

6-4-2018

## The effects of habits on motor skill learning

Nicola J. Popp  
*Western University*

Atsushi Yokoi  
*Osaka University*

Paul L. Gribble  
*Western University*

Jörn Diedrichsen  
*Western University*

Follow this and additional works at: <https://ir.lib.uwo.ca/brainscanpub>



Part of the [Neurosciences Commons](#)

---

### Citation of this paper:

Popp, Nicola J.; Yokoi, Atsushi; Gribble, Paul L.; and Diedrichsen, Jörn, "The effects of habits on motor skill learning" (2018). *BrainsCAN Publications*. 2.  
<https://ir.lib.uwo.ca/brainscanpub/2>

## The effects of habits on motor skill learning

Nicola J. Popp<sup>1</sup>, Atsushi Yokoi<sup>2,3</sup>, Paul L. Gribble<sup>1,4,5,6</sup> & Jörn Diedrichsen<sup>1,7,8\*</sup>

<sup>1</sup>The Brain and Mind Institute, University of Western Ontario, Canada,

<sup>2</sup>Graduate School of Frontier Biosciences, Osaka University, Japan,

<sup>3</sup>Center for Information and Neural Networks (CiNet), NICT, Japan,

<sup>4</sup>Department of Psychology, University of Western Ontario, Canada,

<sup>5</sup>Department of Physiology & Pharmacology, Schulich School of Medicine & Dentistry, University of Western Ontario, Canada,

<sup>6</sup>Haskins Laboratories, USA,

<sup>7</sup>Department of Statistical and Actuarial Sciences, University of Western Ontario, Canada,

<sup>8</sup>Department of Computer Science, University of Western Ontario, Canada

### Acknowledgments

This work is supported by a James S. McDonnell Foundation Scholar award, a Natural Sciences and Engineering Council of Canada (NSERC) Discovery Grant (RGPIN-2016-04890) and the Canada First Research Excellence Fund (BrainsCAN) to J.D., a NSERC Discovery Grant (RGPIN 238338) and a Canadian Institutes of Health Research Grant (PJT-153447) to P.L.G. We thank Aaron L. Wong for helpful comments on earlier versions of this manuscript.

### Correspondence address

Jörn Diedrichsen, The Brain and Mind Institute, University of Western Ontario, London, Canada. [jdiedric@uwo.ca](mailto:jdiedric@uwo.ca)

### Author contributions

N.J.P. and J.D. designed the experiment. N.J.P., A.Y. and J.D. programmed the experiment. N.J.P. collected the data and analyzed the data together with J.D., N.J.P., J.D., and P.L.G. wrote the manuscript.

### Conflict of interest

The authors declare no conflict of interest.

## Abstract

1 Skill learning involves the formation of stable motor patterns. In musical and athletic  
2 training, however, these stable patterns can also impede the attainment of higher levels  
3 of performance, and hence constitute a motor habit. We developed an experimental  
4 paradigm to induce a specific motor pattern in a sequence production task and  
5 investigated how it affected subsequent optimization over a 3-week training period.  
6 Participants initially practiced small segments of 2 to 3 finger movements, which were  
7 then combined to form longer sequences. This initial training induced a persistent  
8 chunking behavior, with shorter inter-press-intervals within a chunk and longer ones at  
9 chunk boundaries. We were able to induce chunking that was either beneficial or  
10 detrimental to performance, and could show that the degree to which these detrimental  
11 chunk structures were maintained, predicted lower levels of final performance. We also  
12 identified two optimization processes by which participants overcame the detrimental  
13 motor habits.  
14

## Introduction

15 Humans are capable of astonishing feats of motor skill in athletics, musical performance  
16 and dance. But what does it take to become an expert? The first obvious factor is  
17 practice: it is estimated that 10,000 hours of training are necessary to develop high-level  
18 motor skills (Ericsson et al., 1993; Hayes, 2013). Perhaps the motor system simply  
19 needs to gather a large amount of experience to optimize the motor commands that are  
20 necessary to achieve skilled movement. Thus, given enough practice, motor expertise  
21 may emerge automatically.  
22

23 However, simply practicing for many hours will not automatically lead to expert  
24 performance. There are numerous examples in which motor skill acquisition is slow or  
25 fails (Haith & Krakauer, 2018). This is sometimes attributed to the formation of habits:  
26 automatic (Hélie, Waldschmidt, & Ashby, 2010; Moors & De Houwer, 2006) and highly  
27 entrenched behavioral patterns that resist change through retraining (Ashby, Ell, &  
28 Waldron, 2003; Graybiel & Grafton, 2015; Hardwick, Forrence, Krakauer, & Haith, 2017;  
29 Jager, 2003; Seger & Spiering, 2011).

30 Animal models have been integral to the study of habit formation and its neural  
31 underpinnings (Jog, Kubota, Connolly, Hillegaart, & Graybiel, 1999; Robbins & Costa,  
32 2017; Smith & Graybiel, 2014, 2016; Wickens, Horvitz, Costa, & Killcross, 2007).  
33 However, the majority of animal experiments investigating this concept have focused on  
34 habits in the context of action selection – i.e. choosing *what* action to perform. In  
35 contrast, our paper addresses the question of habits in motor performance – i.e. habits  
36 in *how* to perform a chosen action. For example, a tennis player could have a habit in  
37 action selection, whereby she always chooses a forehand over a backhand to return a  
38 serve. Independently, she could have a motor habit, whereby she executes the  
39 forehand without rotating her hips.

40 Critical to the definition of a habit is that the behavior is maintained, even though  
41 it is no longer adaptive (Adams, 1982; Dezfouli & Balleine, 2012; Dickinson, 1985). Most  
42 experiments, therefore, demonstrate the existence of a habit by teaching subjects a  
43 behavior under one reward contingency and show that it persists even when the reward  
44 contingency switches (Ashby et al., 2003; Smith & Graybiel, 2013b). In a similar way,  
45 we define motor habits here as a stable way of performing an action that is maintained,  
46 even if it prevents optimal performance. This does not imply that motor habits always  
47 *have to be* dysfunctional. Their automatic nature can be beneficial by increasing  
48 processing speed (Hardwick et al., 2017) or by reducing cognitive load (Haith &  
49 Krakauer, 2018; Hélie & Cousineau, 2011). Thus, habits can be either functional or  
50 dysfunctional, but their defining criterion is that they are resistant to change even under  
51 circumstance where a change would be beneficial.

52 To investigate the influence of habit formation on motor skill learning, we  
53 introduce a novel experimental paradigm that enables us to induce beneficial and  
54 detrimental motor habits and to test whether participants can overcome these habits  
55 with practice. As an experimental model of skill acquisition, we used the discrete  
56 sequence production task (DSP), in which participants perform an explicitly known  
57 series of finger presses as fast as possible (Abrahamse, Ruitenberg, de Kleine, &  
58 Verwey, 2013; Verwey, 2001). Learning in this task depends on both cognitive and  
59 motor processes (Diedrichsen & Kornysheva, 2015; Wong, Lindquist, Haith, &

60 Krakauer, 2015). Initial performance relies strongly on forming a declarative memory of  
61 the sequence and can, therefore, be sculpted through explicit instructions (de Kleine &  
62 Verwey, 2009; Verwey, Abrahamse, & de Kleine, 2010; Verwey, Abrahamse, &  
63 Jiménez, 2009). An important determinant of the structure of declarative memory is  
64 “chunking” – the process by which participants separate a long sequence into smaller  
65 subsets (Verwey, 1996; Verwey & Dronkert, 1996) to aid memorization and improve  
66 performance by reducing memory capacity demands (Halford, Wilson, & Phillips, 1998;  
67 Miller, 1956; Wymbs, Bassett, Mucha, Porter, & Grafton, 2012).

68         The structure of the declarative memory representation of a sequence may then  
69 constrain subsequent motor optimization processes (Bo & Seidler, 2009; Seidler, Bo, &  
70 Anguera, 2012). For example, it has been suggested that sequential movements may  
71 be optimized within a chunk, but not across chunk boundaries (Ramkumar et al., 2016).  
72 We hypothesized therefore that the initial cognitive chunking of the sequence influences  
73 the learning of execution-related skills in subsequent motor training. That is, we tested  
74 the hypothesis that cognitive chunking can evolve into a motor habit.

75         We trained participants to perform the same set of 7 sequences, each consisting  
76 of 11 isometric keypresses. Training occurred on 14 separate days, spread over 3  
77 weeks. In the induction phase (Fig. 1a) we imposed a specific chunk structure by  
78 instructing participants to practice a set of 2-3 digit chunks. They then learned the 11-  
79 digit sequences as being composed of four of the pre-trained 2-3 digit chunks. We  
80 induced chunk structures that were designed to be either aligned or misaligned with  
81 biomechanically easy or difficult finger transitions within the sequence and therefore  
82 were predicted to be beneficial or detrimental to performance. Each participant learned  
83 3 sequences using the misaligned chunk structure and 3 distinct sequences with the  
84 aligned chunk structure (Fig. 1d). To test for patterns of spontaneous chunking, a  
85 separate group of participants (control) was trained on the same sequences but did not  
86 receive chunk training and instead practiced the complete sequences during the initial  
87 training.

88         In the subsequent optimization phase (Fig. 1a), participants were instructed to  
89 improve their performance through practice. During this phase, we did not make any

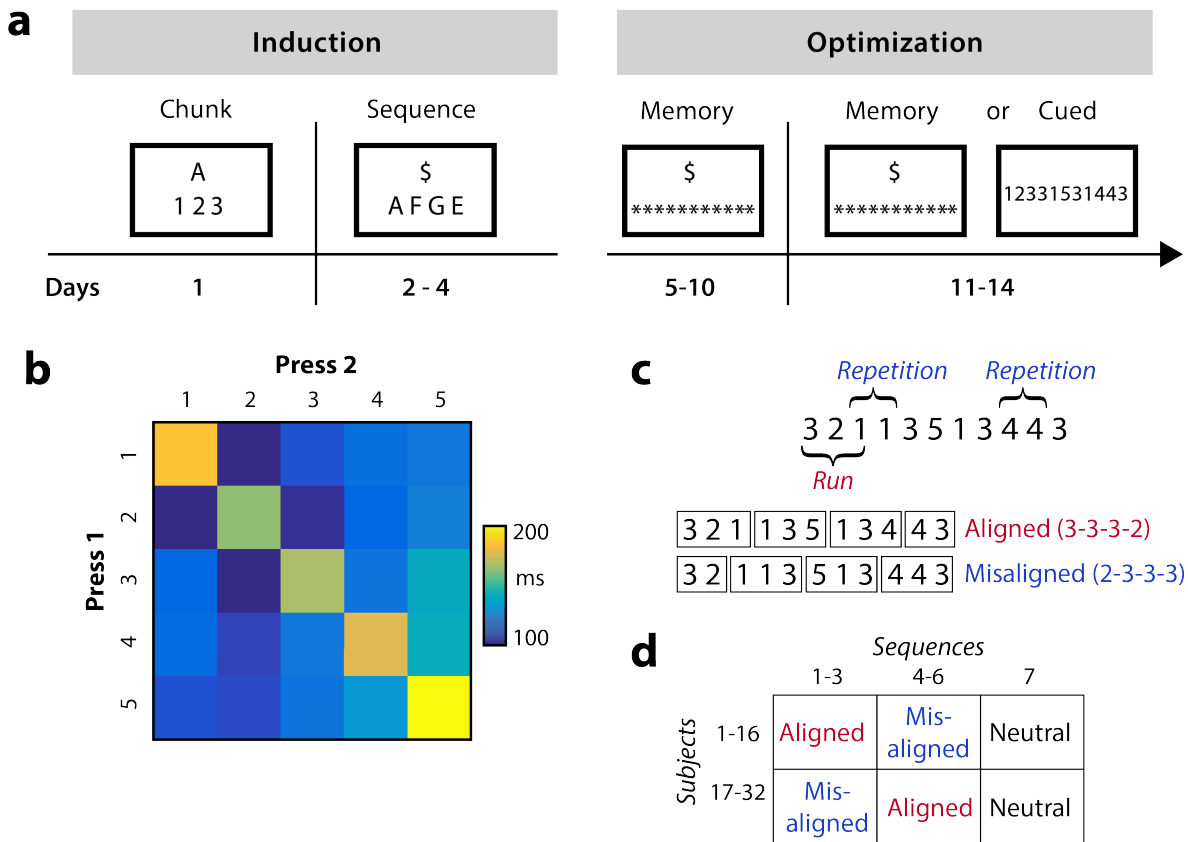
90 further mention of chunks (see Methods). Because participants performed the same  
91 sequences (but differed in the chunk structures with which they had learned the  
92 sequences), we could draw strong inferences about whether their performance was  
93 dictated by biomechanical demands (which were identical across participants) or  
94 whether it was affected by the chunk structure that was imposed during the induction  
95 phase. Using a Bayesian model, we estimated changes in chunk structure. This allowed  
96 us to investigate three questions: First, can explicit instructions at the beginning of  
97 training lead to stable motor performance patterns? Second, to what degree are these  
98 patterns maintained if they impede the participants' ability to reach skilled performance  
99 – i.e. can these patterns be considered a motor habit? Finally, what are the optimization  
100 processes that allow participants to overcome bad habits (misaligned chunk structures)  
101 through practice?

## 102 **Results**

103 Over 15 days we trained 32 participants to produce sequences of 11 isometric  
104 keypresses from memory on a keyboard-like device. Participants were rewarded with  
105 points for executing sequences as fast as possible while keeping the proportion of  
106 incorrect keypresses in each block of trials below 15%. We maintained the participants'  
107 motivation by gradually decreasing the movement time (MT) threshold at which they  
108 received points.

109 We manipulated how participants memorized the sequences by splitting the  
110 sequences into several chunks, each composed of 2-3 keypresses. We wanted to test  
111 whether the different ways of chunking (hereafter “chunk structures”) imposed in the  
112 induction phase (Fig. 1a) would affect performance optimization in the subsequent two  
113 weeks of training. On the first day, we trained participants to produce eleven 2-3 press  
114 chunks in response to a visually presented letter. For example, “A” corresponded to the  
115 chunk “3,2,1” (middle finger, index finger, thumb). At the end of the first day, participants  
116 could reliably produce the chunks from memory with an average accuracy of 92.7%. On  
117 days 2-4, we combined these chunks to form 7 different 11-press sequences. Each  
118 sequence was associated with a specific character symbol (e.g. \$ see Supp. Table 1).

119 At the end of day 4, participants were able to recall all sequences from memory using  
 120 the sequence cue with an accuracy of 92.5%.



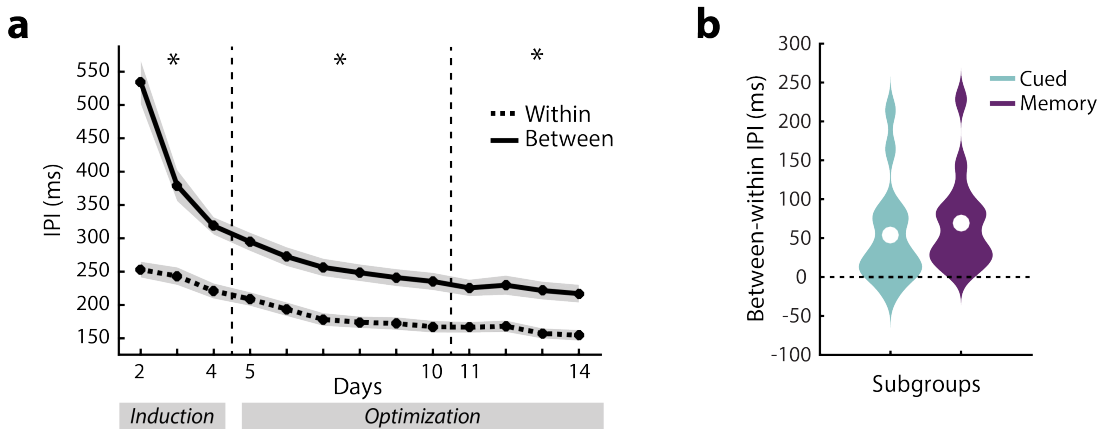
**Figure 1. Experimental procedure.** (a) Experimental timeline depicting the training at each stage. In the induction phase participants memorized chunks and sequences. In the optimization phase participants trained to perform these sequences as fast as possible from memory. In the last week of training, half of the participants were directly cued with the sequence, while the other half performed the sequences from memory. (b) Data from an independent dataset, in which participants performed all possible combinations of 2 and 3-digit transitions. Matrix indicates the median inter-press interval (IPI) to produce the transition between pairs of keypresses. (c) Top: Example sequence containing a 3-digit run and two digit repetitions. Bottom: The sequence was instructed using two possible chunk structures. In the aligned structure, the chunk boundaries fell between repetitions, in the misaligned structure the chunk boundary broke up the run. (d) The assignment of chunk structures to sequences was counterbalanced between participants.

## 121 **Chunk induction induces a stable motor pattern**

122 To assess whether the imposed chunk structure influenced participants' motor behavior,  
123 we examined inter-press time intervals (IPIs). An increased IPI is commonly taken as a  
124 sign of a chunk boundary, as the cognitive processes (memory recall, action selection)  
125 involved in switching from one chunk to another require additional time (Verwey, 1999;  
126 Verwey et al., 2010). Hence, we would expect our participants to exhibit shorter IPIs  
127 between keypresses that belonged to a chunk imposed during day 1 (within-chunk IPIs)  
128 and larger IPIs for the boundaries between chunks (between-chunk IPIs). We indeed  
129 found significantly longer between-chunk IPIs compared to within-chunk IPIs in the first  
130 few days of training (Fig. 2a: days 2-4:  $t_{(31)} = 7.728$ ,  $p = 5.098e-09$ ).

131 In the optimization phase (day 5-14), we ceased to cue sequences using the  
132 alphabetic letters associated with the chunks. Instead, participants were asked to recall  
133 the sequences from memory in response to the symbolic sequence cues (e.g. "\$").  
134 From this point forward, no further reference to the imposed chunk structure was made.  
135 Across days 5-10, the difference between the within- and between-chunk IPIs remained  
136 stable;  $t_{(31)} = 7.165$ ,  $p = 2.351e-08$  (Fig. 2a). Importantly, this difference cannot be  
137 attributed to biomechanical difficulty of the finger transitions. The within-chunk IPIs for  
138 one group were the between-chunk IPIs for the other group and vice versa; IPIs that  
139 were within-chunk for all participants (e.g. the first and last IPI of a sequence) were  
140 excluded from this analysis. In summary, even though after day 4 we cued the  
141 sequences only with a single symbol, participants persisted in performing the  
142 sequences consistent with the chunk structures imposed early in training.





**Figure 2. Within- vs. between-chunk inter-press intervals (IPIs).** (a) Time course of IPIs that were within an instructed chunk (dashed line), or on the boundary between chunks (solid line). Asterisks indicate significant differences between average within- and between-chunk IPIs in the corresponding week (separated by dashed lines). Shaded area denotes between-subject standard error. (b) Difference of between- and within-chunk IPIs in the last week of training, split by whether participants had to recall the sequences from memory or were cued with the sequence numbers. Violin plots indicate distribution of individual participants, white circles indicate means.

143 In the last four days of training (days 11-14) we tested whether the persistence of  
144 the imposed chunk structure reflected a motor habit or whether it reflected memory  
145 recall. We split each experimental group into two subgroups: half of the participants  
146 continued to perform the sequences from memory, while the other half were cued using  
147 the numbers (Fig. 1a) that indicated the necessary keypresses, therefore removing any  
148 memory recall demands. Both the memory ( $t_{(15)} = 4.865$ ,  $p = 2.059e-04$ , Fig. 2b) and the  
149 cued subgroup ( $t_{(15)} = 3.403$ ,  $p = 0.004$ ) showed a significant difference between the  
150 within- and between-chunk IPIs and there was no reliable difference between the two  
151 subgroups in this effect ( $t_{(30)} = -0.749$ ,  $p = 0.460$ ). Thus, removing the requirement for  
152 memory recall did not abolish chunking. Because none of the subsequent analyses  
153 showed any significant difference between the two subgroups, we will report their  
154 combined results for the remainder of the article. Overall, these results suggest the

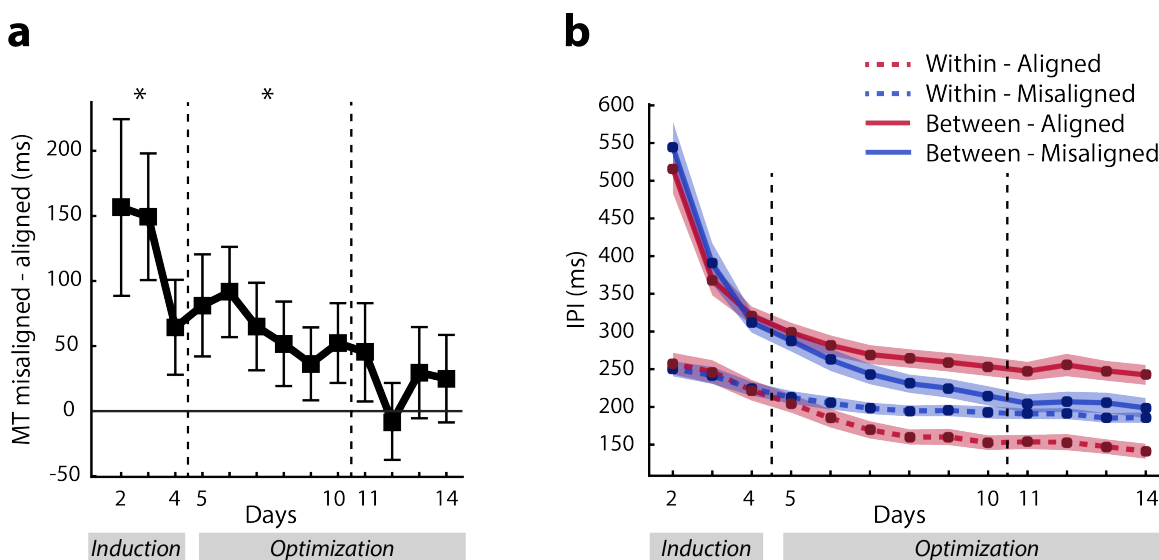
155 explicit chunk training early in learning established a stable performance pattern that  
156 outlasted 10 days of subsequent practice.

### 157 **Misaligned chunk structure impairs performance**

158 To show that this initial instruction led to the emergence of a motor habit (as  
159 defined above), we needed to not only show that this initial instruction induced a stable  
160 temporal pattern of IPIs, but also that this pattern was maintained when it leads to  
161 slower execution speeds than other patterns. We therefore designed chunk structures  
162 that were predicted to be either beneficial or detrimental to performance. These  
163 predictions were based on a separate experiment (see Methods), in which we trained 7  
164 participants on all possible 2 and 3 keypress combinations over the course of 3 days  
165 and measured their execution speed. Transitions between two adjacent fingers could be  
166 performed faster than two repeated presses of the same finger ( $t_{(6)} = 13.965$ ,  $p =$   
167  $8.404e-06$ ; see Fig. 1b). Given that the 2-3 press sequences hardly taxed the cognitive  
168 system, these results can be taken as a characterization of the biomechanical  
169 constraints of our specific task (see Methods).

170 We used these results to design two different ways of separating the sequences into  
171 chunks. In one case, we placed chunk boundaries so that they were **aligned** with digit  
172 transitions that were performed more slowly (as measured in the independent dataset) –  
173 i.e. they were preferentially placed between digit repetitions (Fig. 1c). The time required  
174 to perform these difficult finger transition can therefore simultaneously be used to recall  
175 a next chunk, which should benefit overall performance. In the **misaligned** chunk  
176 structure, we placed chunk boundaries at digit transitions that can be performed quickly,  
177 thereby breaking up transitions between adjacent fingers or runs (Fig. 1c). Participants  
178 would, therefore, have to slow down their performance at these fast transitions to recall  
179 the next chunk, which should slow overall performance. Each participant learned 3 of  
180 the 7 sequences with a misaligned chunk structure and 3 sequences with an aligned  
181 chunk structure, with the assignment counterbalanced across groups. For the last  
182 remaining sequence, both ways of chunking were predicted to be equally fast, as both  
183 possible chunk structures were aligned with the biomechanical requirements (neutral  
184 chunk structure, Fig. 1d & Supp. Table 1).

185 We predicted that training on the misaligned chunk structure would lead to poorer  
186 performance. To quantify performance, we used movement time (MT), the time between  
187 the first finger press and the last finger release. Indeed, in the induction phase (days 2-  
188 4), the sequences instructed with the misaligned chunk structure were performed slower  
189 than the sequences instructed with the aligned chunk structure (one-sample t-test:  $t_{(31)} =$   
190 2.693,  $p = 0.006$ ; Fig. 3a). Hence, we were not only able to manipulate *how* participants  
191 performed a sequence, but also *how well* they could perform it. This difference was  
192 maintained in the second week of training (days 5-10:  $t_{(31)} = 2.313$ ,  $p = 0.014$ ).  
193 Importantly, this shows that the stable pattern of IPIs indeed constitutes a motor habit.



**Figure 3. Change in chunk structure and performance for aligned and misaligned instructed sequences. (a) Differences in movement time (MT) between sequences instructed with an aligned or misaligned chunk structure. Asterisk indicates a significant difference from 0 (no difference). (b) Within- or between-chunk IPIs across training days, separated by whether they were in the aligned or misaligned instructed sequences. Error bars denote between-subject standard error.**

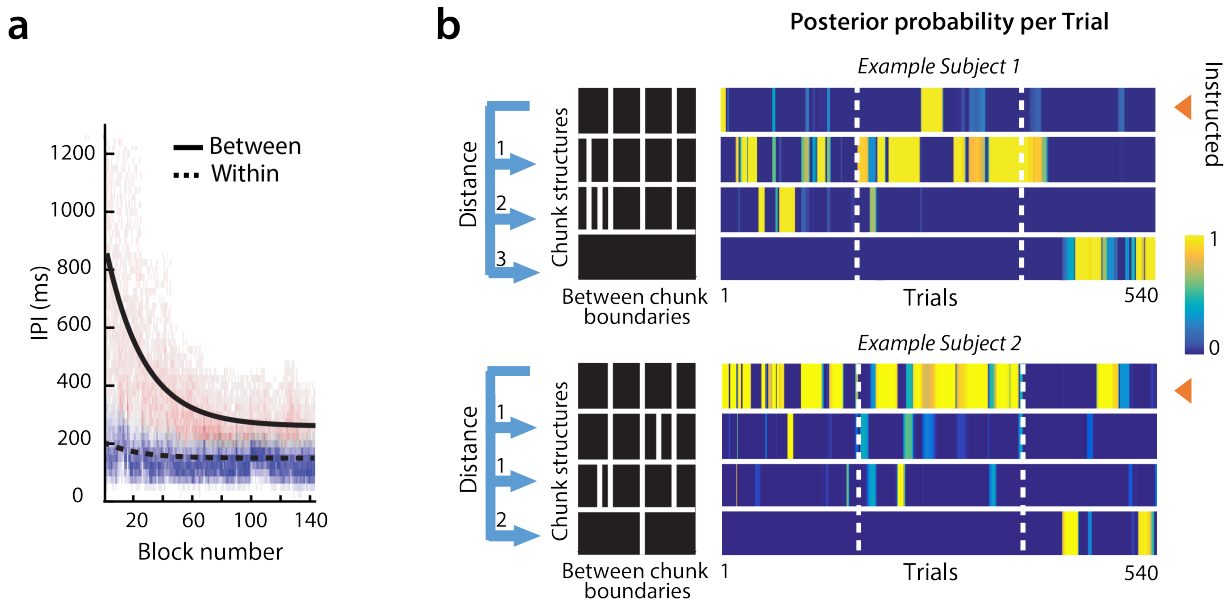
## 194 **Misaligned chunk structure is changed more rapidly**

195 Interestingly, the difference in performance between the sequences instructed with the  
196 aligned compared to the misaligned chunk structure was no longer significant in the last  
197 four days of training (days 11-14:  $t_{(31)} = 0.764$ ,  $p = 0.225$ ; Fig. 3a). This suggests that  
198 participants were able to overcome the “bad” habit of a misaligned chunk structure to  
199 some degree. To investigate this, we separated the IPI analysis (Fig. 2a) by whether the  
200 intervals came from sequences that were instructed using an aligned or misaligned  
201 structure. While the difference between within- and between-chunk IPIs for “aligned  
202 sequences” was stable over the entire training period, the difference for the “misaligned  
203 sequences” disappeared in the last four days of training (Fig. 3b). The three-way  
204 interaction between day x within/between x instruction (aligned or misaligned) was  
205 significant ( $F_{(12,372)} = 19.790$ ,  $p < 1e-16$ ). Thus, in the last four days of training  
206 participants seemed to diverge from the misaligned chunk structure while maintaining  
207 the aligned chunk structure.

## 208 **Tracking changes in chunking**

209 A disadvantage of the above analysis, however, is that we cannot discern how  
210 participants restructured their chunking and whether they completely abandoned the  
211 misaligned chunk structure. For a clearer understanding of how participants changed  
212 their chunk structure, we used a Bayesian model to estimate the probability of each  
213 possible chunk structure, given the observed series of IPIs, on a trial-by-trial basis  
214 (Acuna et al., 2014). The state variable in this Hidden Markov Model indicates which of  
215 the 1023 possible chunk structures is present on each trial. Using the expectation-  
216 maximization (EM) algorithm (Dempster, Laird, & Rubin, 1977; Welch, 2003), we  
217 simultaneously estimated the 9 free parameters of the model (for details see Methods),  
218 and the posterior probability for each possible chunk structure on each trial. We  
219 accounted for the effects of biomechanical difficulty by regressing out the patterns of  
220 IPIs across finger transitions (Fig. 1b) from each block before modeling. Importantly, our  
221 version of the model could capture separate learning-related changes to the within- and  
222 between-chunk intervals (Fig. 4a). Our method, therefore, allowed us to estimate  
223 participants’ chunk structure independently of the overall speed of performance. We  
224 confirmed this independence using simulated data (see Methods).

225           Figure 4b shows two examples of individual participants and sequences. In the  
226 first panel, the participant chunked the sequence according to the initial instructions at  
227 first, then inserted 1 or 2 additional chunk boundaries, and at the end of training  
228 performed the sequence as a single chunk. In comparison, the other participant  
229 maintained the instructed chunk structure for most of the training period.



**Figure 4. Probabilistic chunking model fitted to example participant data. (a)**

The change of within- and between-chunk IPIs were modeled using two separate exponential functions across training. The density plot shows individual IPIs, with the color indicating the probability of a between- (pink) or within-chunk interval (blue). **(b)** Posterior probability for two example participants (for one sequence per participant) over the course of the experiment. Only the 4 most likely chunk structures out of the 1023 possible structures are shown. The color scale indicates the posterior probability of a given chunk structure for each trial - with yellow indicating higher probabilities. The dashed vertical lines indicate the boundaries between training phases (Days 2-4; 5-10 & 11-14). The black box (left) indicates the chunk boundaries as white lines within the 11-press sequence (max. 10 boundaries) for the chosen chunk structures. The first row indicates the instructed chunk structure (arrow). The other three rows illustrate other chunk structures that were highly probable at some point during the experiment. The distance measure expresses how many chunks need to be added or removed to transform one structure (in this case the instructed chunk structure) into the other.

## 230 **Movement towards a single chunk structure**

231 To characterize changes in chunk structure, we first defined a metric that quantified the  
232 difference between two chunking structures: we counted the number of chunk  
233 boundaries that differ – i.e. the number of chunks that needed to be split or merged to  
234 transform one chunk structure into the other (Fig. 4b - distance). We then used this  
235 measure to calculate the distance between the chunk structure used by the participant  
236 and three reference structures of interest: (1) the aligned-, (2) misaligned, and (3) a  
237 structure that consisted of a single chunk. These distances defined a coordinate system  
238 that enabled us to visualize changes in chunk structure. We then projected participants'  
239 estimated chunk structure into this space (Fig. 5a). On the horizontal axis, we plotted  
240 the expected distance of participants' chunk structure to the single-chunk structure.  
241 Given the definition of our distance, this measure simply counts the number of chunk  
242 boundaries. On the vertical axis, we plotted how close the estimated chunk structure  
243 was to the aligned and misaligned chunk structure.

244 Previous literature has suggested that participants group smaller chunks together  
245 with training (Kuriyama, Stickgold, & Walker, 2004; Ramkumar et al., 2016; Sakai,  
246 Kitaguchi, & Hikosaka, 2003; Song & Cohen, 2014; Verstynen et al., 2012; Verwey,  
247 1996; Wymbs et al., 2012), a process that may help to improve performance  
248 (Abrahamse et al., 2013; Ramkumar et al., 2016; Verwey, 1999, 2001; Verwey et al.,  
249 2010; Verwey & Wright, 2014). In nearly all previous studies, however, the estimated  
250 number of chunks is biased by the overall movement speed. Using a modified  
251 probabilistic model (see Methods), we were able to disambiguate the two and critically  
252 test this assumption. We estimated the number of chunk boundaries for each participant  
253 averaged across sequences (the neutral sequence was excluded). Interestingly, on the  
254 2<sup>nd</sup> day, participants separated sequences into more chunks than the 4 chunks we  
255 instructed (Fig. 5a,  $t_{(31)} = 4.224$ ,  $p = 0.0002$ ). This tendency continued on day 3, where  
256 participants tended to subdivide the sequences into even smaller chunks (Fig. 5b; day 2  
257 vs. 3:  $t_{(31)} = 2.023$ ,  $p = 0.052$ ). After day three the number of chunk boundaries  
258 decreased as shown by a significant effect of day in a repeated measures ANOVA  
259 ( $F_{(11,341)} = 11.710$ ,  $p < 1e-16$ ). However, even in the last phase of training, participants  
260 performed the sequences with an average of 2.9 chunk boundaries (we instructed 3

261 chunk boundaries). Thus, while there was a clear tendency towards merging chunks  
262 after an initial increase, participants did not perform the sequence as a single chunk,  
263 even after 3 weeks of practice.

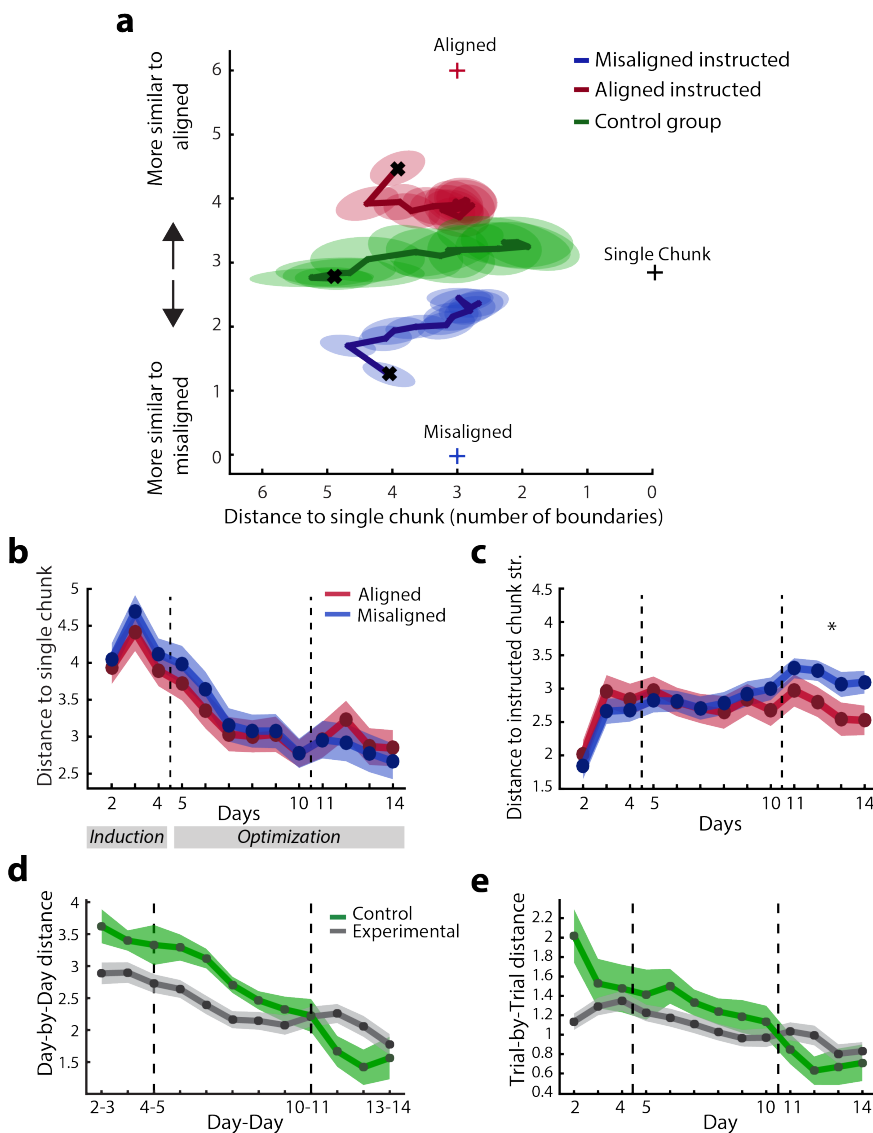
#### 264 **Participants abandoned the misaligned chunk structure to a greater degree**

265 Next, we probed how much participants diverged from the initial instructions.  
266 Participants slowly changed their chunk structure for both aligned and misaligned  
267 instructed sequences with training. The average distance to the instructed chunk  
268 structure increased systematically over time (repeated measures ANOVA, effect of day,  
269  $F_{(12,372)} = 7.055$ ,  $p < 1e-16$ , Fig. 5c).

270 Consistent with our IPI analysis (Fig. 3b), we observed that participants  
271 abandoned the misaligned chunk structure to a greater degree than the aligned chunk  
272 structure (Day x Instruction interaction:  $F_{(12,372)} = 5.610$ ,  $p < 1e-16$ ). In the last four days  
273 of training, the sequences that were instructed with the misaligned chunk structure were  
274 more dissimilar to the misaligned chunk structure than the sequences that were  
275 instructed with the aligned chunk structure were to the aligned chunk structure:  $t_{(31)} =$   
276  $2.294$ ,  $p = 0.029$  (Fig. 5c). Additionally, we found a significant Day x Instruction  
277 interaction ( $F_{(12,372)} = 2.215$ ,  $p = 0.011$ ) for the distance to a single chunk (Fig. 5b),  
278 suggesting a stronger tendency towards performing a sequence as a single chunk when  
279 trained on the misaligned chunk structures. Together these results indicate that  
280 participants changed their chunking behavior more readily for sequences that were  
281 trained using the misaligned chunk structure than when trained using the aligned chunk  
282 structure.

283 Despite the divergence from the misaligned chunk structure with training, our  
284 analysis also revealed that participants did not overcome the influence of the instruction  
285 completely. In the third week, sequences produced after training with a misaligned  
286 chunk structure were still performed closer to the misaligned structure than to the  
287 aligned structure ( $t_{(31)} = 6.962$ ,  $p < 1e-16$ ). This shows that even training on misaligned  
288 chunk structures had a lasting influence on participants' motor behavior.





**Figure 5. Changes in chunk structure with learning.** (a) The average chunk structure over 13 days of practice for aligned (red) and misaligned (blue) instructed sequences for the experimental participants. The results of the control group are shown in green. The horizontal axis represents the distance to the single-chunk structure, i.e. the number of chunk boundaries. The vertical axis shows the distance to the aligned or misaligned chunk structure. The crosses indicate the positions of the three reference structures (aligned, misaligned and single). Ellipses denote the between-subject standard error. (b) Average distance of participants' chunk structure to the single chunk structure across days. (c) Distance to the instructed chunk structure. (d) Day-by-day changes in chunk structure. (e) Trial-by-trial changes in chunk structures within each day. Error bars indicate between-subject standard error.

## 289 **Chunk structure “crystallizes” with training**

290 Would longer training allow participants to completely overcome the influence of the  
291 instruction and to perform all sequences as a single chunk? Although experiments with  
292 longer training are necessary to provide a definitive answer, our data indicate that this  
293 process, if occurring, may take a very long time. The amount of change in the chunk  
294 structure for each sequence reduced dramatically in the last week of training,  
295 suggesting that a stable motor habit formed. This phenomenon is akin to the  
296 development of an invariant temporal and spectral structure in bird-song, a process that  
297 has been termed “crystallization” (Brainard & Doupe, 2002). To estimate crystallization,  
298 we calculated the distance between the chunk structures from one day to the next (Fig.  
299 5d) and within each day from one trial to the next (Fig. 5e). The analysis was performed  
300 separately for each sequence and participant. Overall, both the day-to-day distance  
301 ( $F_{(11,330)} = 18.794, p < 1e-16$ ) and the trial-by-trial distance decreased significantly  
302 across training days ( $F_{(12,456)} = 13.245, p < 1e-16$ ). Therefore, participants appeared to  
303 settle onto a stable pattern in the last week. Consequently, additional training would  
304 likely only lead to slow changes in their chunk structure.

305 In summary, our analyses provide a clearer picture of how chunking changes  
306 with learning. Firstly, in line with previous research (Kuriyama et al., 2004; Ramkumar et  
307 al., 2016; Sakai et al., 2003; Song & Cohen, 2014; Verstynen et al., 2012; Verwey,  
308 1996; Wymbs et al., 2012) participants gradually moved towards performing the  
309 sequence as a single chunk by dividing the sequence into fewer chunks. Secondly,  
310 participants diverged from the instructions over time with a quicker deviation from the  
311 misaligned chunk structure. Nevertheless, they did not completely overcome the initial  
312 instruction, nor did they perform the sequences as a single chunk at the end of training.  
313 Considering that the chunk structure crystallized in the last four days of training, these  
314 results demonstrate the formation of a stable motor habit that is still influenced by the  
315 initial instruction.

## 316 **Spontaneously emerging chunk structures**

317 To investigate how participants would spontaneously chunk the sequences, we tested  
318 an additional control group (N=8), which did not receive any explicit chunk training.

319 Rather, participants were presented with the entire sequences on the first day and had  
320 to memorize them without any reference to chunks (see Methods for details). Even  
321 though memorization was more difficult, the control group did not differ significantly from  
322 the experimental groups in terms of their explicit knowledge on day 4 ( $t_{(36)} = 1.288$ ,  $p =$   
323  $0.206$ ), or in their overall MT across training (main effect of group:  $F_{(1,38)} = 0.101$ ,  $p =$   
324  $0.753$ ; interaction between group and day ( $F_{(1,38)} = 1.387$ ,  $p = 0.168$ ).

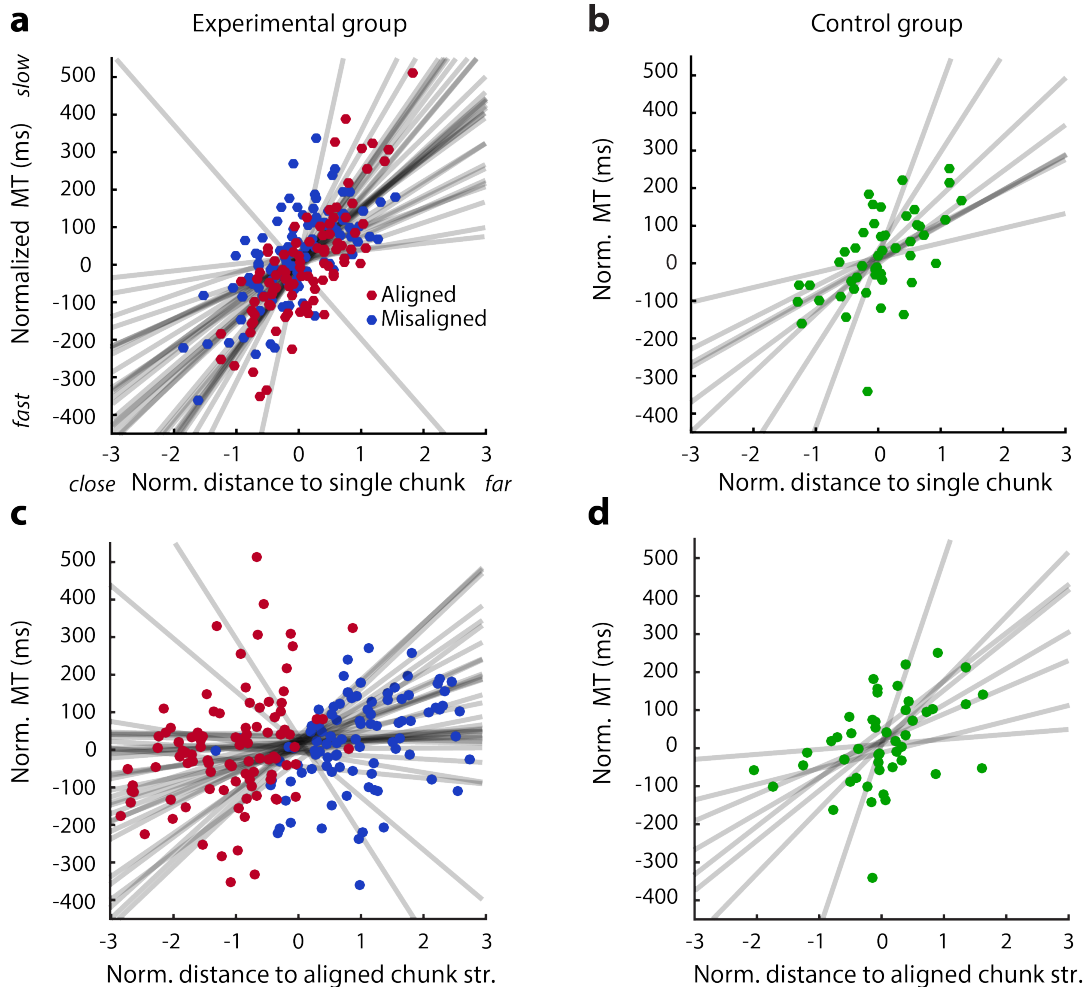
325         Similar to the experimental groups, the control group initially subdivided the  
326 sequences into small chunks and then slowly combined them into larger chunks. The  
327 distance to a single chunk structure decreased significantly over days ( $F_{(12,84)} = 17.977$ ,  
328  $p < 1e-16$ ), and reached a level that was not statistically different from the experimental  
329 participants on the last day of training ( $t_{(38)} = -0.940$ ,  $p = 0.353$ ). Interestingly, on the first  
330 day, the control group performed the sequences closer to the misaligned chunk  
331 structure than to the aligned chunk structure ( $t_{(7)} = -2.799$ ,  $p = 0.027$ ). With training,  
332 participants then moved closer to the aligned chunk structure, as indicated by a  
333 significant change in the difference between the distance to the aligned and misaligned  
334 chunk structure across days ( $F_{(12,84)} = 5.303$ ,  $p < 1e-16$ ). The control group also showed  
335 clear crystallization over time (see Figure 5d&e). Compared to the experimental groups,  
336 control participants showed a higher day-to-day and trial-by-trial change in the  
337 beginning of training, which then reduced more quickly (Group x Day interaction; day-to-  
338 day:  $F_{(11,330)} = 3.780$ ,  $p = 4.003e-05$ ; trial-by-trial:  $F_{(12,456)} = 4.254$ ,  $p = 2.167e-06$ ). In  
339 summary, the control group showed similar behavioral patterns to the experimental  
340 participants, indicating that similar processes of habit formation are also at play in the  
341 absence of explicit instructions.

## 342 **Two optimization processes correlate with faster final performance**

343 How did these changes in chunk structure determine how fast participants could  
344 execute the sequences at the end of training? We first asked whether performing the  
345 sequences using larger chunks would facilitate performance. For each participant, we  
346 therefore regressed the MT for 6 sequences (last 4 days, excluding the neutral  
347 sequence) against the corresponding distance to the single chunk structure (Fig. 6a).  
348 The majority of the participants showed a positive relationship between the number of

349 chunks and MT: a one-sample t-test indicated that the individual slopes were  
350 significantly greater than 0 (Fig. 6a,  $t_{(31)} = 6.104$ ,  $p = 4.560e-07$ ). This significant  
351 relationship was also found for the control participants (Fig. 6b,  $t_{(7)} = 3.429$ ,  $p = 0.006$ ).  
352 Thus, performing the sequences with fewer chunks led to better performance.

353 Secondly, we investigated whether performing the sequences in alignment with  
354 the biomechanical constraints was also beneficial. We regressed the MT for 6  
355 sequences in the last four days of training against the corresponding distance to the  
356 aligned chunk structure. On average the individual slopes again were significantly  
357 greater than 0, both for the experimental (Fig. 6c;  $t_{(31)} = 2.220$ ,  $p = 0.017$ ), and control  
358 group (Fig. 6d,  $t_{(7)} = 2.720$ ,  $p = 0.015$ ). Finding a better way of chunking (for the same  
359 number of chunk boundaries) therefore also improved performance.

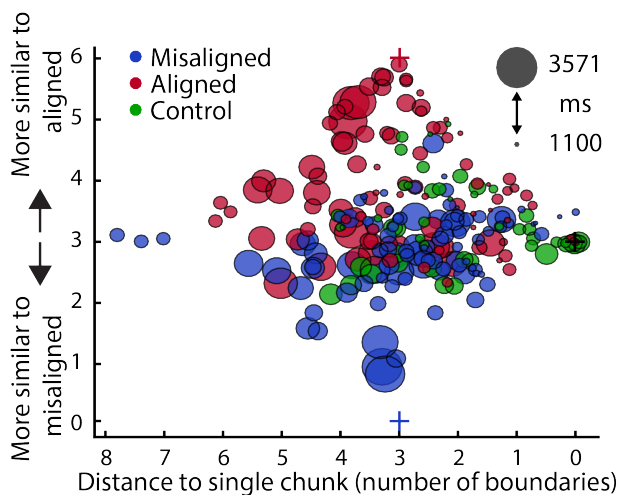


**Figure 6. Relationship between the distance to the aligned/single chunk structure and MT. (a)** Scatterplot between the normalized (per subj.) distance to a single chunk and normalized MT in the last four days of practice. A separate regression line is fitted to the 6 sequences for each participant. Red dots indicate sequences with aligned instructions, blue dots sequences with misaligned chunking instructions. **(b)** Same as **a** but for the control group. **(c&d)** same as **a** & **b** but for the normalized distance to the aligned chunk structure.

360 To visualize the relationship between the chosen chunk structure and the MT in  
361 the last four days of training, we plotted the MT and chunk structure for each sequence  
362 and participant in the 2-dimensional space defined in Fig. 5a (Fig. 7). This visualization

363 clearly shows the performance benefit from being closer to a single chunk as well as  
364 being closer to the aligned chunk structure.

365 Overall, these results suggest that the two optimization processes - joining  
366 chunks and aligning the remaining chunk boundaries with biomechanical constraints -  
367 positively influence participants' ultimate performance. Furthermore, sequences for  
368 which participants could not develop a better way of chunking were performed  
369 substantially slower.



**Figure 7. Relationship between chunking and speed (days 11-14).** The x-axis indicates the distance to a single chunk and the y-axis the relative distance to the two instructed chunk structures. Each data point indicates the average chunk structure and MT of a single sequence and participant in the last four days of training. The diameter of each circle represents the MT with larger circles indicating slower performance.

## The amount of musical training did not systematically affect chunk behavior

370 One possible confound is the amount of musical training that participants' were exposed  
371 to prior to the experiment. We found that participants with piano experience (55%)  
372 performed the sequences faster compared to the non-experienced participants ( $t_{(38)} =$   
373  $6.297, p = 2.227e-07$ ). This is perhaps not surprising, given the similarity of our task with  
374 playing the piano. Furthermore, the number of practice years significantly correlated  
375 with MT ( $t_{(38)} = -3.850, p = 4.401e-04$ ). Importantly, however, the amount of participants'  
376 prior musical experience neither influenced the distance to the instructed chunk  
377 structure in the last week of training ( $t_{(30)} = -0.291, p = 0.773$ ; practice years:  $t_{(30)} =$   
378  $0.059, p = 0.954$ ) nor the distance to a single chunk ( $t_{(38)} = -0.602, p = 0.551$ ; practice  
379 years:  $t_{(38)} = -0.380, p = 0.706$ ). Therefore, musical training did not seem to have a  
380 qualitative influence on participants' chunking behavior.

## Discussion

381  
382 In this study, we utilized chunking as a tool to investigate the role of motor habits  
383 in skill learning. We influenced the structure of the initial declarative sequence  
384 representation by manipulating how participants memorized them (Park, Wilde, & Shea,  
385 2004). By experimentally imposing two different chunk structures on the same physical  
386 sequence, we could make causal inferences on the effects of cognitive chunking on  
387 motor skill development. This is an important advance over previous observational  
388 studies (Ramkumar et al., 2016; Wright, Rhee, & Vaculin, 2010; Wymbs et al., 2012),  
389 which did not experimentally control how participants chose to chunk the sequence.

390 This paradigm yielded three main results. First, consistent with previous studies  
391 (de Kleine & Verwey, 2009; Verwey et al., 2010, 2009; Verwey & Dronkert, 1996), our  
392 data demonstrate that a stable chunking pattern can be induced through cognitive  
393 manipulations during sequence learning. Importantly, participants did not completely  
394 overcome this imposed chunk structure, even after 2 weeks of additional training.  
395 Participants' chunk structure crystallized towards the end of training, making it unlikely  
396 that the influence of the initial instruction would disappear completely with longer  
397 practice. Finally, the chunking structure remained stable, even when the task changed  
398 from a memory-guided to a stimulus-guided task. Thus, the initial instruction led to the

399 formation of specific motor patterns that were still clearly measurable after three weeks  
400 of training.

401         Second, we tested whether this stable pattern of chunking could be considered a  
402 motor habit. To do so, we designed two different ways of instructing the sequence, one  
403 aligned and the other misaligned with its biomechanical requirements. This manipulation  
404 either facilitated or impeded performance in the first two weeks of practice. We could  
405 show that participants did not overcome the misaligned structure completely, even  
406 though it was detrimental to their performance. Thus, the stable chunking pattern meets  
407 the requirements (as laid out in our definition) for being called a motor habit. Therefore,  
408 we believe that studying sequential chunking can provide valuable insights into the  
409 neural systems underlying motor habits. Indeed, it has recently been suggested that  
410 chunking plays an integral role in the formation and expression of habits (Dezfouli,  
411 Lingawi, & Balleine, 2014; Graybiel, 2008) and is neurally represented in the dorsal  
412 lateral striatum as action “start and stop signals” (Barnes, Kubota, Hu, Jin, & Graybiel,  
413 2005; Graybiel, 1998; Jin, Tecuapetla, & Costa, 2014; Smith & Graybiel, 2013a, 2014).

414         Finally, our results also indicate that the “bad” habit was not completely  
415 immutable. Participants were able to modify the misaligned chunk structure, and did so  
416 more rapidly than the aligned chunk structure. As a consequence, the performance  
417 detriment imposed by the misaligned instruction was no longer significant on the group  
418 level in the last week of training.

419         We identified two ways by which participants overcame the limitation induced by  
420 the bad habit. After initially breaking up the instructed sequences into 5 chunks on  
421 average, participants then joined chunks together, decreasing the amount of additional  
422 time spent on chunk boundaries. While previous research has suggested that the size  
423 of chunks increases with training, these findings were usually conflated with the overall  
424 speed of the action (Solopchuk, Alamia, Olivier, Ze, & Zénon, 2016; Song & Cohen,  
425 2014; Wymbs et al., 2012). Using a Bayesian model to assess chunk structure  
426 independent of performance, we could demonstrate a positive relationship between  
427 chunk concatenation and execution speed, both in the experimental as well as in the  
428 control group that developed a chunking strategy without explicit instructions. However,



429 our results also indicate that participants did not merge all sequences into a single  
430 chunk after 3 weeks of training, but on average subdivided each sequence into 3-4  
431 chunks. This suggests that the number of motor actions that can be joined in a single  
432 chunk may be limited (Langan & Seidler, 2011; Ramkumar et al., 2016; Verwey &  
433 Eikelboom, 2003; Verwey, Lammens, & Van Honk, 2002).

434 A second (and novel) finding was that participants also optimized performance by  
435 rearranging chunk boundaries in a biomechanically efficient manner. Consistent with  
436 our prediction based on the difficulty of individual digit transitions, placing chunk  
437 boundaries at digit transitions that take more time to execute resulted in faster  
438 performance for the full sequence. This optimization process was also observable in the  
439 control group that memorized and practiced sequences on their own terms.

440 Conversely, we observed that sequences that were not chunked in line with  
441 these strategies were performed slower. Therefore, if a more beneficial way of chunking  
442 was not found, participants still showed a detriment, suggesting that other learning  
443 mechanisms cannot fully make up for a persistent bad habit. Considering that  
444 participants' behavior became highly invariant in the last week of practice, we predict  
445 that some bad habit will remain and continue to influence participants' performance  
446 even after prolonged training.

447 In many motor tasks, there are numerous strategies and processes that can lead  
448 to excellent performance (Verstynen et al., 2012; Verwey et al., 2010). Examining  
449 Figure 7, one can observe that the shortest MTs were achieved anywhere in the space  
450 between the aligned and single chunk structure. Occasionally, good performance was  
451 also reached in other positions in chunk space. Participants adopted quite idiosyncratic  
452 chunk structures for each sequence at the end of training. This suggests that there may  
453 be considerable inter-individual variability in which technique works best for reaching a  
454 high level of performance. While we based our biomechanical constraint estimates on a  
455 representative sample, it might not perfectly reflect the constraints experienced by each  
456 participant. Alternatively, a number of ways of chunking may work approximately equally  
457 well, such that the cost of changing an established habit may outweigh the small benefit  
458 that could be gained from changing the structure. A similar observation can be made in

459 sports, where even top-ranked athletes use slightly different techniques to reach similar  
460 levels of performance. This variation may reflect individual biomechanical differences  
461 but also differences in instruction and training combined with subsequent habit  
462 formation.

463         The establishment of a novel experimental paradigm to study motor habit  
464 formation will allow us to explore ways to encourage learners to abandon or change a  
465 current habit. While our attempt at accelerating this process by changing the task from a  
466 memory-based to a stimulus-based task was ultimately not successful, there are many  
467 other techniques that would be possible. In many disciplines, teachers have developed  
468 ways to help students overcome bad habits. For instance, the Hanon piano exercise  
469 helps students play difficult passages of a musical piece by breaking up learned  
470 phrases into new chunks to explore different rhythms. Playing a passage slower than  
471 intended has also been suggested to break bad habits (Chang, 2004). Overall, the  
472 general advice from the diverse literature on learning piano is to diversify training and to  
473 practice with careful awareness to prevent bad habits from forming (Sadnicka,  
474 Kornysheva, Rothwell, & Edwards, 2018). This suggests that changes in context and  
475 the exploration of novel ways of moving can aid performance and the abandonment of  
476 bad habits.

477         While our experimental design enabled us to manipulate participants' habits in a  
478 laboratory setting, sequence learning only captures a specific aspect of motor skill  
479 acquisition. Nevertheless, similar persistence of habits has been observed in other  
480 motor learning paradigms (Diedrichsen, White, Newman, & Lally, 2010). In bimanual  
481 coordination, for instance, Park et al. (2013) showed that an acquired pattern stayed  
482 remarkably stable even over 8 years of not performing the task.

483         The current study shows that motor habits can be cognitively induced and can  
484 remain stable for extended time periods, even though they may prevent further  
485 performance gains. Furthermore, the study provides the first insights into the learning  
486 processes that are involved in overcoming a detrimental habit. Our experimental  
487 paradigm allows the further study of how we can aid the abandonment of bad habits.

488

## Methods

### 489 **Participants**

490 Forty neurologically healthy participants were recruited for the study (30 females; ages:  
491 19 to 33). Thirty-two were randomly split into two experimental groups and the  
492 remaining eight participants were assigned to the control group. All participants were  
493 right-handed based on the Edinburgh Handedness Inventory and completed informed  
494 consent. On average, participants had received 4.68 ( $\pm$  5.55) years of musical training,  
495 with 55% percent having played the piano for more than half a year. The study protocol  
496 was approved by the ethics board of the University of Western Ontario.

### 497 **Apparatus**

498 A custom-built five-finger keyboard was used. The keys were not depressible, but were  
499 equipped with a force transducer (FSG-15N1A, Sensing and Control, Honeywell)  
500 underneath each key which reliably measured participants' isometric force production  
501 with a repeatability of  $<0.02\text{N}$  and a dynamic range of 16N (Wiestler & Diedrichsen,  
502 2013; Wiestler, Waters-Metenier, & Diedrichsen, 2014; Yokoi et al., 2017). The signal  
503 was amplified and sampled at 200 Hz.

### 504 **Discrete sequence production task**

505 We used a discrete sequence production task (DSP), in which participants had to  
506 execute sequences of 2, 3, or 11 keypresses as fast as possible while keeping their  
507 error rate under 15% within each block. A trial was termed erroneous if participants  
508 pressed a wrong key anywhere within the sequence. No pause between presses was  
509 required and thus some co-articulation between fingers emerged with faster execution.  
510 A finger press was detected when the given finger produced a force above 3N.  
511 Subsequently, a finger was detected as released when the force of the same finger fell  
512 below 1.5N. In order for a subsequent finger to be registered as pressed the previous  
513 finger had to be released. This rule prevented participants to press with more than 2  
514 fingers at once. The force magnitude applied to each key was represented by 5 lines on  
515 an LCD monitor, with the height of the line representing the force in the corresponding  
516 finger. A white asterisk (memory-guided conditions) or digit (cued condition) for each  
517 finger press was presented above the lines. Immediately after the press threshold was

518 reached, participants received visually and auditory feedback. If the press was correct,  
519 the white cue changed its color to green and a sound was presented. If the press was  
520 incorrect, the cue turned red and a lower-pitch sound was presented. After each trial,  
521 participants received points based on their accuracy and movement time (MT; the time  
522 between the first press and last release). Correct sequences performed faster than the  
523 current MT threshold were rewarded with 1 point. MTs that were 20% faster than the  
524 threshold were rewarded with 3 points. Incorrect presses or MTs exceeding the  
525 threshold resulted in 0 points. At the end of each block, participants received feedback  
526 on their error rate, median MT, points obtained during the block, and total points  
527 obtained during the session. In order to maintain motivation, we adjusted the MT  
528 threshold by lowering the threshold by 500ms after each block in which the participants  
529 performed with an error rate of 15% or lower and had a median MT faster than the  
530 current threshold. This manipulation resulted in an approximately stable overall success  
531 rate of 61% SD: 13% (0.27% 1pt, 0.34 % 3pt) across the entire experiment.

### 532 **Study design**

533 To impose a particular way of chunking, we first had participants memorize and perform  
534 smaller 2-3 press chunks. These chunks were then combined to form the training  
535 sequences. All participants were trained on the same 7 sequences, each consisting of  
536 11 digit presses (see suppl. Table 1). Each participant completed 14 training sessions in  
537 total: one session per day across a 3-week period (excluding weekends). Each session  
538 lasted approximately 1 hour, excluding the two initial sessions and the last session  
539 which took 2 hours. Participants completed at least 10 blocks of 28 trials per training  
540 day. Each block comprised 4 repetitions of each of the 7 sequences. Each trial started  
541 with the visual presentation of the sequence to be executed and was completed once  
542 the participants pressed the amount of presented numbers (irrespective of whether the  
543 pressed keys were correct or incorrect).

544 To verify that the chunking behavior was influenced by the instruction, we used  
545 two different ways of chunking. We split each sequence either into one 2-digit and three  
546 3-digit chunks (2-3-3-3, misaligned) or into three 3-digit chunks and one 2-digit chunk  
547 (3-3-3-2, aligned). Each participant practiced half of the sequences with one chunk

548 structure and the other half of the sequences with the other chunk structure. This  
549 resulted in in two different sets of chunks (suppl. Table 2). The control group did not  
550 receive any explicit chunking instructions.

551 *Days 1-4: Chunk induction & initial sequence learning*

552 Experimental group: At the beginning of training the experimental groups were pre-  
553 trained on a specific set of eleven 2- or 3-digit chunks (2 two-press chunks and 9 three-  
554 press chunks). Participants received one of two different sets of chunks (suppl. Table  
555 2). Each chunk was consistently associated with a letter of the alphabet (A-K).  
556 Participants were explicitly told to learn this association. Each chunk was presented  
557 twice in succession. In half of the blocks, on the first trial of each chunk presentation,  
558 the numbers corresponding to the finger presses accompanied the letter on the screen  
559 while on the second trial participants had to recall the presses solely based on the letter  
560 (numbers were interchanged with stars). This trial order was reversed on every second  
561 block. To ensure that participants had memorized the chunks we added speeded recall  
562 blocks at the end of days 1 and 2. After practicing the 2-3 press chunks on day 1 and at  
563 the beginning of day 2, participants trained on the seven 11-press sequences. Each  
564 sequence was associated with a symbol (e.g. \$; suppl. Table 1). Each sequence was  
565 presented twice in succession and participant had to perform the sequences from  
566 memory using the sequence cue on one trial or with the help of the chunk letters on the  
567 next trial. We tested participants' sequence knowledge with a self-paced recall block at  
568 the end of days 2-4 (The first two participants did not perform the recall blocks).

569 Control group: The control group did not receive any chunk training but instead trained  
570 directly on the seven 11-press sequences. On the first day, the control participants  
571 practiced the sequences using the digits presented on the screen. We matched the  
572 amount of training across groups by ensuring that all participants were required to  
573 produce the same number of finger presses. On the first day, the control participants  
574 were not aware that they would have to memorize the sequences later on. On days 2-4  
575 they were then instructed to memorize the sequences using the same sequence cues  
576 as the experimental groups and were subsequently tested on their sequence  
577 knowledge. The rest of the experimental design was identical for all groups.

578 *Days 5-10: Optimization - Memory Recall*

579 For the days 5-10 of training participants practiced exclusively on the entire eleven-  
580 press sequences and chunks were no longer mentioned or trained on. Each sequence  
581 was presented twice in succession and participants had to recall the sequence from  
582 memory on both trials using the sequence cue.

583 *Days 11-14: Optimization - Memory recall or cued presentation*

584 During the last four days of training, half of the experimental participants performed the  
585 sequences from memory while for the other half and for the control participants we  
586 removed the sequence cue and presented participants with the actual numbers that  
587 corresponded to the sequences (Fig. 1a). Participants completed an additional  
588 generalization test on day 15. The results of this test are not reported in this article.

589 **Biomechanical baseline study**

590 We conducted a separate study to determine the influence of biomechanical difficulty on  
591 the finger transition speed. 7 participants (5 females, ages: 21-27) participated in this 3-  
592 day study. Participants executed all possible two-finger transitions (25) and three-finger  
593 transitions (125), each 8 times per day (each sequence was presented twice in a row).  
594 Each day participants completed 8 blocks with 150 trials each. The setup and  
595 motivational structure were identical to the main experiment. We found that on our  
596 device, finger repetitions (e.g. 2-2) were executed more slowly than presses of  
597 neighboring fingers (e.g. 2-1) To press the same finger twice, the force applied to the  
598 key had to first exceed the press threshold (3N), then go below the release threshold  
599 (1.5N) and then cross the press threshold again. This rapid alternation of forces takes  
600 time to produce. In contrast, for two adjacent fingers, the second finger can be already  
601 pressed before the finger is released (have already reached the press threshold),  
602 making it easier to rapidly produce this force pattern. Even though participants improved  
603 the overall speed from 622ms on the first to 522ms on the third day, the 5x5 pattern of  
604 relative IPI was stable across both participants (average correlation  $r = 0.689$ ) and days  
605 ( $r = 0.894$ ).

## 606 **Aligned vs. misaligned chunk structures**

607 To determine how to design our sequences and chunk structures to aid or impede  
608 performance we used the finding from the biomechanical baseline study that finger  
609 repetitions (e.g. 11) are performed slower than presses of adjacent fingers (e.g. 12).

610 We designed the sequences such that they would include both fast transitions  
611 (runs e.g. 123) and slow finger repetitions (113; suppl. Table 1). Depending on which  
612 chunk structure was instructed, these transitions would either fall on a chunk boundary  
613 or lie within a chunk. We counterbalanced this within and between participants, meaning  
614 that each participant trained on 3 sequences with the aligned chunk structure and 3 with  
615 the misaligned chunk structure (suppl. Table 1). One control sequence was added  
616 which included a within-chunk run for both groups.

## 617 **Statistical Analysis**

618 We recorded and analyzed the force traces for each finger. For each trial, we calculated  
619 the reaction time (RT, time between presentation and first crossing of the threshold),  
620 movement time (MT, time between first press and last release) and inter-press-intervals  
621 (IPIs; time between force peaks of two consecutive presses). All analyses were  
622 performed using custom-written code for MATLAB (the MathWorks). We excluded trials  
623 that contained one or more incorrect presses from our analyses, as well as trials with an  
624 MT or a press with an IPI three standard deviations above the mean. The data were  
625 analyzed using mixed-effects analysis of variance (mixed ANOVA), Pearson's  
626 correlation and paired and one sample t-tests. All t-tests were two-sided. A probability  
627 threshold of  $p < 0.05$  for the rejection of the null hypothesis was used for all statistical  
628 tests. For the regression analyses as well as for calculating the MT difference between  
629 the sequences with misaligned and aligned instruction we normalized the data for each  
630 participant by subtracting the mean performance for each day due to a wide range of  
631 performance speeds.

## 632 *Probabilistic model for estimating chunk structure*

633 We used an extended version of a Bayesian model of chunking behavior,  
634 developed by Acuna et al. (2014). The algorithm uses a Hidden Markov Model to  
635 estimate the posterior probability that a specific chunk structure is active on a given trial.

636 As we had 10 digit transitions, each of which could either coincide with a chunk  
637 boundary or not, we had to consider  $2^{10}-1=1023$  possible chunk structures. Between  
638 trials, the hidden Markov process could either stay in the same chunk structure with  
639 probability  $p$  or jump to any other chunk structure with probability  $(1-p)/1022$ . The IPIs  
640 were modeled as a Gaussian random variable, with a different mean and variance,  
641 depending on whether the transition was within- or between-chunks. In contrast to  
642 Acuna et al.(Acuna et al., 2014), where learning effects were removed in a  
643 preprocessing step using a single exponential, we modeled the learning within our  
644 model with two separate exponentials for the IPI mean. This captured the faster  
645 reduction in the between- compared to the within-chunk intervals (Fig. 2a). The  
646 inclusion of separate learning curves for within- and between-chunk IPIs into the model  
647 allowed us to estimate participants' chunk structure independently of the overall  
648 performance speed. This is an important advance over previous methods that used a  
649 constant cutoff value to distinguish between within- and between chunk intervals. For  
650 these methods, faster performance would automatically decrease the number of chunk  
651 boundaries detected. To confirm that our algorithm did not show this bias, we simulated  
652 artificial data using parameter estimates for individual participants. We simulated  
653 sequences that switched between 4 different chunk structures, each of which contained  
654 4 chunks. Even though IPIs decreased by about 300ms with learning, the estimated  
655 average number of chunks remained stable across the entire simulated experiment  
656 (average distance to single chunk: 3.35).

657 The model did not use errors and IPIs covariance structure, as these did not  
658 relate systematically to the imposed chunk structure even early in training. We used an  
659 Expectation-Maximization algorithm to simultaneously estimate the posterior probability  
660 of each chunk structure for each trial, as well as the 9 parameters of the model: 3  
661 parameters each for the exponential curve for the within- and between-chunk IPIs, 1  
662 variance parameter for each, and the transition probability  $p$ .

663 As a preprocessing step, we regressed the IPIs for each subject against the  
664 average biomechanical profile, which was estimated as the average IPI profile for all  
665 possible 2 digit-presses from our biomechanical baseline experiment (Fig. 1b). The



666 fitted values were removed from the IPIs. Removing temporal regularities that could be  
667 modeled with biomechanics alone should result in chunking estimates that more closely  
668 reflect cognitive and learning influences. Qualitatively comparable results were also  
669 obtained using the raw IPIs, without biomechanical factors removed.

#### 670 *Expected distance*

671 We quantified how much participants changed their chunking behavior over time by  
672 calculating the expected distance between two estimated chunk structures. The  
673 distance between two chunk structures,  $d(i,j)$ , was defined as how many of the 10  
674 transitions would have to change from a chunk boundary to a non-boundary (and vice  
675 versa) to transform one structure into the other (for an example, see Fig. 4b). A distance  
676 of 0 would indicate no change and the average distance between two randomly chosen  
677 chunk structures is 5. Because we did not know for certain which chunk structure  
678 participants adopted in each trial, we calculated the expected distance. For this, we first  
679 calculated a 1023 X 1023 matrix containing the distances between any chunk structure  
680  $i$ , and chunk structure  $j$ . From the posterior probability distribution, we could then derive  
681 how likely each of these chunk structure changes was,  $p(i,j)$ . The expected value of the  
682 distance was then simply calculated as

$$683 \quad E(d) = \sum_{i=1}^{1023} \sum_{j=1}^{1023} p(i,j)d(i,j).$$

#### 684 *Code availability*

685 Bayesian algorithm code available on GitHub:  
686 [https://github.com/jdiedrichsen/chunk\\_inference](https://github.com/jdiedrichsen/chunk_inference).

687 Custom MATLAB code is available from the corresponding author on request.

#### 688 *Data availability*

689 The datasets generated during and analyzed during the current study are available from  
690 the corresponding author on request.

**Supplementary Table 1. Sequences and chunk structures for the experimental group.** Displayed are the 7 sequences used together with the associated sequence cue. The black vertical lines indicate the chunk boundaries that were imposed. Chunk structures were either aligned with the biomechanical requirements (red) or misaligned (blue). The last sequence (green) was included as a control sequence that was chunked either with a 3-3-3-2 or 2-3-3-3 structure but performance wise should lead to similar speeds as for both chunk structures the boundaries were placed at biomechanically slow transitions. This sequence was not included in the analyses. Half of the participants were instructed based on “Group1” assignment of aligned and misaligned chunk structures and the other half based on “Group2” assignment

Sequence	Group 1	Group 2
?	1 2 3 5 1 3 3 2 1 3 4	1 2 3 5 1 3 3 2 1 3 4
+	4 3 5 5 1 2 3 5 3 3 2	4 3 5 5 1 2 3 5 3 3 2
%	4 3 5 5 1 2 3 5 3 3 2	4 3 5 5 1 2 3 5 3 3 2
\$	3 2 1 1 3 5 1 2 3 4 3	3 2 1 1 3 5 1 2 3 4 3
&	3 2 1 1 3 5 1 3 4 4 3	3 2 1 1 3 5 1 3 4 4 3
@	3 4 1 1 3 5 1 3 4 4 3	3 4 1 1 3 5 1 3 4 4 3
# (control sequence)	3 4 1 2 3 5 1 2 3 4 3	3 4 1 2 3 5 1 2 3 4 3

| Chunk Boundary    ■ Aligned    ■ Misaligned

**Supplementary Table 2. Instructed chunks and sequences for the experimental group.**

The tables depict the finger presses (1-5) that were associated with the chunk cues (A-K) and the chunks that were associated with the sequences cues (symbols). Half of the participants trained with the Group 1 chunks and the other half practiced the Group 2 chunks

Chunks Group 1			Chunks Group 2		
Chunk	Presses		Chunk	Presses	
A	3	2	A	1	2
B	3	4	B	4	3
C	1	1 3	C	1	2 3
D	1	2 3	D	1	3 4
E	3	2 1	E	1	3 5
F	3	4 3	F	2	3 5
G	3	5 3	G	3	2 1
H	4	3 5	H	3	3 2
I	4	4 3	I	3	4 1
J	5	1 2	J	3	5 1
K	5	1 3	K	5	5 1

Sequences Group 1					Sequences Group 2				
Seq.	Chunks				Seq.	Chunks			
?	D	K	E	B	?	A	J	H	D
+	H	K	E	B	+	B	K	H	D
%	H	J	G	A	%	B	K	F	H
\$	A	C	J	F	\$	G	E	C	B
&	A	C	K	I	&	G	E	D	B
@	B	C	K	I	@	I	E	D	B
#	B	D	J	F	#	I	F	C	B

691

References

692 Abrahamse, E. L., Ruitenberg, M. F. L., de Kleine, E., & Verwey, W. B. (2013). Control of  
 693 automated behavior: insights from the discrete sequence production task. *Frontiers in*  
 694 *Human Neuroscience*, 7(March), 1–16. <https://doi.org/10.3389/fnhum.2013.00082>

695 Acuna, D. E., Wymbs, N. F., Reynolds, C. A., Picard, N., Turner, R. S., Strick, P. L., ... Kording, K. P.

- 696 (2014). Multifaceted aspects of chunking enable robust algorithms. *Journal of*  
697 *Neurophysiology*, 112(8), 1849–1856. <https://doi.org/10.1152/jn.00028.2014>
- 698 Adams, C. D. (1982). Variations in the sensitivity of instrumental responding to reinforcer  
699 devaluation. *The Quarterly Journal of Experimental Psychology Section B*, 34(2), 77–98.  
700 <https://doi.org/10.1080/14640748208400878>
- 701 Ashby, F. G., Ell, S. W., & Waldron, E. M. (2003). Procedural learning in perceptual  
702 categorization. *Memory and Cognition*, 31(7), 1114–1125.  
703 <https://doi.org/10.3758/BF03196132>
- 704 Barnes, T. D., Kubota, Y., Hu, D., Jin, D. Z., & Graybiel, A. M. (2005). Activity of striatal neurons  
705 reflects dynamic encoding and recoding of procedural memories, 437(October).  
706 <https://doi.org/10.1038/nature04053>
- 707 Bo, J., & Seidler, R. D. (2009). Visuospatial working memory capacity predicts the organization  
708 of acquired explicit motor sequences. *Journal of Neurophysiology*, 101(6), 3116–3125.  
709 <https://doi.org/10.1152/jn.00006.2009>
- 710 Brainard, M. S., & Doupe, A. J. (2002). What songbirds teach us about learning. *Nature*,  
711 417(6886), 351–358. <https://doi.org/10.1038/417351a>
- 712 Chang, C. C. (2004). *Fundamentals of Piano Practice*. Brain (3rd ed.). CreateSpace Independent  
713 Publishing Platform. Retrieved from <http://www.pianopractice.org/>
- 714 Dempster, A. P., Laird, N. M., & Rubin, D. B. (1977). Maximum likelihood from incomplete data  
715 via the EM algorithm. *Journal of the Royal Statistical Society Series B Methodological*,  
716 39(1), 1–38. <https://doi.org/http://dx.doi.org/10.2307/2984875>
- 717 Dezfouli, A., & Balleine, B. W. (2012). Habits, action sequences and reinforcement learning.  
718 *European Journal of Neuroscience*, 35(7), 1036–1051. [https://doi.org/10.1111/j.1460-](https://doi.org/10.1111/j.1460-9568.2012.08050.x)  
719 9568.2012.08050.x
- 720 Dezfouli, A., Lingawi, N. W., & Balleine, B. W. (2014). Habits as action sequences: Hierarchical

- 721 action control and changes in outcome value. *Philosophical Transactions of the Royal*  
722 *Society B: Biological Sciences*, 369(1655). <https://doi.org/10.1098/rstb.2013.0482>
- 723 Dickinson, A. (1985). Actions and Habits: The Development of Behavioural Autonomy.  
724 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 308(1135), 67–78.  
725 <https://doi.org/10.1098/rstb.1985.0010>
- 726 Diedrichsen, J., & Kornysheva, K. (2015). Motor skill learning between selection and execution.  
727 *Trends in Cognitive Sciences*, 19(4), 227–233. <https://doi.org/10.1016/j.tics.2015.02.003>
- 728 Diedrichsen, J., White, O., Newman, D., & Lally, N. (2010). Use-Dependent and Error-Based  
729 Learning of Motor Behaviors. *Journal of Neuroscience*, 30(15), 5159–5166.  
730 <https://doi.org/10.1523/JNEUROSCI.5406-09.2010>
- 731 Ericsson, K. A., Krampe, R. T., Tesch-romer, C., Ashworth, C., Carey, G., Grassia, J., ... Schneider,  
732 V. (1993). The role of deliberate practice in the acquisition of expert performance.  
733 *Psychological Review*, 100(3), 363–406. <https://doi.org/10.1037//0033-295X.100.3.363>
- 734 Graybiel, A. M. (1998). The basal ganglia and chunking of action repertoires. *Neurobiology of*  
735 *Learning and Memory*, 70(1–2), 119–136. <https://doi.org/10.1006/nlme.1998.3843>
- 736 Graybiel, A. M. (2008). Habits, Rituals, and the Evaluative Brain. *Annual Review of Neuroscience*,  
737 31(1), 359–387. <https://doi.org/10.1146/annurev.neuro.29.051605.112851>
- 738 Graybiel, A. M., & Grafton, S. T. (2015). The Striatum: Where Skills and Habits Meet. *Cold Spring*  
739 *Harbor Perspectives in Biology*, 7(8), a021691.  
740 <https://doi.org/10.1101/cshperspect.a021691>
- 741 Haith, A. M., & Krakauer, J. W. (2018). The multiple effects of practice: skill, habit and reduced  
742 cognitive load. *Current Opinion in Behavioral Sciences*, 20, 196–201.  
743 <https://doi.org/10.1016/j.cobeha.2018.01.015>
- 744 Halford, G. S., Wilson, W. H., & Phillips, S. (1998). Processing capacity defined by relational  
745 complexity: implications for comparative, developmental, and cognitive psychology. *The*

- 746 *Behavioral and Brain Sciences*, 21(6), 803–864.  
747 <https://doi.org/10.1017/S0140525X98001769>
- 748 Hardwick, R. M., Forrence, A. D., Krakauer, J. W., & Haith, A. M. (2017). Skill Acquisition and  
749 Habit Formation as Distinct Effects of Practice. *BioRxiv*. <https://doi.org/10.1101/201095>
- 750 Hayes, J. R. (2013). *The Complete Problem Solver*. Taylor & Francis. Retrieved from  
751 <https://books.google.ca/books?id=uqttX7YEhIMC>
- 752 Hélie, S., & Cousineau, D. (2011). The cognitive neuroscience of automaticity: Behavioral and  
753 brain signatures. *Cognitive Sciences*, 6(1), 25–43.
- 754 Hélie, S., Waldschmidt, J. G., & Ashby, F. G. (2010). Automaticity in rule-based and information-  
755 integration categorization. *Attention, Perception, & Psychophysics*, 72(4), 1013–1031.  
756 <https://doi.org/10.3758/APP.72.4.1013>
- 757 Jager, W. (2003). Breaking ‘bad habits’: a dynamical perspective on habit. *In Human Decision*  
758 *Making and Environmental Perception: Understanding and Assisting Human Decision*  
759 *Making in Real-Life Settings* (L. Hendrickx, W. Jager, and L. Steg, Eds.), *Liber Amicorum for*  
760 *Charles Vlek, University of Groningen, Groningen, Netherlands*, (January 2003), 149–160.
- 761 Jin, X., Tecuapetla, F., & Costa, R. M. (2014). Basal ganglia subcircuits distinctively encode the  
762 parsing and concatenation of action sequences. *Nature Neuroscience*, 17(3), 423–430.  
763 <https://doi.org/10.1038/nn.3632>
- 764 Jog, M. S., Kubota, Y., Connolly, C. I., Hillegaart, V., & Graybiel, A. M. (1999). Building neural  
765 representations of habits. *Science (New York, N.Y.)*, 286(5445), 1745–1750.  
766 <https://doi.org/10.1126/science.286.5445.1745>
- 767 Kleine, E. De, & Verwey, W. B. (2009). Representations underlying skill in the discrete sequence  
768 production task: effect of hand used and hand position. *Psychological Research*  
769 *Psychologische Forschung*, 73(5), 685–694. <https://doi.org/10.1007/s00426-008-0174-2>
- 770 Kuriyama, K., Stickgold, R., & Walker, M. P. (2004). Sleep-dependent learning and motor-skill

- 771 complexity. *Learning & Memory*, 11(6), 705–713. <https://doi.org/10.1101/lm.76304>
- 772 Langan, J., & Seidler, R. D. (2011). Age differences in spatial working memory contributions to  
773 visuomotor adaptation and transfer. *Behavioural Brain Research*, 225(1), 160–8.  
774 <https://doi.org/10.1016/j.bbr.2011.07.014>
- 775 Miller, G. A. (1956). The magical number seven, plus or minus two: some limits on our capacity  
776 for processing information. *Psychological Review*, 63(2), 81–97.  
777 <https://doi.org/10.1037/h0043158>
- 778 Moors, A., & De Houwer, J. (2006). Automaticity: A theoretical and conceptual analysis.  
779 *Psychological Bulletin*, 132(2), 297–326. <https://doi.org/10.1037/0033-2909.132.2.297>
- 780 Park, J. H., Wilde, H., & Shea, C. H. (2004). Part-Whole Practice of Movement Sequences.  
781 *Journal of Motor Behavior*, 36(1), 51–61. <https://doi.org/10.3200/JMBR.36.1.51-61>
- 782 Park, S.-W., Dijkstra, T. M. H., & Sternad, D. (2013). Learning to never forget—time scales and  
783 specificity of long-term memory of a motor skill. *Frontiers in Computational Neuroscience*,  
784 7(September), 1–13. <https://doi.org/10.3389/fncom.2013.00111>
- 785 Ramkumar, P., Acuna, D. E., Berniker, M., Grafton, S. T., Turner, R. S., & Kording, K. P. (2016).  
786 Chunking as the result of an efficiency computation trade-off. *Nature Communications*, 7,  
787 12176. <https://doi.org/10.1038/ncomms12176>
- 788 Robbins, T. W., & Costa, R. M. (2017). Habits. *Current Biology*, 27(22), R1200–R1206.  
789 <https://doi.org/10.1016/j.cub.2017.09.060>
- 790 Sadnicka, A., Kornysheva, K., Rothwell, J. C., & Edwards, M. J. (2018). A unifying motor control  
791 framework for task-specific dystonia. *Nature Reviews Neurology*, 14(2), 116–124.  
792 <https://doi.org/10.1038/nrneurol.2017.146>
- 793 Sakai, K., Kitaguchi, K., & Hikosaka, O. (2003). Chunking during human visuomotor sequence  
794 learning. *Experimental Brain Research*, 152(2), 229–242. [https://doi.org/10.1007/s00221-](https://doi.org/10.1007/s00221-003-1548-8)  
795 003-1548-8

- 796 Seger, C. A., & Spiering, B. J. (2011). A critical review of habit learning and the Basal Ganglia.  
797 *Frontiers in Systems Neuroscience*, 5(August), 1–9.  
798 <https://doi.org/10.3389/fnsys.2011.00066>
- 799 Seidler, R. D., Bo, J., & Anguera, J. A. (2012). Neurocognitive contributions to motor skill  
800 learning: The role of working memory. *Journal of Motor Behavior*, 44(6), 445–453.  
801 <https://doi.org/10.1080/00222895.2012.672348>
- 802 Smith, K. S., & Graybiel, A. M. (2013a). A dual operator view of habitual behavior reflecting  
803 cortical and striatal dynamics. *Neuron*, 79(2), 361–374.  
804 <https://doi.org/10.1016/j.neuron.2013.05.038>
- 805 Smith, K. S., & Graybiel, A. M. (2013b). Using optogenetics to study habits. *Brain Research*,  
806 1511, 102–114. <https://doi.org/10.1016/j.brainres.2013.01.008>
- 807 Smith, K. S., & Graybiel, A. M. (2014). Investigating habits: strategies, technologies and models.  
808 *Frontiers in Behavioral Neuroscience*, 8(February), 1–17.  
809 <https://doi.org/10.3389/fnbeh.2014.00039>
- 810 Smith, K. S., & Graybiel, A. M. (2016). Habit formation coincides with shifts in reinforcement  
811 representations in the sensorimotor striatum. *Journal of Neurophysiology*, 115(3), 1487–  
812 1498. <https://doi.org/10.1152/jn.00925.2015>
- 813 Solopchuk, O., Alamia, A., Olivier, E., Ze, A., & Zénon, A. (2016). Chunking improves symbolic  
814 sequence processing and relies on working memory gating mechanisms. *Learning &*  
815 *Memory*, 23(3), 108–112. <https://doi.org/10.1101/lm.041277.115>
- 816 Song, S., & Cohen, L. (2014). Impact of conscious intent on chunking during motor learning.  
817 *Learning & Memory (Cold Spring Harbor, N.Y.)*, 21(9), 449–51.  
818 <https://doi.org/10.1101/lm.035824.114>
- 819 Verstynen, T., Phillips, J., Braun, E., Workman, B., Schunn, C., & Schneider, W. (2012). Dynamic  
820 Sensorimotor Planning during Long-Term Sequence Learning: The Role of Variability,  
821 Response Chunking and Planning Errors. *PLoS ONE*, 7(10), e47336.



- 822 <https://doi.org/10.1371/journal.pone.0047336>
- 823 Verwey, W. B. (1996). Buffer loading and chunking in sequential keypressing. *Journal of*  
824 *Experimental Psychology: Human Perception and Performance*, 22(3), 544–562.  
825 <https://doi.org/10.1037/0096-1523.22.3.544>
- 826 Verwey, W. B. (1999). Evidence for a multistage model of practice in a sequential movement  
827 task. *Journal of Experimental Psychology: Human Perception and Performance*, 25(6),  
828 1693–1708. <https://doi.org/10.1037/0096-1523.25.6.1693>
- 829 Verwey, W. B. (2001). Concatenating familiar movement sequences: The versatile cognitive  
830 processor. *Acta Psychologica*, 106(1–2), 69–95. [https://doi.org/10.1016/S0001-](https://doi.org/10.1016/S0001-6918(00)00027-5)  
831 [6918\(00\)00027-5](https://doi.org/10.1016/S0001-6918(00)00027-5)
- 832 Verwey, W. B., Abrahamse, E. L., & de Kleine, E. (2010). Cognitive processing in new and  
833 practiced discrete keying sequences. *Frontiers in Psychology*, 1(JUL), 32.  
834 <https://doi.org/10.3389/fpsyg.2010.00032>
- 835 Verwey, W. B., Abrahamse, E. L., & Jiménez, L. (2009). Segmentation of short keying sequences  
836 does not spontaneously transfer to other sequences. *Human Movement Science*, 28(3),  
837 348–361. <https://doi.org/10.1016/j.humov.2008.10.004>
- 838 Verwey, W. B., & Dronkert, Y. (1996). Practicing a Structured Continuous Key-Pressing Task:  
839 Motor Chunking or Rhythm Consolidation? *Journal of Motor Behavior*, 28(1), 71–79.  
840 <https://doi.org/10.1080/00222895.1996.9941735>
- 841 Verwey, W. B., & Eikelboom, T. (2003). Evidence for Lasting Sequence Segmentation in the  
842 Discrete Sequence-Production Task. *Journal of Motor Behavior*, 35(2), 171–181.  
843 <https://doi.org/10.1080/00222890309602131>
- 844 Verwey, W. B., Lammens, R., & Van Honk, J. (2002). On the role of the SMA in the discrete  
845 sequence production task: A TMS study. *Neuropsychologia*, 40(8), 1268–1276.  
846 [https://doi.org/10.1016/S0028-3932\(01\)00221-4](https://doi.org/10.1016/S0028-3932(01)00221-4)

- 847 Verwey, W. B., & Wright, D. L. (2014). Learning a keying sequence you never executed:  
848 Evidence for independent associative and motor chunk learning. *Acta Psychologica*, *151*,  
849 24–31. <https://doi.org/10.1016/j.actpsy.2014.05.017>
- 850 Welch, L. R. (2003). Hidden Markov Models and the Baum-Welch Algorithm. *IEEE Information*  
851 *Theory Society Newsletter*, *53*(4), 1,10-13. <https://doi.org/10.1023/A:1007425814087>
- 852 Wickens, J. R., Horvitz, J. C., Costa, R. M., & Killcross, S. (2007). Dopaminergic Mechanisms in  
853 Actions and Habits, *27*(31), 8181–8183. <https://doi.org/10.1523/JNEUROSCI.1671-07.2007>
- 854 Wiestler, T., & Diedrichsen, J. (2013). Skill learning strengthens cortical representations of  
855 motor sequences. *ELife*, *2*(2), 1–20. <https://doi.org/10.7554/eLife.00801>
- 856 Wiestler, T., Waters-Metenier, S., & Diedrichsen, J. (2014). Effector-Independent Motor  
857 Sequence Representations Exist in Extrinsic and Intrinsic Reference Frames. *Journal of*  
858 *Neuroscience*, *34*(14), 5054–5064. <https://doi.org/10.1523/JNEUROSCI.5363-13.2014>
- 859 Wong, A. L., Lindquist, M. A., Haith, A. M., & Krakauer, J. W. (2015). Explicit knowledge  
860 enhances motor vigor and performance: motivation versus practice in sequence tasks.  
861 *Journal of Neurophysiology*, *114*(1), 219–232. <https://doi.org/10.1152/jn.00218.2015>
- 862 Wright, D. L., Rhee, J.-H., & Vaculin, A. (2010). Offline improvement during motor sequence  
863 learning is not restricted to developing motor chunks. *Journal of Motor Behavior*, *42*(5),  
864 317–24. <https://doi.org/10.1080/00222895.2010.510543>
- 865 Wymbs, N. F., Bassett, D. S., Mucha, P. J., Porter, M. A., & Grafton, S. T. (2012). Differential  
866 Recruitment of the Sensorimotor Putamen and Frontoparietal Cortex during Motor  
867 Chunking in Humans. *Neuron*, *74*(5), 936–946.  
868 <https://doi.org/10.1016/j.neuron.2012.03.038>
- 869 Yokoi, A., Bai, W., Diedrichsen, J., Yokoi, X. A., Bai, W., & Diedrichsen, X. J. (2017). Restricted  
870 transfer of learning between unimanual and bimanual finger sequences. *Journal of*  
871 *Neurophysiology*, *117*(3), 1043–1051. <https://doi.org/10.1152/jn.00387.2016>

872