invested
 529 in the planning of the immediately upcoming press (+1, 2, blue). The further in
 530 time a press is from the current press (0, 4, red), the smaller the corresponding
 531 planning investment. Once a press has been initiated, the resources are
 532 redistributed by shifting the planning curve one step ahead, thus allowing for
 533 continuous online planning of future presses (e.g., +2, 3, yellow). **B.**
 534 Hypothetical neuronal population activity in a brain region involved in both
 535 planning and execution processes. Each plane refers to an independent
 536 subspace of the multidimensional population activity with possible neural
 537 trajectories for the current action (0), and future actions (+1, +2), color-coded

538 *as in A. Shaded areas reflect single trial variability. The current neural state is*
539 *indicated by a black dot. Here, planning of the next (+1) and future actions (+2)*
540 *evolve in orthogonal subspaces. C. Alternatively, planning of future movement*
541 *transitions may occur in an integrated manner.*

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