

1 *Repetita iuvant: repetition facilitates online* 2 *planning of sequential movements*

3
4 Abbreviated title: Sequence repetition facilitates online planning

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33 **Abstract**

34 Beyond being essential for long-term motor-skill development, movement repetition has
35 immediate benefits on performance, increasing speed and accuracy of a second execution.
36 While repetition effects have been reported for single reaching movements, it has yet to be
37 determined whether they also occur for movement sequences, and what aspects of sequence
38 production are improved. We addressed these questions in two behavioral experiments using a
39 discrete sequence production (DSP) task in which human volunteers had to perform short
40 sequences of finger movements. In Experiment 1, we presented participants with randomly
41 varying sequences and manipulated 1) whether the same sequence was repeated on
42 successive trials, and 2) whether participants had to execute the sequence (Go), or not (No-
43 Go). We establish that sequence repetition led to immediate improvements in speed without
44 associated accuracy costs. The largest benefit was observed in the middle part of a sequence,
45 suggesting that sequence repetition facilitated online planning. This claim was further supported
46 by Experiment 2, in which we kept a set of sequences fixed throughout the experiment, thus
47 allowing participants to develop sequence-specific learning: once the need for online planning
48 decreased, the benefit of repetition disappeared. Finally, we found that repetition-related
49 improvements only occurred for the trials that had been preceded by sequence production,
50 suggesting that action selection and sequence pre-planning may not be sufficient to reap the
51 benefits of repetition. Together, these results show that repetition can enhance representations
52 at the level of movement sequences (rather than of individual movements) and facilitate online
53 planning.

54

55 **Key words:**

56 Motor planning; Repetition effects; Sequence production; Skill learning.

57

58 **New & Noteworthy**

59 Even for overlearned motor skills such as reaching, movement repetition improves performance.
60 How brain processes associated with motor planning or execution benefit from repetition,
61 however, remains unclear. Here we report the novel finding of repetition effects for sequential
62 movements. Our results show that repetition benefits are tied to improved online planning of
63 upcoming sequence elements. We also highlight how actual movement experience appears to
64 be more beneficial than mental rehearsal for observing short-term repetition effects.

65

66 **Introduction**

67 Repeated practice is an essential ingredient for motor learning. However, even the immediate
68 repetition of the same stimulus, or response, often leads to better performance (i.e., “repetition
69 effect”). Stimulus repetition enhances perceptual processing (Bentin and McCarthy 1994;
70 Eichelman 1970) and improves stimulus-response (S-R) mapping (Bertelson 1961, 1963, 1965).
71 Conversely, switching usually incurs a performance cost (Adams 1961; Eimer et al. 1995;
72 Hyman 1953; Kleinsorge 1999; Smith 1968). Within the movement domain, repetition can
73 provide short-term benefits to motor output (Vleugels et al. 2019), even for well-learned skills
74 (Ajemian et al. 2010; Phatak et al. 2020). As a common example, athletes and musicians
75 rehearse action sequences moments before a big match or performance. Previous research on
76 reaching movements has shown that movements are biased towards the direction experienced
77 in the recent history, and repeated movements can be executed with less variability (Chapman
78 et al. 2010; Diedrichsen et al. 2010; Marinovic et al. 2017; Verstynen and Sabes 2011). Yet, the
79 mechanisms by which movement repetition facilitates task performance remain elusive.

80 A recent study (Mawase et al. 2018) provided some insight into the possible origins of
81 this effect. The authors argue that repetition accelerates movement pre-planning – the ability of
82 the system to reach a well-prepared state, from which movements can be initiated and
83 produced quickly and efficiently. The paper also presents some arguments that this effect was
84 not caused by speeding up perceptual or action selection processes. However, many real-life
85 motor skills are more complex than single, point-to-point reaches – they tend to involve the
86 production of sequential movements. In this context, the general term planning can refer to
87 either pre-planning, planning-related processes that occur prior to movement onset (during the
88 preparation phase), or to online planning, planning-related processes that occur after movement
89 onset (during the movement phase; Ariani and Diedrichsen, 2019). If repetition only improves
90 the planning of individual movements, we should not find a repetition effect at the sequence

91 level – that is, switching between two different orderings of the same movement elements
92 should be as good as repeating the same ordering. Conversely, if repetition accelerates
93 planning at the level of a sequence, we would expect to observe a repetition effect only when
94 the ordering remains consistent.

95 Using a discrete sequence production (DSP) task, we have recently shown that faster
96 performance for trained sequences relies on improvements in online planning – the ability to
97 plan future elements in parallel with the execution of preceding sequence elements (Ariani and
98 Diedrichsen 2019). Given the hypothesis that repetition improves movement planning (Mawase
99 et al. 2018), we would therefore expect to observe a repetition benefit not only on reaction time,
100 which depends on pre-planning and movement initiation, but also on sequence movement time,
101 which depends on online planning and movement execution. To test these ideas, here we used
102 a DSP task in which participants were explicitly cued to produce short sequences of finger
103 movements (Exp. 1). On any given trial, the sequence could either be the same as in the
104 previous trial (Repetition), or a different sequence (Switch), with equal probability (0.5).
105 Participants were given enough time (2.5 s) to complete stimulus identification and action
106 selection before the go signal. The use of such a delayed-movement paradigm ensured that
107 repetition effects could not be caused by improved perceptual processes. Our findings indicated
108 that sequence repetition improved both reaction times (the time between go signal and the first
109 keypress) and sequence movement times (the time between first and the last keypress in the
110 sequence).

111 Next, we asked the exploratory question of whether these benefits are caused by
112 processes occurring before movement onset (stimulus identification and sequence pre-
113 planning), or by processes occurring during sequence production (initiation, execution, and
114 online planning). While our design encouraged participants to pre-plan each sequence during
115 the preparation phase, we manipulated whether they had to perform the sequence, or not, with
116 a Go/No-Go paradigm. This allowed us to compare Repetition and Switch trials, depending on

117 the whether the previous (N-1) trial involved pre-planning alone (No-Go condition), or included
118 also the initiation, execution, and online planning of the sequence (Go condition).

119 Finally, in a separate behavioral experiment on an independent sample of participants
120 (Exp. 2), we examined how the repetition effect changed with the gradual development of
121 sequence-specific learning by monitoring the effect over the course of training on a fixed set of
122 sequences.

123 **Methods**

124 **Participants.** Forty-nine right-handed volunteers participated in Experiment 1 (33 F, 16 M; age
125 18–39, mean 22.73 years, SD 5.04). An independent sample of forty right-handed volunteers
126 participated in Experiment 2 (24 F, 16 M; age 18–36, mean 22.28 years, SD 3.44). Handedness
127 was assessed using the Edinburgh Handedness Inventory (Exp. 1: mean 86.33, SD = 15.67;
128 Exp. 2: mean 78.59, SD = 16.74). While some participants had some musical training, none of
129 them was a professional musician (musical experience, Exp. 1: mean 4.67 years, SD 6.01; Exp.
130 2: mean 3.14 years, SD 3.77). None of the participants had a history of neurological disorders.
131 Experimental procedures were approved by the ethics committee at Western University
132 (London, Ontario, Canada). All participants gave written informed consent and received
133 monetary compensation for their participation. Four participants withdrew from Exp. 1 before
134 study completion and were thus excluded from data analysis (final N = 45). In Exp. 2, one
135 participant failed to follow the instructions. The session was terminated before completion and
136 the data excluded from successive analysis (final N = 39).

137
138 **Apparatus.** Sequences of finger presses were executed on a custom-made keyboard device
139 comprised of five keys corresponding to each finger of the right hand. The isometric force
140 exerted by each finger was continuously recorded by force transducers under each key (FSG-
141 15N1A, Sensing and Control, Honeywell; dynamic range, 0-25 N) at a rate of 500 Hz. To
142 account for sensor drifts, we recalibrated the zero-force baseline at the beginning of each block
143 of trials. Each key was independently deemed to be *pressed* when the force exceeded a
144 threshold of 1 N and *released* as soon as the force returned below 1 N. (Fig. 1C; P = press, R =
145 release).

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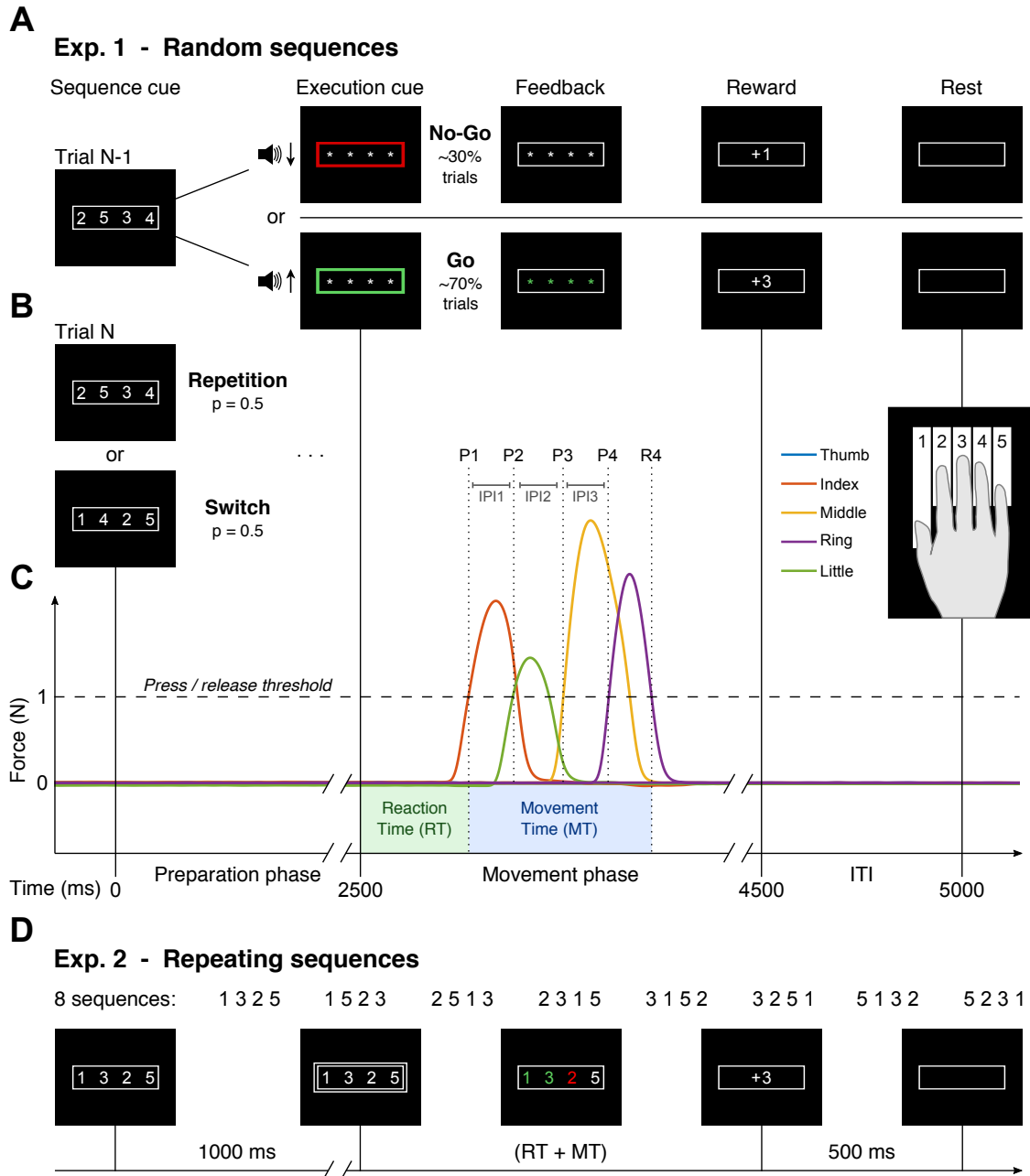


Figure 1. The discrete sequence production (DSP) task. **A.** Exp. 1 example trial: a sequence cue (white numbers on the computer screen) is followed by a production cue (outline changes color, numbers are masked). Online visual feedback about keypresses was given during the movement phase (green asterisks for correct presses, red for incorrect presses), followed by reward points depending on performance. 30% of the trials in a block were No-Go trials (red outline + low-pitch sound, top), 70% were Go trials (green outline + high-pitch sound, bottom). **B.** The next trial could be either a Repetition of the same sequence (0.5 probability), or a Switch to a new sequence. **C.** Example trial in Exp. 1 with the following trial timing: preparation phase: 2.5 sec; movement phase: 2 sec; ITI: 0.5 sec. Dashed horizontal line indicates force threshold (1 N) to determine the moment of each keypress and release (dotted lines). P1 = press of first key; R4 = release of fourth key; IPI1 = first inter-press interval. Total time (TT) = RT + MT. **D.** Exp. 2 design: 8 repeating sequences, trial structure, and timing. The go signal here is given via white box around the sequence cue.

148

149 Visual stimuli to instruct one sequence of finger presses were presented on a computer monitor
150 and consisted of a string of 4 numeric characters displayed in white on black background
151 (Sequence cue) and framed by a white rectangle (Fig. 1A; character height 1.5 cm, visual angle
152 approx. 2°).

153

154 **Task.** We used a discrete sequence production (DSP) task in which participants were required
155 to produce sequences of keypresses with the five fingers of their right hand (Fig. 1A). Each
156 sequence was cued by 4 numbers ranging from 1 to 5, instructing which fingers had to be
157 pressed (e.g., 1 = thumb, 2 = index, ... 5 = little). The sequence had to be produced by
158 sequentially pressing the fingers corresponding to the numbers on the screen, from left to right.
159 On each trial, participants were presented with a 4-item sequence and asked to prepare for the
160 corresponding finger presses (preparation phase). After a fixed delay of 2.5 seconds, an audio-
161 visual production cue would mark the beginning of the movement phase (a fixed 2 seconds). On
162 Go trials, the production cue was a green frame accompanied by a high-pitch tone (Fig. 1A,
163 bottom), indicating that participants had to perform the planned sequence of finger presses as
164 quickly and accurately as possible (Go condition). On other trials, the production cue was a red
165 frame accompanied by a low-pitch tone (Fig. 1A, top), instructing the participants to remain as
166 still as possible without pressing any key until the end of the movement phase (No-Go
167 condition). To encourage sequence pre-planning before the production cue, at the beginning of
168 the movement phase the sequence cue was replaced by 4 asterisks masking the numbers.
169 Moreover, the sequence of keypresses had to be completed within 2 seconds from the
170 production cue (timeout error after that). With each keypress, the corresponding asterisk turned
171 either green (correct press) or red (wrong press). Performance was evaluated in terms of both
172 execution speed and press accuracy. Speed was defined in terms of total time (TT), which
173 consisted of the reaction time (RT: from the onset of the Sequence cue to the first keypress)

174 plus the movement time (MT: from the onset of the first keypress, P1, to the release of the last
175 keypress, R4). A single press error invalidated the whole trial, so accuracy was calculated as
176 percent error rate (ER) per block of trials (number of error trials / number of total trials x 100). At
177 the end of the movement phase, during the 500 ms inter-trial interval (ITI), participants were
178 presented with performance points appearing in place of the asterisks.

179

180 **Feedback.** To motivate participants to improve in speed ($TT = RT + MT$) and accuracy ($1 - ER$)
181 of sequence production, we gave participants performance feedback on each trial. The
182 performance score was based on the following point system: -1 points for timing errors (i.e.,
183 anticipation of the production cue, or movement initiation in No-Go trials); 0 points for correct
184 timing but wrong finger press (any one wrong keypress); +1 points for correct timing and press
185 (i.e., movement initiation in Go trials, or no movement in No-Go trials); and +3 points for correct
186 timing, correct press, and TT 2% or more faster than TT threshold. TT threshold would decrease
187 by 2% from one block to the next if both of the following performance criteria were met: median
188 TT in the current block faster than best median TT recorded hitherto, and mean ER in the last
189 block < 25%. If either one of these criteria was not met, the thresholds for the next block
190 remained unchanged. At the end of each block of trials, the median TT, mean ER, and points
191 earned were displayed to the participants. At the end of the session, monetary compensation
192 corresponded to the amount of performance points accumulated (points < 750 = 10 \$; 750 ≤
193 points < 1000 = 12 \$; points ≥ 1000 = 15 \$).

194 Penalizing timing errors (-1 points) more than press errors (0 points) might have made
195 participants more cautious and increased their RTs. Thus, to encourage full preparation of the
196 sequence, for the last 20 participants of Exp. 1 we gave equal weight to timing and press errors
197 (both 0 points). To check whether the penalty for timing errors affected RT performance, out of
198 the 45 participants not excluded from data analysis, we compared the reaction times of
199 participants who received the penalty (N = 27) and those who did not (N = 18). An independent

200 samples *t*-test showed no statistical difference in RTs between the two groups (with or without
201 penalty for timing errors), suggesting that participants adopted a similar strategy regardless of
202 the penalty (penalty group: 443 ± 15 ms; no-penalty group: 453 ± 19 ms; difference: -10 ± 23
203 ms; $t_{43} = -0.437$, $p = 0.664$).

204 The scoring system in Exp. 2 was identical to the one in Exp. 1 without any additional
205 penalty for eventual timing errors (0 points). Participants in Exp. 2 were paid a flat hourly rate (7
206 \$), regardless of the specific amount of points accumulated.

207

208 **Design.**

209 **Exp. 1.** To investigate the nature of the repetition effect, we used a 2-by-2 design independently
210 manipulating whether a particular sequence was repeated or whether the previous trial was a
211 Go or No-Go trial. Sequences in Exp. 1 were randomly determined (see below). On any given
212 trial, there was a 0.5 probability that the sequence was the same as the previous trial
213 (Repetition) or that it was different (Switch; Fig. 1B). Independently, we varied whether each trial
214 was a Go trial (70%) or a No-Go trial (30%). We designed a majority of the trials to be go-trials
215 to encourage full sequence pre-planning before the production cue. The order of trials was
216 randomly interleaved, creating all possible combinations of the factors repetition type and
217 execution type of the previous trial. Note that, given that the trial structure was kept fixed across
218 all experimental conditions (i.e., 2.5 sec preparation phase + 2 sec movement phase + 0.5 sec
219 ITI), there was no difference in time elapsed after a Go, or No-Go trial. Each block was
220 composed of 48 trials (12 repetitions for each of the 4 sequences), and participants underwent 1
221 session of 12 blocks each. In order to limit strong learning effects that might lead to ceiling
222 performance, for each block of trials, we randomly selected four different 4-item sequences from
223 a large pool of all permutations with repetition of the numbers 1 to 5, taken 4 items at a time.
224 Moreover, to keep sequences of a similar level of difficulty, we removed from the permutation
225 pool all sequences in which any number repeated (i.e., each number could only appear once

226 per sequence), or that included “runs” (more than 2 fingers in either increasing or decreasing
227 order; e.g., 1-2-3, or 3-2-1).

228

229 **Exp. 2.** To explore how sequence-specific learning affects sequence repetition, we designed a
230 second experiment where one set of 8 sequences remained fixed over time. Participants
231 underwent training for two consecutive days to ensure the development of enough sequence-
232 specific learning. However, for the purposes of this study, we will not be examining
233 consolidation effects, which will be discussed in future work. We used 8 4-item sequences
234 including all fingers of the right hand except for the ring finger. The sequences were selected
235 according to the following criteria: 1) each finger was used only once per sequence; 2) each
236 finger started 2 of the 8 sequences; 3) each finger was pressed in every ordinal position twice
237 across sequences; and 4) no more than 2 neighboring fingers pressed in a row (i.e., as in Exp.
238 1, we excluded “runs”).

239 In contrast to Exp. 1, Exp. 2 did not contain any No-Go trials and the preparation phase
240 was shortened to a fixed 1 s. Also, the production cue was presented only visually (white box
241 around the sequence cue), the sequence cue was not masked, and the duration of the
242 movement phase was not fixed (i.e., TT dictated the actual duration of the trial, with the ITI
243 occurring right after the last keypress). Finally, sequence repetition was not randomized, but
244 counter-balanced across sequences. Each sequence was executed from a minimum of once
245 (i.e., a Switch) to a maximum of five times in a row (i.e., executing once and repeating four
246 times). To ensure a comparable number of trials per each repetition condition, we manipulated
247 the proportion of same-sequence executions in a row as follows: 0.33 one-execution trials
248 (Switch), 0.22 two-executions trials (One-repetition), 0.22 three-executions trials (Two-
249 repetitions), 0.11 four-executions trials (Three-repetitions), 0.11 five-executions trials (Four-
250 repetitions). Each of the 8 sequences was presented in each repetition condition the same
251 number of times (balanced design across sequences), and the factors sequence type and

252 repetition condition were then pseudo-randomized within a block of trials. In addition,
253 unbeknownst to the participants, we included a variable number (from 1 to 4) of one-execution
254 trials (Switch) as dummy trials at the beginning (assuming warm-up) and end (assuming
255 tiredness) of each block, which were subsequently excluded from data analysis. Overall, this led
256 to a final proportion of 0.59 repetition trials (across repetition conditions), and 0.41 switch trials.
257 Each experimental block consisted of 50 trials (including dummy trials), and participants
258 performed 12 blocks (~ 4-5 min each) per experimental session per day (i.e., 24 blocks in total
259 per participant). No explicit information about the sequence types, or instruction to memorize the
260 sequences, was given. Nonetheless, the extensive repetition (more than 130 trials per
261 sequence) ensured that participants would learn the finger transitions associated with each
262 sequence, usually already by the end of the first testing day.

263

264 **Data analysis.** Data were analyzed offline using custom code written in MATLAB (The
265 MathWorks, Inc., Natick, MA). Statistical analyses for assessing movement repetition effects on
266 reaction times (RT) and sequence movement time (MT) included two-tailed paired-samples t-
267 tests (Repetition vs. Switch), and 2-by-2 within-subject repeated measures ANOVAs with factors
268 repetition type (Repetition / Switch) and previous trial type (No-Go / Go). Error trials (both timing
269 and press errors), No-Go trials, and dummy trials (Exp. 2 only, see Design section) were
270 excluded from data analysis. For visualization purposes only, data were normalized by
271 subtracting from each data point each participant's mean and adding back the grand mean of
272 the group. Statistical analyses, computed on raw data, were not affected by this normalization
273 procedure.

274

275 **Results**

276 ***Sequence repetition reduces both reaction and movement times***

277 Our experiment was designed to test whether there are short-term (i.e., trial-to-trial) benefits for
278 the repetition of sequential movements. We compared trials in which the movement sequence
279 was the same as on the previous trial (i.e., Repetition trials) to trials preceded by a different
280 sequence (i.e., Switch trials). We found that RT improved upon repetition of the same sequence
281 (Fig. 2A). Participants could react more quickly to the Go cue when then previous trial contained
282 the same sequence (paired-samples t-test, $t_{44} = 2.890$, $p = 0.006$). Notably, this RT advantage
283 was present even though participants had more than enough time (2.5 s) to finish pre-planning
284 the 4-item sequence before the production cue (Ariani and Diedrichsen 2019). These results
285 extend previous insights by Mawase et al. (2018) by showing that repetition facilitates the
286 triggering of a planned movement, an effect that cannot simply be accounted by improved
287 identification of the visual stimuli, or a bias in selection processes. Repetition also accelerated
288 sequence production, as indicated by a significant repetition effect on sequence MT (Fig. 2C).
289 On Repetition trials, the sequence was performed 36 ms (± 5 ms) faster than on Switch trials, a
290 robust effect across participants (paired-samples t-test, $t_{44} = 7.473$, $p = 2.330e-09$).

291 Next we asked whether the repetition effect would increase with further repetitions of the
292 same sequence. For RT, the repetition effect was limited to the first repetition (Switch-Rep1
293 difference: 15 ± 4 ms; $t_{44} = 3.753$, $p = 5.081e-04$; Fig. 2B). After that, no further RT advantage
294 was observed for successive sequence repetitions (Rep1-Rep2 difference: -2 ± 4 ms; $t_{44} = -$
295 0.537 , $p = 0.594$; Rep2-Rep3+ difference: -4 ± 3 ms; $t_{44} = -1.138$, $p = 0.261$). In contrast, for MT
296 the improvements were not limited to the first repetition (Switch-Rep1 difference: 23 ± 4 ms): a
297 second repetition (i.e., performing the same sequence three times in a row) was almost nearly
298 as beneficial to further reduce sequence MT (Rep1-Rep2 difference: 21 ± 4 ms; $t_{44} = 4.712$, $p =$
299 $2.478e-05$; Fig. 2D). After the second repetition, performance appeared to reach a plateau

300 (Rep2-Rep3+ difference: 4 ± 6 ms; $t_{44} = 0.705$, $p = 0.484$).

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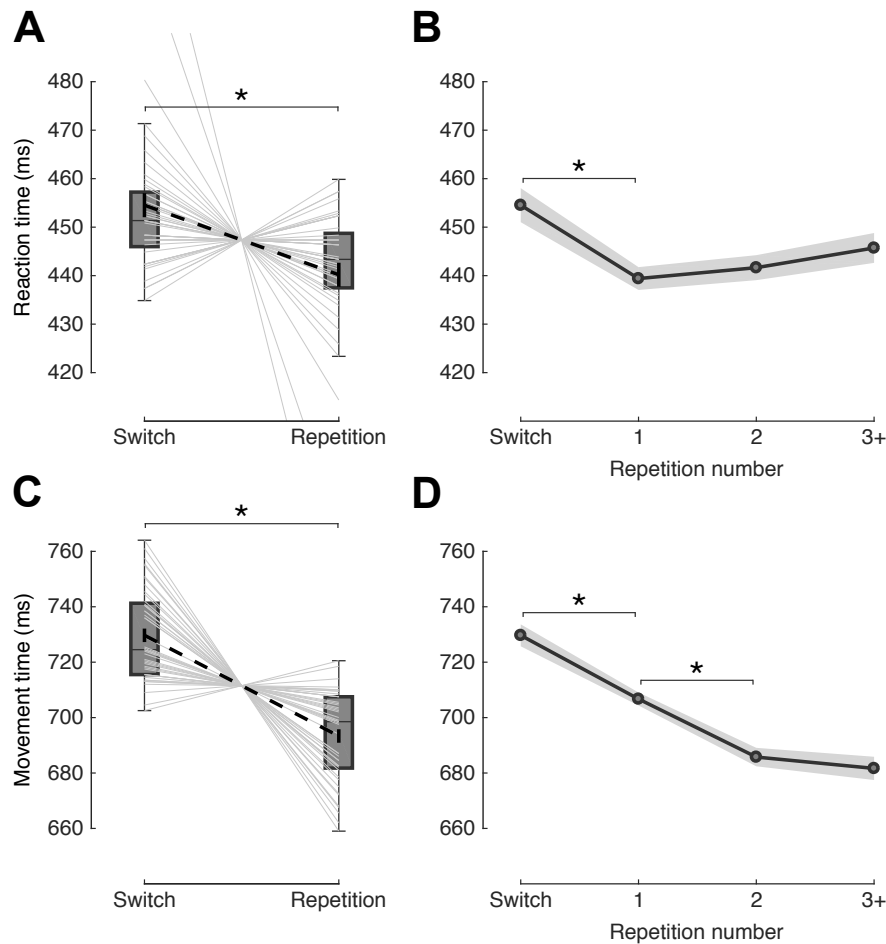


Figure 2. Immediate repetition leads to better performance. **A.** Distribution of median reaction times (RT) separately for Switch and Repetition trials. Light-gray lines represent individual participants. Dashed black line shows group mean across conditions, with relative standard error. **B.** Mean RT as a function of repetition number (1 means that a sequence was performed twice in a row, 3+ means the average of a sequence being repeated 4 or more times in a row). Shaded areas represent between-subject standard error of the mean. **C.** Distribution of median sequence movement times (MT) separately for Switch and Repetition trials. Other conventions as in panel A. **D.** Mean sequence MT as a function of repetition number. Other conventions as in panel B. * $p < 0.05$, two-tailed paired-samples t -test.

302

303

304 Importantly, faster RT and MT in Repetition trials did not come at the cost of decreased
305 accuracy. In fact, the opposite was true: accuracy increased from $81.8 \pm 1.1\%$ correct trials in
306 Switch trials to $85.6 \pm 1.2\%$ in Repetition trials (paired-samples t -test $t_{44} = -5.532$, $p = 1.637e-$

307 06). Moreover, timing errors (i.e., false starts by anticipation of the production cue) decreased
308 from 4 % to 2.9 % (paired-samples t-test $t_{44} = 2.777$, $p = 0.008$).

309 Overall, our results suggest that repetition of a sequence improves both the initiation of a
310 pre-planned movement, as well as the speed by which the repeated sequence can be
311 performed. The accuracy advantage proved that this effect did not arise at the expense of
312 reduced execution accuracy.

313

314 ***The repetition benefit arises from improved online planning***

315 The results so far indicate that sequence repetition improves initiation (RT) and movement (MT).
316 Should this be taken as an indication that repetitions improve execution-related, rather than
317 planning-related processes? Not necessarily so. In a previous study we have demonstrated that
318 sequence MT (the time from first to last keypress) is not only a function of motoric processes,
319 but is also strongly influenced by the speed of online planning (Ariani and Diedrichsen 2019).
320 Even for short sequences, only the first 2-3 keypresses can be fully pre-planned, whereas later
321 movements appear to be planned online, that is during of the execution of the beginning of the
322 sequence. If movement repetition facilitates online planning, this effect should therefore be more
323 prevalent in latter parts of the sequence. If, however, movement repetition facilitates execution
324 processes, it should influence the speed of all presses in the sequence, no matter if these are
325 performed in the beginning or later.

326 To examine this issue, we inspected the 3 inter-press intervals (IPIs) between the onsets
327 of the 4 keypresses separately. The second transition was the slowest, while the first and last
328 transition were nearly equally fast (Fig. 3A). This indicates a “2-and-2” rhythm, in which each 4-
329 item sequence begins with two quick presses, followed by a brief pause, and then again by two
330 quick presses. Given that the sequences changed randomly from block to block, all possible
331 finger transitions could occur with equal probability at each position of the sequence. Therefore,
332 this effect cannot be explained by biomechanical factors (e.g., some transitions being harder

333 than others). Instead, the pattern of results suggests a clear influence of online planning: the
334 first two keypresses can be fully pre-planned and can therefore be executed quickly; then
335 execution needs to slow down until online planning of the remaining two keypresses is finished.
336

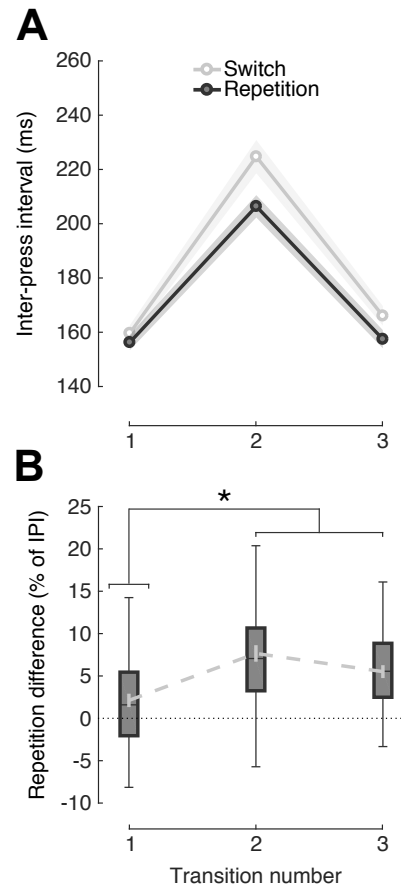


Figure 3. Sequence repetition benefits online planning of repeating sequence elements. A. Mean inter-press intervals (IPI) as a function of transition number, separately for Switch (light) and Repetition (dark) trials. Shaded areas represent between-subject standard error of the mean. **B.** Same data as in A but normalized by mean IPI for each transition separately. Dashed gray line denotes group mean across conditions, with relative standard error. * $p < 0.05$, two-tailed paired-samples t -test.

337

338

339 Importantly, we found that the repetition effect was most pronounced on the second
340 transition (Switch-Repetition difference, 2nd vs 3rd transition: 10 ± 3 ms; $t_{44} = 3.205$, $p = 0.003$;
341 Fig. 3A). After normalizing the Switch-Repetition difference by mean IPI of each transition, we

342 found that the repetition benefit, expressed as percentage of average IPI (Fig. 3B), was
343 significantly greater on the second and third transitions than on the first transition ($t_{44} = 5.380$, p
344 $= 2.729e-06$). Taken together, the pattern of IPIs is consistent with the view that repetition
345 affects sequence movement times by accelerating processes related to online planning and
346 does not speed up the actual production of individual keypresses.

347

348 ***Repetition effects may require actual movement experience***

349 So far, the results suggest that sequence repetition accelerates subsequent pre- and online
350 planning processes. Next, we addressed the question of whether pre-planning of a sequence
351 would be sufficient to produce a benefit on subsequent trials RT, or whether the execution of the
352 sequence (involving initiation, motor processes, and online planning) may be required. For this
353 purpose, we compared Switch and Repetition trials separately for whether the previous trial (N-
354 1) had been a Go, or a No-Go trial. Our logic was that if the repetition effect resulted from
355 stimulus processing, selection, and pre-planning, we should see a repetition benefit even if the
356 previous trial had been a No-Go trial. Conversely, if the repetition effect requires the initiation or
357 execution of the sequence, then we should only observe it when the previous trial had been
358 executed (i.e., N-1 was a Go trial). To avoid repetition trials which were preceded both by a Go
359 and by a No-Go trial of the same sequence, we restricted this analysis to the first repetition of a
360 sequence (i.e., max two executions in a row).

361 We found that the repetition effect on RT was significant when the previous trial had
362 been a Go ($t_{44} = 4.534$, $p = 4.421e-05$), but not when it had been a No-Go ($t_{44} = 0.986$, $p =$
363 0.330 ; Fig. 4A). Importantly, the interaction between repetition type (Switch vs. Repetition) and
364 previous trial type (No-Go vs. Go) was significant (2-by-2 within-subject ANOVA, $F_{1,44} = 5.303$, p
365 $= 0.026$). The same pattern of results was observed for MT (Fig. 4B): significant repetition effect
366 only on N-1 Go trials ($t_{44} = 5.464$, $p = 2.055e-06$), and significant interaction between repetition
367 and previous trial type ($F_{1,44} = 4.898$, $p = 0.032$). As expected, the effect was also visible when

368 we split up the MT into IPIs (Fig. 4C). Only for the second transition did we find a significant
369 interaction between repetition type and previous trial type ($F_{1,44} = 4.271$, $p = 0.044$).
370

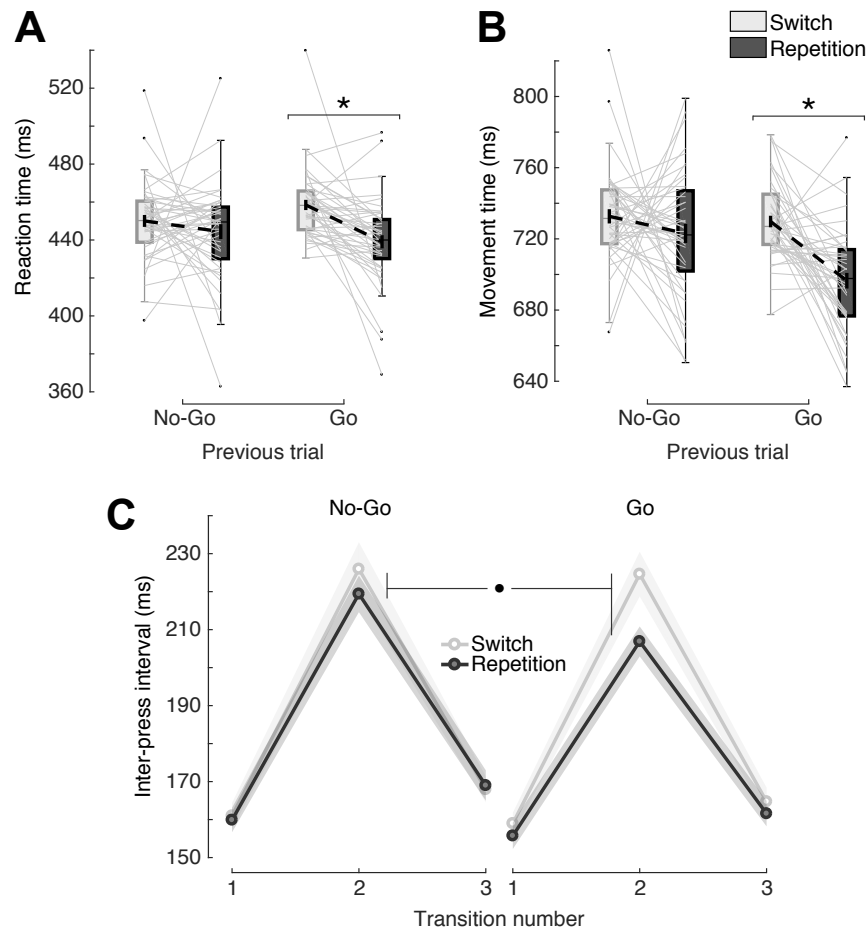


Figure 4. The repetition effect appears to require movement experience. **A.** Distribution of median movement times (MT) separately for Switch (light) and Repetition (dark) trials as a function of whether the previous ($N-1$) trial was a Go, or a No-Go trial. To avoid contamination between Go and No-Go trials in long repetition chains, selected trials were restricted to a maximum of one repetition. Solid light-gray lines represent individual participants. Dashed black lines represent group means across conditions. Black dots are considered group outliers. **B.** Distribution of median reaction times (RT) separately for Switch (light) and Repetition (dark) trials as a function of whether the previous ($N-1$) trial was a Go, or a No-Go trial. Other conventions as in panel A; **C.** Mean inter-press intervals (IPI) as a function of transition number, separately for Switch (light) and Repetition (dark) trials and split by whether the preceding trial was a No-Go (left) or a Go (right) trial. Shaded areas represent between-subject standard error of the mean. * $p < 0.05$, two-tailed paired-samples t -test; * $p < 0.05$, for interaction in 2-by-2 within-subject repeated measures ANOVA.

371

372

373 Again, faster reaction and movement in repetition trials did not trade-off with sequence
374 execution accuracy. The strong and consistent improvements in accuracy after a repetition ($F_{1,44}$
375 = 26.698, $p = 5.543e-06$) was not different depending on whether the previous trial had been a
376 Go or a No-Go trial ($F_{1,44} = 0.159$, $p = 0.691$), nor it was the decrease in timing errors (main
377 effect of repetition, $F_{1,44} = 6.238$, $p = 0.016$; interaction between repetition and previous trial
378 execution, $F_{1,44} = 0.190$, $p = 0.665$).

379 Taken together, our results are consistent with the view that the repetition effect relies on
380 the experience of performing, or at least initiating the execution of a sequence. The act of
381 processing the visual stimuli, selecting, and pre-planning the upcoming sequence movements
382 (all processes that we assumed would be performed on No-Go trials as well) was not sufficient
383 to obtain faster RT or MT on Repetition trials. Therefore, the benefit of rehearsal in a motor
384 sequence task appears to require processes that are only activated when the movement is
385 actually initiated or executed.

386

387 ***Repetition improves the speed of even the fastest movements and participants***

388 Immediate movement repetition makes participants faster at initiating and producing a motor
389 sequence. This effect may have been caused by an improvement in movement speed across
390 the board – that is, even the fastest trials should get even faster after repetition. Alternatively,
391 the effect could have been caused by the fact that repetition makes slow trials less likely: such
392 slow trials may be the result of errors in planning, lack of concentration or focus on the task. In
393 other words, repetition may simply ease the computational burden on the subject and make
394 suboptimal trials less likely, without actually affecting the top speeds in sequence production. To
395 investigate this idea, we divided the whole distribution of sequence movement times into 11 bins
396 for each repetition condition and participant separately. This analysis was performed separately
397 for trials for which the previous trial (N-1) was a No-Go or a Go trial (Fig. 5A). For Go trials, the
398 repetition effect was present for the whole range of sequence execution speeds. Importantly,

399 this was true even for the fastest MTs: the mean repetition difference for the fastest bin was 41
 400 \pm 19 ms (one-sample t -test vs. zero $t_{44} = 2.124$, $p = 0.039$).

401

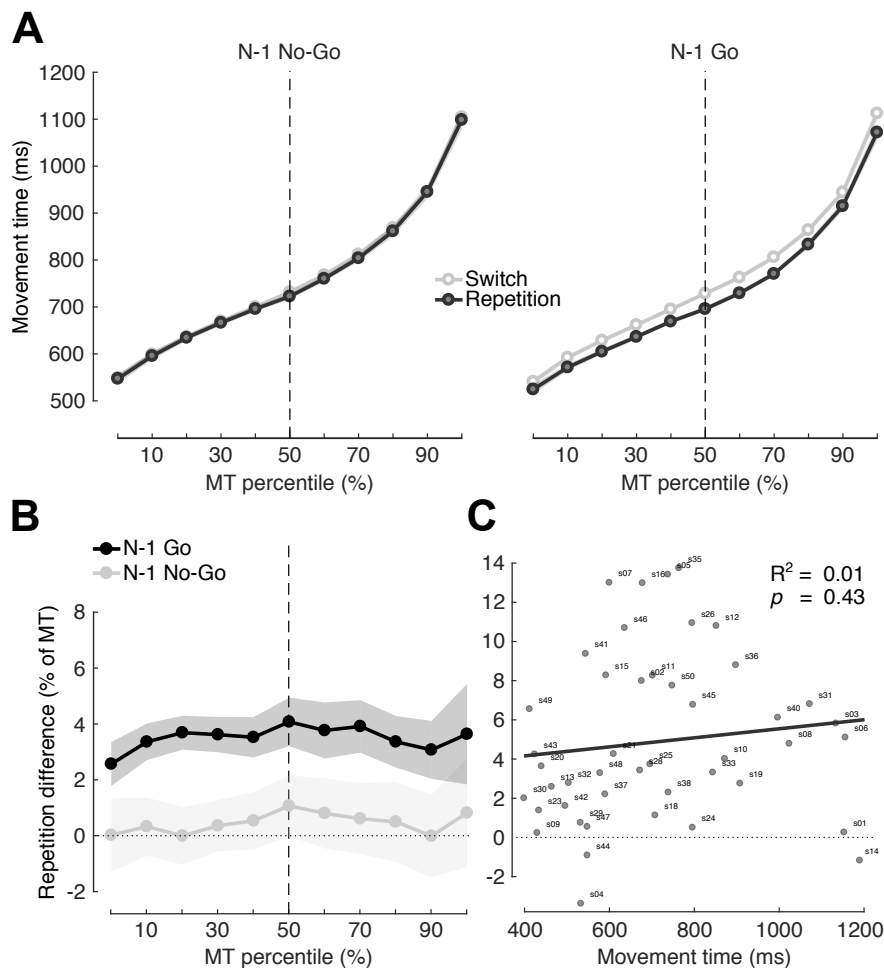


Figure 5. The repetition benefit remains constant across a wide range of movement speeds. A. Sequence MT as a function of MT percentile (11 bins), separately for Switch (light) and Repetition (dark) trials, and by previous trial No-Go (left), or Go (right). Dashed vertical line denotes the MT bin that includes the median MT. Shaded areas represent between-subject standard error of the mean. **B.** Repetition difference normalized by median MT for each bin separately as a function of MT percentile, and by previous trial No-Go (light), or Go (dark). Other figure conventions are the same as in A. **C.** Repetition difference normalized by median MT plotted against MT for each participant. Solid line represents linear regression. Dotted line as landmark for lack of repetition difference. R^2 = proportion of variance in repetition difference explained by execution speed.

402

403

404 To better quantify this difference, we plotted the repetition difference normalized by the MT of

405 the corresponding percentile bin (i.e., [Switch MT – Repetition MT] / Overall MT for each bin;
406 Fig. 5B). Again, this analysis confirmed that for N-1 Go trials the percentage repetition effect
407 was significant (one-sample t -test vs. zero across all percentiles, $t_{44} = 4.792$, $p = 1.908e-05$) and
408 did not differ across the range of speeds (paired-samples t -test first vs. last percentile, $t_{44} = -$
409 0.516 , $p = 0.609$). As expected, for N-1 No-Go trials the effect was not significant ($t_{44} = 1.064$, p
410 $= 0.293$). Thus, the repetition benefit was not simply a consequence of preventing occasionally
411 slow executions (i.e., an attentional effect). Rather, after a repetition, participants were more
412 likely to beat their currently best speed.

413 Lastly, we investigated whether repetition was equally beneficial for all subjects, or only
414 for participants that were relatively slow performers to begin with. Indeed, for participants that
415 were already faster overall, the benefit of repetition may not have constituted a large proportion
416 of their movement time. For each participant, we plotted the median Switch-Repetition
417 difference normalized by MT as a function of median sequence movement time (Fig. 5C). The
418 correlation between sequence production speed and size of the repetition effect was not
419 significantly different from zero ($r = 0.119$, $t_{44} = 0.790$, $p = 0.434$), so we found no evidence that
420 inter-subject variability had a strong influence on the relative repetition benefit. Overall, we
421 showed that movement repetition enables faster sequence MT across the board – both for fast
422 and slow trial, and for fast and slow participants.

423

424 ***Does sequence-specific learning affect the repetition benefit?***

425 In Exp. 1, sequences varied randomly from block to block, effectively preventing participants
426 from learning a specific set of keypress transitions. Therefore, it is likely that overall
427 performance improvements largely reflected sequence-general learning processes (e.g., faster
428 single-item selection, or task familiarization). But how does sequence-specific learning (i.e.,
429 extensively practicing a fixed set of sequences) change the repetition effect? One possibility is
430 that practice may diminish, and eventually erase, the repetition effect. This would be consistent

431 with our previous finding that sequence-specific learning reduces the time that participants need
432 to pre-plan and online-plan the sequences (Ariani and Diedrichsen 2019).
433

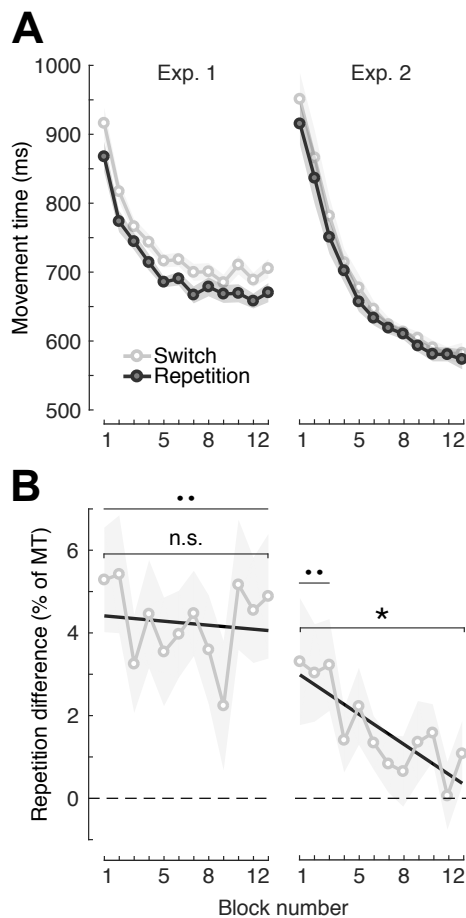


Figure 6. Sequence-specific learning reduces the repetition effect. A. Sequence movement time separately for Switch (light) and Repetition (dark) trials as a function of block number in Exp. 1 (left) and Exp. 2 (right). Shaded areas represent between-subject standard error of the mean. **B.** Switch-Repetition difference normalized as percentage of MT for each block in Exp. 1 (left) and Exp. 2 (right). Shaded areas represent between-subject standard error of the mean. Black solid line represents linear regression line. Dashed horizontal line indicates absence of repetition effect. * $p < 0.05$, two-tailed paired-samples t -test; ** $p < 0.05$, two-tailed one-sample t -test vs zero difference.

434

435

436 To test this hypothesis, we designed a second study (Exp. 2) in which a set of 8 sequences was
437 kept constant throughout the experiment (12 blocks of 50 trials each). We still randomly varied,
438 however, whether a sequence would repeat or change between trials. We then analyzed how

439 the repetition effect changed over the course of learning. For illustrative purposes, we re-
440 analyzed the results of the first experiment (Exp. 1, N = 45, sequence-general; Fig. 6A-6B, left
441 column) in the same format as the results for the second experiment (Exp. 2, N = 39, sequence-
442 specific; Fig. 6A-6B, right column) and focused on the comparison between the first day of both
443 experiments.

444 In Exp. 1, where sequence-specific learning was nearly impossible, a clear repetition
445 benefit was present from the first block (Fig. 6A, left; Switch-Repetition difference: 49 ± 12 ms,
446 $t_{44} = 3.973$, $p = 2.600e-04$) and remained roughly constant despite sequence-general learning,
447 until the last block (last block Switch-Repetition difference: 35 ± 11 ms, $t_{44} = 3.315$, $p = 0.002$;
448 Fig. 6A, left). Importantly, once adjusted by overall MT for each block (Fig. 6B, left), there was
449 no difference in repetition benefit from block 1 to block 12 (paired-samples t -test, $t_{44} = 0.214$, $p =$
450 0.832).

451 In Exp. 2, we found that the repetition benefit was present in the first few blocks (one-
452 sample t -test between mean blocks 1-3 vs. zero difference, $t_{38} = 2.424$, $p = 0.020$; Fig. 6B, right)
453 despite the overall improvement in sequence execution speed (Fig. 6A, right). However, this
454 effect quickly vanished after a few blocks of practice (repetition difference on block 4, $t_{38} =$
455 1.806 , $p = 0.078$; Fig. 6B, right).

456 These results show that the repetition effect gradually decreases with practice.
457 Importantly, sequence-specific, but not sequence-general learning was associated with such
458 decrease.

459 **Discussion**

460 In two behavioral experiments, we establish that repeating a sequence of movements led to
461 immediate improvements in reaction times and movement speed (Fig. 2) without any associated
462 cost in performance accuracy. The repetition benefit during sequence production was largest in
463 the middle part of a sequence (Fig. 3), and was absent for the first two presses, suggesting that
464 repetition did not affect execution-related processes (which should be involved in all presses),
465 but rather online planning (which was most relevant in the middle of the sequence). The finding
466 that sequence repetition facilitated online planning was consistent with the observation that the
467 repetition effect decreased with sequence-specific, but not sequence-general practice (Fig. 6).
468 That is, once sequence-specific learning reduced the role of online planning, the benefit of
469 repetition disappeared. Finally, we observed that repetition-related improvements only occurred
470 for the trials that had been preceded by sequence production (which involves movement
471 initiation, execution, and online planning), suggesting that action selection and pre-planning may
472 not be sufficient to drive the repetition effect (Fig. 4-5).

473

474 ***Sequence-level repetition effects in motor sequence production***

475 Repetition of a sequence of finger movements resulted in immediate improvements in speed
476 and accuracy of sequence production. This indicates that repetition also affects processes
477 governing the planning or execution of the entire movement sequence, rather than just
478 individual movements. To understand the implications of this finding, it may be useful to
479 consider our findings in the framework of neuronal state-spaces (Churchland et al., 2010, Fig.
480 7). In this framework, neural activity in movement-related brain regions (e.g., primary and pre-
481 motor cortex) can be decomposed into neuronal dimensions representing the current movement
482 (execution state-space) and neuronal dimensions representing the next upcoming movements
483 (planning state-space). Pre-planning would be equivalent to bringing the neuronal population

484 state into a specific location of planning state-space (Churchland et al. 2006b). Upon movement
485 initiation, the neuronal state changes dramatically (Elsayed et al. 2016; Kaufman et al. 2016)
486 and subsequently evolves mainly in the dimensions that span the execution state-space,
487 generating the patterns required for producing muscular output. While neurons in the dorsal pre-
488 motor cortex (PMd) likely contribute more to the planning state-space, neurons in the primary
489 motor cortex (M1) contribute more to the execution state-space. However, although execution-
490 and planning-related signals are mixed in these two regions, with many neurons responding to
491 both processes (Alexander and Crutcher 1990; Prut and Fetz 1999; Riehle and Requin 1989),
492 planning and execution processes can be kept from interfering with each other by using
493 orthogonal neural dimensions of the same overlapping population of neurons (Kaufman et al.
494 2014).

495 In this framework, repetition effects for individual finger movements would be caused by
496 the fact that the correct pre-planning state can be reached faster and with more accuracy after
497 repetition (Mawase et al. 2018), possibly by lingering activity in the planning state-space (Fig.
498 7A). Now consider the production of a short sequence. Here, the planning-related neural state
499 needs to traverse multiple locations, each triggering the corresponding elementary movements
500 in the execution state-space (Fig 7B). During movement, the neural state in the planning state-
501 space would already start to plan the next movement (i.e., online planning). If movement
502 repetition simply primed one location in the planning state-space, then any advantage of pre-
503 planning the first individual movement element would be washed out after completing the
504 sequence. Thus, the presence of a repetition effect at the level of sequences indicates that
505 movement repetition primes the entire pathway through the planning state-space. This is
506 consistent with the hypothesis of an intermediate level between movement selection and
507 execution (Diedrichsen and Kornysheva 2015).

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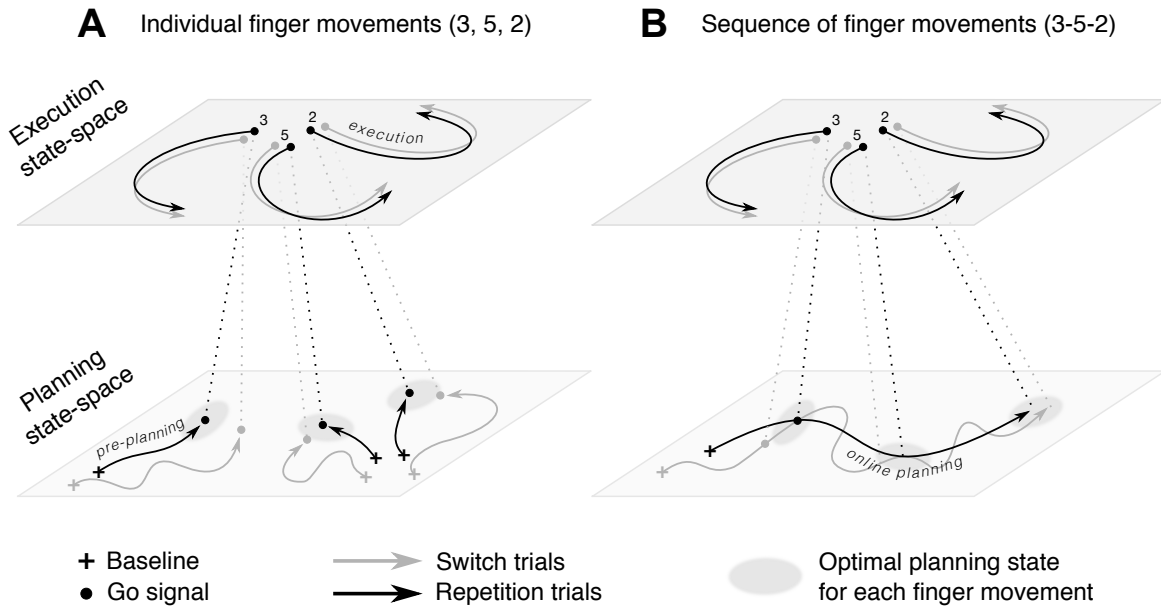


Figure 7. Conceptual visualization of planning and execution in a neural state-space framework. Changes in the pattern of neuronal firing can be characterized by movements of the neuronal state in a low-dimensional state-space. During the preparation phase, these changes mostly occur in the planning state-space (lower plane), whereas during the movement phase, these changes are more pronounced in the execution state-space (upper plane). Different finger movements (numbers, see Fig. 1) are characterized by a unique pattern in the planning state-space, and a unique trajectory in the execution state-space. Dotted lines indicate temporal correspondence between state-space events across planning and execution planes. **A.** Individual finger movements. During pre-planning (after stimulus onset), the neural state trajectory moves from a baseline location (cross) towards the optimal planning state (gray spotlight) until the go signal (dot) triggers execution dynamics. On repetition trials the correct planning state would be reached more quickly and with higher accuracy, enabling faster movement initiation when the go signal is given. **B.** Sequence of finger movements. Note that in this scenario what improves upon repetition is the neural state trajectory on the planning plane (i.e., online planning), leaving neural dynamics unchanged on the execution plane.

509

510

511 **RT advantage does not reflect improved stimulus processing or action selection**

512 In a previous study we found that benefits of a prolonged preparation phase asymptote after
513 ~1.5 seconds (Ariani and Diedrichsen 2019). Thus, by using a delayed-response paradigm, we
514 can be relatively confident that our RT measure mainly reflects the initiation of a pre-planned
515 response, as processes of stimulus identification and action selection should have been
516 completed during the preparatory delay (2.5 s). Thus, our study provides stronger evidence than

517 Mawase et al. (2018), who used a Free-RT/Timed-response paradigm, that the repetition benefit
518 on RT cannot be explained by faster perceptual processing of the target stimuli. By masking the
519 sequence cue at the moment of the go signal, we purposely encouraged participants to
520 complete the perceptual processing and response selection in the preparatory period. The
521 faster response initiation after a repetition may indicate that the planning state was closer to the
522 ideal state, which allowed for faster triggering of the desired sequence (Ames et al. 2014;
523 Churchland et al. 2006a, 2006b; Michaels et al. 2018).

524

525 ***Faster sequence production is due to more efficient online planning***

526 Repetition accelerated not only RT, but also MT, for repeated sequences. Critically, a detailed
527 analysis of the inter-press-intervals revealed that the transition between the first two
528 keypresses, which was likely fully pre-planned, was not influenced by the repetition. Rather, the
529 repetition advantage was observed on the second and, to some degree, third transitions. This
530 finding is consistent with the view that repetition benefits arose as a consequence of facilitated
531 online planning (Fig. 7B). Our current design cannot disambiguate whether this result was a
532 consequence of participants splitting the 4-item sequences into 2 chunks, with online planning
533 between the chunks, or whether the slowing down was caused by the necessity for continuous
534 online planning in the middle of the sequence. Either way, sequence repetition shortens MT, not
535 by accelerating how quickly individual movements can be executed, but by improving the speed
536 in which sequence elements, be it chunks or individual presses, can be planned online.

537

538 ***Sequence-specific learning gradually reduces the repetition effect***

539 After one day of practice on a fixed set of sequences we observed behavioral improvements
540 consistent with sequence-specific learning (Ariani and Diedrichsen 2019; Wiestler et al. 2014).
541 This speed advantage went hand in hand with a decrease, and eventual disappearance, of the
542 repetition effect. This result corroborates the interpretation that repetition benefits on sequence

543 production come from improvements in online planning. More efficient online planning for known
544 sequences allows for faster movement speeds, up to the point where participants are limited not
545 by their ability to quickly plan the next response, but by the ability to motorically implement the
546 response (Ariani and Diedrichsen 2019). When online planning ceases to be the main limiting
547 factor, the repetition benefit disappears. An alternative and non-mutually exclusive interpretation
548 is that sequences are planned and executed in movement chunks – in the case of our short 4-
549 item sequences, 2 chunks of 2 keypresses each. After extensive training, participants could
550 gradually learn to associate each sequence with a larger chunk of 4. This would enable them to
551 quickly pre-plan the entire short sequence at once, and then execute it as one chunk, again
552 removing the benefit of online planning during sequence repetition.

553

554 ***Is pre-planning sufficient or is movement required to drive the repetition effect?***

555 The repetition effect on MT was only present when the sequence was actually initiated and
556 executed on the previous trial. Given our claim that the repetition is due to online planning, this
557 finding would be expected, as sequence pre-planning alone would not move the neural state
558 through the entire trajectory in the planning state-space (Fig. 7B). According to this view, neither
559 the pre-planning of the initial part of the sequence, nor the execution of the individual sequence
560 elements is enough to facilitate sequence production with repetition. Instead, it is revisiting the
561 trajectory in the planning state-space that improves subsequent MT.

562 More surprisingly, pre-planning alone did not produce a repetition effect on RT. A priori,
563 it was not obvious why executing a sequence would be required to observe a faster RT. In fact,
564 if repetition facilitates response pre-planning (Mawase et al. 2018), one may have expected the
565 persistence of the effect on RT. A potential explanation for this finding could be that, despite
566 having enough time and information, participants did not fully pre-plan the response during the
567 preparatory period. Indeed, reaction times were relatively long (~400 ms) for triggering a pre-
568 planned sequence. Perhaps participants used the time after the go signal to complete pre-

569 planning. In this view, the completion of pre-planning up to and including movement initiation
570 would be essential for the subsequent repetition benefit. Nonetheless, our experiment was
571 designed to motivate participants to pre-plan the sequence well in advance during the delay. We
572 masked the sequence cue so that they could not rely on it after the go signal. Go and No-Go
573 trials were pseudo-randomly ordered, and we included a higher proportion of Go trials (70%),
574 such that, more often than not, participants would be required to act on the pre-planned
575 sequence. Finally, we rewarded participants on the sum of RT and MT, meaning that an easy
576 way to earn more money would be to shorten RTs. Thus, it is hard to see how more complete
577 pre-planning could be achieved. Instead, the act of initiating the sequence or online planning of
578 the remainder of the sequence appear to be necessary to achieve faster RT on the next trial.
579 However, how the processes related to pre-planning, initiation, and online planning interact with
580 each other remains an open question.

581

582 **Conclusions**

583 Our results show clear repetition effects for sequential movements, thereby extending previous
584 findings that repetition speeds up the preparation of individual movements. The pattern of
585 results is consistent with repetition facilitating trajectories through the preparatory neural state-
586 space. While sequence production recruits widespread cortical sensorimotor areas (Kornysheva
587 and Diedrichsen 2014; Wiestler and Diedrichsen 2013), our results would predict that the
588 neuronal origin of repetition effects should not be found in the primary motor cortex, which
589 mainly appears to be involved in the execution of individual movements (Yokoi et al. 2018;
590 Yokoi and Diedrichsen 2019). Instead, we would expect to observe the effects of repetition in
591 regions involved in (online) motor planning, such as dorsal premotor or superior parietal cortex.

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