The effects of habits on motor skill learning

Abbreviated title: The effects of habits on motor skill learning

Nicola J. Popp¹, Atsushi Yokoi^{2,3}, Paul L. Gribble^{1,4,5,6} & Jörn Diedrichsen^{1,7,8*}

- ¹ The Brain and Mind Institute, University of Western Ontario, N6A 5B7, Canada
- ² Graduate School of Frontier Biosciences, Osaka University, 565-0871, Japan
- ³ Center for Information and Neural Networks (CiNet), NICT, 565-0871, Japan
- ⁴ Department of Psychology, University of Western Ontario, N6A 5C2, Canada
- ⁵ Department of Physiology & Pharmacology, Schulich School of Medicine & Dentistry, University of Western Ontario, N6A 5C1, Canada
- ⁶ Haskins Laboratories, 06511, USA
- ⁷ Department of Statistical and Actuarial Sciences, University of Western Ontario, N6A 5B7, Canada
- ⁸ Department of Computer Science, University of Western Ontario, N6A 5B7, Canada

Correspondence address

Jörn Diedrichsen, The Brain and Mind Institute, University of Western Ontario, London, Canada. jdiedric@uwo.ca

Page count: 46

Figures count. 8

Word counts: Abstract: 245; Introduction: 620; Discussion 1275

Conflict of interest

The authors declare no conflict of interest.

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.

1

Abstract

2 Skill learning involves the formation of stable motor patterns. In musical and athletic 3 training, however, these stable motor habits can also impede the attainment of higher 4 levels of performance. We developed an experimental paradigm to induce a specific 5 motor pattern in the context of a discrete sequence production task and to investigate 6 how these habits affect performance over a 3-week training period. Participants initially 7 practiced small segments of 2 to 3 finger movements ("chunks") and then learned 8 longer sequences composed of these chunks. This initial training induced a persistent 9 temporal pattern during execution, with shorter inter-press-intervals within a chunk and 10 longer ones at chunk boundaries. This pattern remained stable during the subsequent 11 10 days of training, in which participants were asked to produce the sequence as fast as 12 possible from memory. The habit was also preserved when the sequences were directly 13 displayed, removing the need for memory recall. We were able to induce chunking 14 patterns that were either beneficial or detrimental to performance by taking into 15 consideration the biomechanical constraints of the sequences. While we observed an 16 overall reduction in the detrimental effect of the disadvantageous chunking instructions 17 with training, our results show that the degree to which these detrimental chunk 18 structures were maintained, was predictive of lower levels of final performance. In sum, 19 we were able to induce beneficial and detrimental motor habits in a motor sequence 20 production task and show that these initial instructions influenced performance 21 outcomes over a prolonged period of time.

22

23

Significance Statement

24	A habit is defined as an automatized action that resists modification once sufficiently
25	established. Preventing bad habits, while reinforcing good habits, is a key objective
26	when teaching new motor skills. While habit formation is an integral part of motor skill
27	acquisition, previous research has focused on habit formation in terms of action
28	selection. In this paper, we examine habit formation in terms of motor skill execution,
29	after the action has been selected. We were able to induce beneficial or detrimental
30	motor habits in the production of motor sequences. Habits were stable over a prolonged
31	training period. Our results demonstrate how cognitive instruction can lead to persistent
32	motor habits and we explore how these habits are potentially modified with training.

2	Λ
- 3	4
-	

Introduction

35	What does it take to become an expert at a motor skill such as playing the piano?
36	Clearly, practice is key. Some have proposed that 10,000 hours of training are
37	necessary to develop a high level of performance (Ericsson et al., 1993; Hayes, 2013).
38	However, simply practicing for many hours may not lead to expert performance, as
39	numerous examples have shown (Haith and Krakauer, 2018). This is sometimes
40	attributed to the formation of habits: automatic (Hélie, Waldschmidt, & Ashby, 2010;
41	Moors & De Houwer, 2006) and highly entrenched behavioral patterns that resist
42	change through retraining (Ashby et al., 2003; Jager, 2003; Seger and Spiering, 2011;
43	Graybiel and Grafton, 2015; Hardwick et al., 2019).
44	Animal models have been integral to the study of habit formation and its neural
45	underpinnings (Jog et al., 1999; Wickens et al., 2007; Smith and Graybiel, 2014, 2016;
46	Robbins and Costa, 2017). However, the majority of animal experiments investigating
47	habit formation have focused on habits in the context of action selection – i.e. choosing
48	what action to perform. In contrast, in this paper we address the question of habits in
49	motor performance – i.e. habits that influence how to perform a chosen action. For
50	example, a tennis player could be influenced by a habitual pattern in action selection,
51	whereby she always chooses a forehand over a backhand to return a serve. At the
52	same time, she could be influenced by a motor habit, whereby she executes the
53	forehand without rotating her hips.

54 Critical to the definition of a habit is that the behavior is maintained even though it 55 is no longer adaptive (Adams, 1982; Dickinson, 1985; Dezfouli and Balleine, 2012). 56 Most experiments, therefore, demonstrate the existence of a habit by teaching subjects

a behavior under one reward contingency and show its persistence when the reward
contingency switches (Ashby et al., 2003; Smith and Graybiel, 2013a).

59 To investigate the influence of habit formation on motor skill learning we used a 60 discrete sequence production task (DSP) in which participants performed an explicitly 61 learned series of finger presses as fast as possible (Verwey, 2001; Abrahamse et al., 62 2013). Learning in this task depends on both cognitive and motor processes 63 (Diedrichsen & Kornysheva, 2015; Wong, Lindquist, Haith, & Krakauer, 2015). Initial 64 performance relies on forming a declarative memory of the sequence that can be 65 sculpted through explicit instructions (de Kleine & Verwey, 2009; Verwey, Abrahamse, & 66 Jiménez, 2009) and potentially can constrain subsequent motor optimization (Bo and 67 Seidler, 2009; Seidler et al., 2012). We tested the hypothesis that the initial instruction 68 causes the formation of a motor habit which influences the learning of execution-related 69 skills in subsequent motor training.

70 We instructed participants to memorize long sequences of finger presses by first 71 practicing a set of smaller 2-3 digit "chunks" on an isometric keyboard-like device 72 (Miller, 1956; Verwey, 1996; Verwey and Dronkert, 1996; Halford et al., 1998; Wymbs et 73 al., 2012). Two different chunk sets were used. Participants were then trained on seven 74 11-digit sequences. Each sequence was subdivided into chunks (depending on chunk 75 set) so that boundaries between chunks were either aligned or misaligned with 76 biomechanically easy or difficult finger transitions. This manipulation influenced initial 77 performance with sequences learned using the aligned chunk structure being performed 78 faster. After the introduction phase, participants had to recall the sequences from 79 memory and practiced them over the course of 3 weeks.

We investigated three questions: First, do the initial instructions lead to a stable motor performance pattern and how long does it persist? Second, to what degree are these patterns maintained even if they are detrimental to performance? Finally, what learning-related changes are involved in overcoming motor habits?

84

Methods

85 Participants

86 Forty participants who reported no neurological conditions were recruited for the study 87 (30 females; ages: 19 to 33). Thirty-two of them were randomly assigned to learn the 88 sequences with one of the two chunk sets (Figure 1) and the remaining eight 89 participants were assigned to a control group. All participants were right-handed based 90 on the Edinburgh Handedness Inventory and completed informed consent. On average, 91 participants had received 4.68 (\pm 5.55) years of musical training, with 55% percent 92 reported having more than 6 months of experience playing the piano. While participants 93 with piano experience performed the sequences faster than participants with no 94 experience and the number of practice years correlated with execution speed (MT), the 95 amount of participants' prior musical experience did not have a qualitative influence on 96 participants' chunking behavior. The study protocol was approved by the ethics board of 97 the University of Western Ontario.

98 Apparatus

A custom-built five-finger keyboard was used. The keys were not depressible but were
equipped with a force transducer (FSG-15N1A, Sensing and Control, Honeywell)
underneath each key which measured participants' isometric force production with a

repeatability of <0.02 N and a dynamic range of 16 N (Wiestler and Diedrichsen, 2013;
Wiestler et al., 2014; Yokoi et al., 2017). The measured force at each key was digitally
sampled at 200 Hz.

105 Discrete sequence production task

106 We used a discrete sequence production task (DSP) in which participants 107 executed sequences of 2, 3, or 11 keypresses as fast as possible while keeping their 108 error rate under 15%. Each trial started with the visual presentation of the sequence to 109 be executed and was completed once the participants pressed the amount of presented 110 numbers. Each block consisted of 28 trials. A trial was deemed erroneous if participants 111 pressed a wrong key anywhere within the sequence. No pause between presses was 112 required and thus some co-articulation between fingers emerged with faster execution. 113 A keypress was registered when the measured force first exceeded 3N. A key release 114 was marked when the force measured at the same key first fell below 1.5N. To prevent 115 participants from pressing more than 2 keys at once, we implemented a constraint such 116 that in order for a key to be registered as depressed the key previously registered as 117 depressed had to be released.

The magnitude of the force applied to each key was represented by 5 lines on an LCD monitor, with the height of the line representing the force at the corresponding key. A white asterisk (memory-guided conditions) or a digit (cued condition) for each finger press was presented above the lines. Immediately after the keypress threshold was reached, participants received visual and auditory feedback. If the correct key was pressed, the color of the cue changed from white to green and a sound was presented.

124 If the incorrect key was pressed, the cue turned red and a lower-pitch sound was125 presented.

126 After each trial participants received points based on their accuracy and 127 movement time (MT; the time between the first keypress and last key release). Correct 128 sequences performed faster than the MT threshold (see below) were rewarded with 1 129 point. MTs that were 20% faster than the threshold were rewarded with 3 points. 130 Incorrect presses or MTs exceeding the threshold resulted in 0 points. At the end of 131 each block, participants received feedback on their error rate, median MT, points 132 obtained during the block, and total points obtained during the session. In order to 133 motivate participants to continue to improve their performance, we adjusted the MT 134 threshold by lowering it by 500 ms after each block in which the participants performed 135 with an error rate of 15% or lower and had a median MT faster than the current 136 threshold. This manipulation resulted in an approximately stable overall error rate of 137 14.6%, SD: 2.6%. On 27% of trials, participants received 1 point, on 34% of trials 3 138 points.

139 Biomechanical baseline study

To design the chunks and sequences for the main experiment, we conducted a
separate study to determine the influence of biomechanical constraints on finger
transition speed. 7 participants (5 females, ages: 21-27) participated in this 3-day study.
Participants executed all possible two-finger transitions (e.g. 25) and three-finger
transitions (e.g. 125), each 8 times per day. Each sequence was presented twice in a
row. Each day, participants completed 8 blocks with 150 trials each. The setup and
motivational structure were the same as reported above. We found that on our device,

147 transitions between two adjacent fingers (e.g. 12) could be performed faster than two 148 repeated presses of the same finger (e.g. 55; $t_{(6)} = 13.965$, p = 8.404e-06; Fig. 1). Given 149 that the 2-3 press sequences hardly taxed the cognitive system, these results can be 150 taken as a characterization of the biomechanical constraints of our specific task. To 151 press the same finger twice, the force applied to the key had to first exceed the press 152 threshold, then go below the release threshold and then cross the press threshold 153 again. This rapid alternation of forces takes time to produce. In contrast, for two 154 adjacent fingers, the second finger press can be initiated (have already reached the 155 press threshold) before the previous finger is released, making it easier to rapidly 156 produce this force pattern. Even though participants improved their overall speed from 157 157 ms on the first day to 114 ms on the third day, the 5x5 pattern of relative inter-press 158 interval (IPI) was stable both across participants (average correlation r = 0.689) and 159 days (r = 0.894).

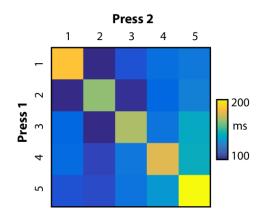


Figure 1. Two-finger transition execution speed.

Biomechanical 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. Indicated values are means over n=7 participants.

161 Experimental design

162 To experimentally impose a particular way of chunking, we instructed participants in the 163 experimental group to memorize and perform a set of 2-3 keypress chunks (Fig. 2a). 164 These chunks were later combined to form the training sequences (Fig. 2b). Our goal 165 was to impose beneficial or detrimental motor habits on participants' performance. For 166 this, we used the finding from the biomechanical baseline study that finger repetitions 167 are performed slower than presses of adjacent fingers. We designed sequences such 168 that they would include both fast transitions (runs e.g. 123) and slow finger repetitions 169 (e.g. 113). Depending on which chunk structure was instructed, these transitions would 170 either fall on a chunk boundary or lie within a chunk. In the "aligned" chunk structure we 171 aligned the boundaries such that they fell on difficult finger transitions, which were 172 executed slowly for biomechanical reasons. The time required to perform these difficult 173 finger transitions can therefore simultaneously be used to recall the next chunk, which 174 should benefit overall performance. Using this chunk structure, the 3-digit "runs" (i.e. 175 123) which are performed quickly were kept intact (not broken up by a chunk transition). 176 We predicted that learning the sequence using this chunk structure would be beneficial 177 to performance speed (Fig. 2c). In the misaligned chunk structure, we placed chunk 178 boundaries in a way that divided up biomechanically easy finger transitions such as 179 runs, thereby breaking up parts of the sequence that could otherwise be performed very 180 guickly. We hypothesized that this would hinder overall performance (Fig. 2c). All 181 participants practiced the same 7 sequences (Fig. 2b). Half of the participants were 182 instructed with the aligned chunk structure for the first 3 sequences, and the misaligned 183 chunk structure for the next 3 sequences (Fig. 2d). For the other half of the participants,

- the assignment of sequences to aligned and misaligned was reversed. The last
- 185 sequence served as a control sequence and was chunked, such that either instruction
- 186 should lead to similarly beneficial performance. The counterbalanced design (Fig. 2d)
- 187 allowed us to draw strong inferences about whether participants' performance was
- 188 dictated by biomechanical demands (which were identical across participants) or
- 189 whether it was affected by the chunk structure imposed during the induction phase
- 190 (which was different between the two chunk sets).

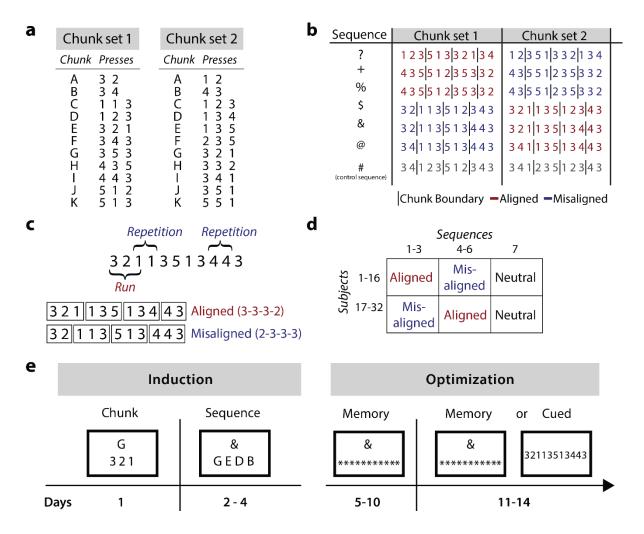


Figure 2. Experimental design. (a) Each participant learned 11 chunks associated with the chunk cues (A-K) from one of the chunk sets. (b) The seven 11-digit sequences that participants trained on. The vertical lines (not shown to the participants) indicate the chunk boundaries induced in training through the chunk set. Sequences were trained with an aligned (red) or misaligned (blue) chunk structure. (c) Example sequence containing a 3-digit run and two-digit repetitions. In the aligned structure, the chunk boundaries fell between repetitions, in the misaligned structure the chunk boundary broke up the run. (d) We counterbalanced across participants which sequences were practiced with which chunk structures. (e) Experimental timeline depicting the training at each stage. In the induction 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 others performed the sequences from memory.

Every participant completed 15 training sessions in total (Figure 2e): one session per day across a 3-week period. Each session lasted approximately 1 hour, excluding the two initial sessions and the last session which each took 2 hours. Participants completed at least 10 blocks of 28 trials per training day. Each block comprised 4 repetitions of each of the 7 sequences.

197 Days 1-4: Chunk induction & initial sequence learning

198 *Experimental group:* On Day 1 the participants were pre-trained on one of the chunk 199 sets (Fig. 2a). Each chunk was associated with a letter of the alphabet (A-K). 200 Participants were explicitly told to learn this association. Each letter A-K was presented 201 twice in succession. In half of the blocks, on the first trial of each pair, the numbers 202 corresponding to the finger presses accompanied the letter on the screen, while on the 203 second trial participants had to recall the presses solely based on the letter (numbers 204 were replaced with stars). This trial order was reversed on every second block. To 205 ensure that participants had memorized the chunks we added speeded recall blocks at 206 the end of days 1 and 2. At the end of the first day, participants could reliably produce 207 the chunks from memory with an average accuracy of 92.7%.

On day 2 participants trained on the seven 11-press sequences. Each sequence was associated with a symbol (e.g. \$; suppl. Fig. 2b). Each symbol was presented twice in succession and participants had to perform the sequences from memory using the symbol cue on one trial or with the help of the chunk letters on the next trial. We tested participants' sequence knowledge with a self-paced recall block at the end of days 2-4 (The first two participants did not perform the recall blocks). At the end of day 4,

214 participants were able to recall all sequences from memory using the sequence cues215 with an accuracy of 93.1%.

216 Control group: The control group did not receive any chunk training but instead trained 217 directly on the seven 11-press sequences. On day 1 they were presented with the 11 218 digits corresponding to the 11-press sequences. We matched the amount of training 219 across groups by ensuring that all participants were required to produce the same 220 overall number of finger presses. On day 1, the control participants were not aware that 221 they would have to memorize the sequences later on. On days 2-4 they were instructed 222 to memorize the sequences using the same symbolic sequence cues as the 223 experimental groups and their memory was tested using recall blocks at the end of each 224 day (Day 4: 90.2% accuracy). The rest of the experimental design was identical for all 225 groups.

226 Days 5-10: Optimization - Memory Recall

On days 5-10 participants practiced exclusively on the eleven-press sequences using
the symbolic cues. Chunks were no longer cued. Each sequence cue was presented
twice in succession and participants had to recall the sequence from memory on both
trials.

231 Days 11-14: Optimization - Memory recall or cued presentation

On the last four days of training half of the experimental participants performed the
sequences from memory (as on days 5-10), while for the other half and for the control
participants we removed the symbolic sequence cue and instead visually presented
participants with the complete set of 11 digits that corresponded to the sequences (Fig.

226 2e). Participants completed an additional generalization test on day 15. The results of237 this test are not reported in this article.

238 Statistical Analysis

239 We recorded and analyzed the force measured at each key. For each trial, we 240 calculated movement time (MT, time between the first press and last release) and inter-241 press-intervals (IPIs; time between force peaks of two consecutive presses). All 242 analyses were performed using custom-written code in MATLAB (The MathWorks). We 243 excluded from our analyses trials that contained one or more incorrect presses, as well 244 as trials with an MT or a press with an IPI three standard deviations above the mean 245 calculated across all days and participants. The data were analyzed using mixed-effects 246 analysis of variance (mixed ANOVA), Pearson's correlation and paired and one-sample 247 t-tests. All t-tests were two-sided. A probability threshold of p<0.05 for the rejection of 248 the null hypothesis was used for all statistical tests. For the regression analyses as well 249 as for calculating the MT difference between the sequences with misaligned and aligned 250 instruction we subtracted the mean performance for each participant and day (across 251 sequences) to normalize and remove the large part of the variance due to interindividual 252 performance differences.

253 Probabilistic model for estimating chunk structure

To estimate participants' chunking behavior from IPIs, we used an extended version of a Bayesian model of chunking behavior, developed by Acuna et al. (2014). The algorithm uses a Hidden Markov Model to estimate the posterior probability that a specific chunk structure is present on a given trial. Here we used only the IPIs on

correct trials, but not the error probability as in the original publication, as the probability
of errors did not relate systematically to the imposed chunk structure early in learning.

As we had 10 digit transitions, each of which could either coincide with a chunk boundary or not, we had to consider $2^{10}-1=1023$ possible chunk structures. Between trials, the hidden Markov process could either preserve the same chunk structure with probability *p* or switch to any other chunk structure with probability (1-p)/1022. The IPIs were modeled as a Gaussian random variable, with a different mean and variance depending on whether the keypress transition was within or between chunks.

266 In contrast to Acuna et al., in which learning effects were removed in a 267 preprocessing step using a single exponential, we modeled learning within our model 268 using two separate exponential terms for the IPI mean. This captured the faster 269 reduction in the between- compared to the within-chunk intervals (Fig. 3a). The 270 inclusion of separate learning curves for within- and between-chunk IPIs allowed us to 271 estimate participants' chunk structure independently of changes in the overall 272 performance speed (Fig. 5a). This is an important advance over previous methods that used a constant cutoff value to distinguish between within- and between-chunk 273 274 intervals. For these methods, faster performance would automatically decrease the 275 number of chunk boundaries detected. To confirm that our algorithm did not show this 276 bias, we simulated artificial data using parameter estimates for individual participants. 277 We simulated sequences that switched between 4 different chunk structures, each of 278 which contained 4 chunks. Even though IPIs decreased by about 300 ms with learning, 279 the estimated average number of chunks remained stable across the entire simulated 280 experiment (average distance to single chunk: $3.35 \sim 4$ chunks and 3 boundaries).

We used an Expectation-Maximization algorithm to simultaneously estimate the posterior probability of each chunk structure for each trial, as well as the 9 parameters of the model: 3 parameters each for the exponential curve for the within- and betweenchunk IPIs, 1 variance parameter for each, and the transition probability *p* (for

285 *implementation details, see <u>https://github.com/jdiedrichsen/chunk_inference</u>.*

As a preprocessing step, we regressed the IPIs for each subject against the average biomechanical profile, which was estimated as the average IPI profile for all possible 2-digit presses from our biomechanical baseline experiment (Fig. 1). The fitted values were removed from the IPIs. Removing temporal regularities that could be modeled with biomechanics alone should result in chunking estimates that more closely reflect cognitive and learning influences. Qualitatively comparable results were also obtained using the raw IPIs, without biomechanical factors removed.

293 Expected distance

294 We quantified how much participants changed their chunking behavior over time by 295 calculating the expected distance between their estimated chunk structure and a 296 reference chunk structure. We defined the distance between two chunk structures, d(i,j), 297 as how many of the 10 keypress transitions would have to change from a chunk 298 boundary to a non-boundary (and vice versa) to transform one structure into the other 299 (for an example, see Fig. 5b). A distance of 0 would indicate no change. The average 300 distance between two randomly chosen chunk structures is 5. Because chunk 301 structures produced by participants on each trial were estimates, we calculated the 302 expected distance. For this, we first calculated a 1023 X 1023 matrix containing the 303 distances between any chunk structure *i*, and chunk structure *j*. From the posterior

304 probability distribution, we could then derive how likely each of these chunk structure 305 changes was, p(i,j). The expected value of the distance was then calculated as $E(d) = \sum_{i=1}^{1023} \sum_{j=1}^{1023} p(i,j) d(i,j).$ 306 307 Data availability 308 The datasets generated and analyzed during the current study will be made available 309 upon publication. 310 Results 311 Over 15 days we trained 32 participants to produce sequences of 11 isometric 312 keypresses from memory on a keyboard-like device. Participants were rewarded with 313 points for executing sequences as fast as possible while keeping the proportion of

314 incorrect keypresses in each block of trials below 15%. We maintained the participants'

315 motivation by gradually decreasing the movement time (MT) threshold at which they

316 received points.

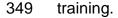
317 We manipulated how participants memorized the sequences by splitting the 318 sequences into several chunks, each composed of 2-3 keypresses. The aim was to test 319 whether the different ways of chunking (hereafter "chunk structures") imposed through 320 the chunk training in the induction phase (Methods, Fig. 2b) would affect performance 321 optimization in the subsequent two weeks of training. Each sequence could be chunked 322 in an aligned or misaligned fashion, predicted to lead to beneficial or detrimental 323 performance respectively (Methods, Fig. 2c). All participants practiced the same 7 324 sequences but differed in the chunking instructions they received for each sequence.

325 Chunk induction induces a stable motor pattern

326 To assess whether the imposed chunk structures influenced participants' motor 327 behavior, we examined inter-press time intervals (IPIs). An increased IPI is commonly 328 taken as a sign of a chunk boundary, as the cognitive processes (memory recall, action 329 selection) involved in switching from one chunk to another require additional time 330 (Verwey, 1999; Verwey et al., 2010). Hence, we would expect our participants to exhibit 331 shorter IPIs between keypresses that belonged to a chunk imposed during day 1 332 (within-chunk IPIs) and larger IPIs for the boundaries between chunks (between-chunk 333 IPIs). For this analysis, we pooled the data from all sequences irrespective of instruction 334 (misaligned vs. aligned). We indeed found significantly longer between-chunk IPIs 335 compared to within-chunk IPIs in the first few days of training (Fig. 3a: days 2-4: $t_{(31)} =$ 336 7.728, p = 5.098e-09), suggesting that our manipulation was successful in inducing a 337 temporally specific pattern of keypresses.

338 In the optimization phase, we ceased to cue sequences using the alphabetic 339 letters associated with the chunks. Instead, participants were asked to recall the entire 340 11-keypress sequences from memory in response to symbolic sequence cues (e.g. "\$"). 341 Across days 5-10, the within and between-chunk IPIs were still significantly different 342 from each other; $t_{(31)} = 7.165$, p = 2.351e-08 (Fig. 3a). This difference cannot be 343 attributed to biomechanical difficulty of the finger transitions, as the within-chunk IPIs for one half of the participants were the between-chunk IPIs for the other half and vice 344 345 versa (Fig. 2b). IPIs that were within-chunk for all participants (e.g. the first and last IPI 346 of a sequence) were excluded from this analysis. In summary, even though after day 4 347 we cued the sequences only with symbols, participants persisted in performing the

348 sequences consistent with the chunk structures that we experimentally imposed early in



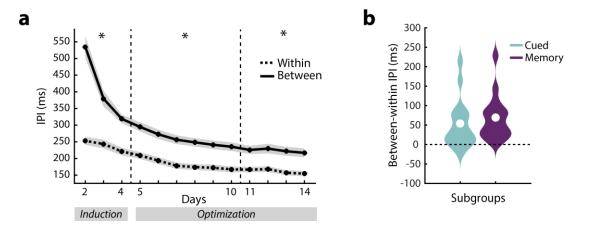


Figure 3. Within- vs. between-chunk inter-press intervals (IPIs). (a) Time course of IPIs that were within an instructed chunk (dashed line), or on the boundary between chunks (solid line). Asterisks indicate significant differences between average within- and between-chunk IPIs in the corresponding 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.

In the last four days of training, we tested whether the persistence of the imposed chunk structure reflected a motor habit or whether it reflected memory recall. Half of the participants continued to perform the sequences from memory, while the other half were cued using the numbers that indicated the necessary keypresses (Fig. 2e), therefore removing any memory recall demands. Both the memory ($t_{(15)} = 4.865$, p = 2.059e-04, Fig. 3b) and the cued subgroup ($t_{(15)} = 3.403$, p = 0.004) showed a significant difference

between the within- and between-chunk IPIs and there was no reliable difference between the two subgroups in this effect ($t_{(30)} = -0.749$, p = 0.460). Thus, removing the requirement for memory recall did not abolish chunking. Because none of the subsequent analyses showed any significant difference between the two subgroups, we will report their combined results for the remainder of the article. Overall, these results suggest the explicit chunk training early in learning established a stable performance pattern that outlasted 10 days of subsequent practice.

363 Misaligned chunk structure impairs performance

364 To show that the initial instruction led to the emergence of a motor habit, we needed to 365 not only show that this initial instruction induced a stable temporal pattern of IPIs, but 366 also that this pattern was maintained even when it leads to slower execution speeds 367 than other patterns. We therefore designed chunk structures that were predicted to be 368 either beneficial or detrimental to performance (aligned vs. misaligned respectively) based on their biomechanical constraints (see Methods). Each participant learned 3 of 369 370 the 7 sequences with a misaligned chunk structure and 3 sequences with an aligned 371 chunk structure, with the assignment counterbalanced across participants (Fig. 2d). This 372 counterbalanced design allowed us to compare execution speed between aligned and 373 misaligned sequences for each participant.

To test our prediction that training with the misaligned chunk structure would lead to poorer performance, we measured participants' movement time (MT) by estimating the time between the first finger press and the last finger release. In the induction phase, sequences instructed with the misaligned chunk structure were performed slower than the sequences instructed with the aligned chunk structure (Fig. 4a) one-

379	sample t-test: $t_{(31)} = 2.693$, $p = 0.006$). Hence, we were not only able to manipulate how
380	participants performed a sequence, but also how well they could perform it.

381	Examining what factors influenced the difference in speed we observed, we
382	found that on average a within-chunk finger run led to an advantage of 28.6 ms and a
383	within-chunk repetition cost 16 ms. An additional factor that influenced participants'
384	speed was whether the 2-digit chunk was placed in the beginning (misaligned) or the
385	end of the sequence (aligned), which led to an advantage of 24.7 ms. The difference in
386	MT found in the first week was maintained in the second week of training (days 5-10:
387	$t_{(31)} = 2.313$, $p = 0.014$). Importantly, this shows that the stable pattern of IPIs indeed
388	constitutes a motor habit. This speed difference was no longer statistically reliable in the
389	last four days of training (days 11-14: $t_{(31)} = 0.764$, $p = 0.225$). This suggests that
390	participants were able to overcome the "bad" habit of a misaligned chunk structure to
391	some degree.

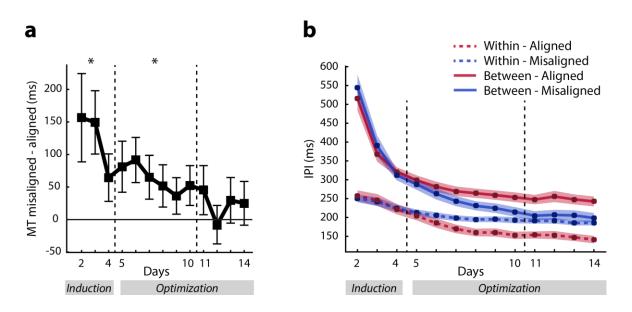


Figure 4. Change in chunk structure and performance for aligned and misaligned instructed sequences. (a) Differences in movement time (MT) between sequences instructed with an aligned or misaligned chunk structure. Asterisk indicates a significant difference from 0 (no difference). (b) Within- or between-chunk IPIs across training days, separated by whether they were in the aligned or misaligned instructed sequences. Error bars denote between-subject standard error.

392 Misaligned chunk structure is changed more rapidly

393 To investigate how participants overcame the detrimental influence of the misaligned 394 chunk structure, we first separated the IPI analysis (Fig. 3a) by whether the intervals 395 came from sequences that were instructed using an aligned or misaligned structure. 396 While the difference between within- and between-chunk IPIs for sequences 397 constructed using aligned chunk structures was stable over the entire training period, 398 the difference was absent for misaligned chunk structures in the last four days of 399 training (Fig. 4b). The three-way day x within/between x aligned/misaligned interaction 400 was significant ($F_{(12,372)} = 19.790$, p = 1e-16). Thus, in the last four days of training

401 participants diverged from the misaligned chunk structure while maintaining the aligned402 chunk structure.

A disadvantage of this analysis, however, is that we cannot discern how participants restructured their chunking and whether they completely abandoned the misaligned chunk structure. For a clearer understanding of how participants changed their chunk structure, we used a model-based approach to analyze our IPI data.

407 Bayesian model of chunk behavior

408 We used a Bayesian model to estimate the probability of each possible chunk structure 409 given the observed series of IPIs on a trial-by-trial basis (Acuna et al., 2014). The state 410 variable in this Hidden Markov Model represents which of the 1023 possible chunk 411 structures is present on each trial. Using an expectation-maximization (EM) algorithm 412 (Dempster et al., 1977; Welch, 2003), we simultaneously estimated the 9 free 413 parameters of the model (for details see Methods), and the posterior probability for each 414 possible chunk structure on each trial. We accounted for the effects of biomechanical 415 difficulty by regressing out the patterns of IPIs across finger transitions predicted from 416 our biomechanical dataset (Fig. 1) before modeling. Importantly, our model could 417 capture separate learning-related changes to the within- and between-chunk intervals 418 (Fig. 5a). Our method, therefore, allowed us to estimate participants' chunk structure 419 independently of the overall speed of performance.

Figure 5b shows two examples of individual participants and sequences. In the first panel, the participant chunked the sequence according to the initial instructions at first, then inserted 1 or 2 additional chunk boundaries, and at the end of training

- 423 performed the sequence as a single chunk. In comparison, the other participant
- 424 maintained the instructed chunk structure for most of the training period.

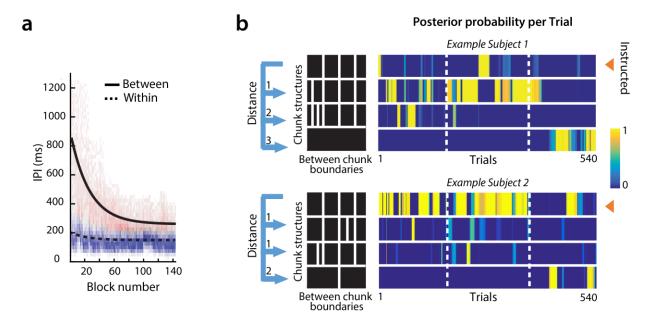


Figure 5. Probabilistic chunking model fitted to example participant data. (a) The change of within- and between-chunk IPIs were modeled using two separate exponential functions across training. The density plot shows individual IPIs, with the color indicating the probability of a between- (pink) or 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.

425 To characterize changes in chunk structure over training we defined a metric that 426 quantified the difference between any two chunking structures. The metric is based on 427 counting the number of chunk boundaries that differ, in other words, the number of 428 chunks that would need to be split or merged to transform one chunk structure into the 429 other (Fig. 5b - distance). We then used this measure to calculate, on each trial, the 430 distance between the chunk structure estimated for the participant and three reference 431 structures of interest: (1) the aligned-, (2) misaligned, and (3) a structure that consisted 432 of a single chunk. These distances defined a coordinate system that enabled us to 433 visualize changes in chunk structure over training. We then projected participants' 434 estimated chunk structures into this space (Fig. 6a). On the horizontal axis is the 435 expected distance of participants' chunk structure to the single-chunk structure. Given 436 our definition of distance, this measure simply counts the number of chunk boundaries. 437 The vertical axis indicates how close the estimated chunk structure is to the aligned and 438 misaligned chunk structure, respectively.

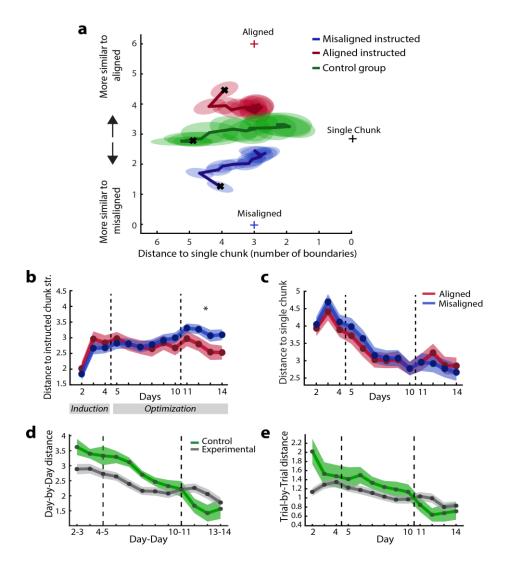


Figure 6. Changes in chunk structure with learning. (a) The average chunk structure over 13 days of practice for aligned (red) and misaligned (blue) instructed sequences for the experimental participants. The results of the control group are shown in green. The horizontal axis represents the distance 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 instructed chunk structure. (c) Distance to the single chunk structure across days. (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.

440 Participants abandoned the misaligned faster than aligned chunk structure

Using this modeling approach, we probed how much participants diverged from the initial instructions and whether they diverged from the misaligned chunk structure to a greater degree as already suggested by our IPI analysis. Participants slowly changed their chunk structure for both aligned and misaligned instructed sequences with training. The average distance to the instructed chunk structure increased systematically over time (repeated measures ANOVA, effect of day, $F_{(12,372)} = 7.055$, p < 1e-16, Fig. 6b).

447 Consistent with our IPI analysis (Fig. 4b), we observed that participants 448 abandoned the instructed misaligned chunk structure to a greater degree than the 449 aligned chunk structure (Day x Instruction interaction: $F_{(12,372)} = 5.610$, p < 1e-16). In the 450 last four days of training, sequences with the misaligned chunk structure were more 451 dissimilar to the instructed chunk structure than sequences with an aligned chunk 452 structure: $t_{(31)} = 2.294$, p = 0.029 (Fig. 6b). Additionally, we found a significant Day x 453 Instruction interaction ($F_{(12,372)} = 2.215$, p = 0.011) for the distance to a single chunk 454 (Fig. 6c), suggesting a stronger tendency towards performing a sequence as a single 455 chunk when trained on the misaligned chunk structure. Together these results indicate 456 that participants changed their chunking behavior more readily for sequences that were 457 trained using the misaligned chunk structure than when trained using the aligned chunk 458 structure.

Despite the divergence from the misaligned chunk structure with training, our analysis also revealed that participants did not overcome the influence of the instruction completely. In the third week, sequences trained with a misaligned chunk structure were still performed using a chunk structure that was closer to the misaligned structure than

to the aligned structure ($t_{(31)} = 6.962$, p < 1e-16). This shows that training with a

464 misaligned chunk structure had a lasting influence on participants' motor behavior.

465 Movement towards a single chunk structure

466 Previous literature has suggested that with training, participants group smaller chunks 467 together to form new larger chunks (Verwey, 1996; Sakai et al., 2003; Kuriyama et al., 468 2004; Verstynen et al., 2012; Wymbs et al., 2012; Song and Cohen, 2014; Ramkumar 469 et al., 2016), a process that may help to improve performance (Verwey, 1999, 2001; 470 Verwey et al., 2010: Abrahamse et al., 2013: Verwey and Wright, 2014: Ramkumar et 471 al., 2016). However, in nearly all previous studies the estimated number of chunks is 472 biased by the overall movement speed. As verified by simulations (see Methods), our 473 probabilistic model was able to disambiguate the two factors. We estimated the number 474 of chunk boundaries for each participant averaged across sequences (the neutral 475 sequence was excluded). On the 2nd day, participants separated sequences into more 476 chunks than the 4 chunks we instructed (Fig. 6c, $t_{(31)} = 4.224$, p = 0.0002). This 477 tendency continued on day 3, on which participants tended to subdivide the sequences 478 into even smaller chunks (day 2 vs. 3: $t_{(31)} = 2.023$, p = 0.052). After day three the 479 number of chunk boundaries decreased as shown by a significant effect of day in a 480 repeated measures ANOVA ($F_{(11,341)} = 11.710$, p < 1e-16). However, even in the last 481 phase of training, participants performed the sequences with an average of 2.9 chunk 482 boundaries (we instructed 3 chunk boundaries). Thus, while there was a clear tendency 483 towards merging chunks after an initial increase, participants did not perform the 484 sequence as a single chunk, even after 3 weeks of practice.

485 Chunk structure crystallizes with training

486 Would longer training allow participants to completely overcome the influence of the 487 instruction and to perform all sequences as a single chunk? Although experiments with 488 longer training are necessary to provide a definitive answer, our data indicate that this 489 process, if occurring, may take a very long time. The amount of change in the chunk 490 structure for each sequence reduced dramatically in the last week of training, 491 suggesting that a stable motor habit formed. This phenomenon is akin to the 492 development of an invariant temporal and spectral structure in bird-song, a process that 493 has been termed "crystallization" (Brainard and Doupe, 2002). As a measure of 494 crystallization, we calculated the distance between the chunk structures from one day to 495 the next (Fig. 6d) and within each day from one trial to the next (Fig. 6e). The analysis 496 was performed separately for each sequence and participant. Overall, both the day-to-497 day distance ($F_{(11,330)} = 18.794$, p < 1e-16) and the trial-by-trial distance decreased 498 significantly across training days ($F_{(12,456)} = 13.245$, p < 1e-16). Therefore, participants 499 appeared to settle onto a stable pattern in the last week. Consequently, additional 500 training would likely only lead to slow changes in their chunk pattern.

In summary, our analyses provide a clear representation of how chunking changes with learning. Firstly, participants diverged from the instructions over time with a quicker deviation from the misaligned chunk structure. Secondly, in line with previous research (Verwey, 1996; Sakai et al., 2003; Kuriyama et al., 2004; Verstynen et al., 2012; Wymbs et al., 2012; Song and Cohen, 2014; Ramkumar et al., 2016) participants gradually moved towards performing the sequence as a single chunk by dividing the sequence into fewer chunks. Nevertheless, they did not completely overcome the initial

instruction, nor did they perform the sequences as a single chunk at the end of training.

- 509 Considering that the chunk structure crystallized in the last four days of training, these
- 510 results demonstrate the formation of a stable motor habit that is still influenced by the
- 511 initial instruction.
- 512 Spontaneously emerging chunk structures
- 513 To investigate how participants might spontaneously chunk the sequences, we tested
- an additional control group (N=8), who did not receive any explicit chunk training.
- 515 Participants were presented with the sequences in entirety on the first day and were
- asked to memorize them without any reference to chunks (see Methods for details).
- 517 Even though memorization was more difficult, the control group did not differ
- 518 significantly from the experimental groups in terms of their explicit knowledge on day 4
- 519 ($t_{(36)} = 1.288$, p = 0.206), or in their overall MT across training (main effect of group:
- 520 $F_{(1,38)} = 0.101$, p = 0.753; interaction between group and day ($F_{(1,38)} = 1.387$, p = 1.387

521 0.168).

522 Similar to the experimental groups, the control group initially subdivided the 523 sequences into small chunks and then slowly combined them into larger chunks. The 524 distance to a single chunk structure decreased significantly over days ($F_{(12.84)} = 17.977$, 525 p < 1e-16, Fig. 6a), and reached a level that was not statistically different from the 526 experimental participants on the last day of training ($t_{(38)} = -0.940$, p = 0.353). 527 Interestingly, on the first day, the control group performed the sequences closer to the 528 misaligned chunk structure than to the aligned chunk structure ($t_{(7)} = -2.799$, p = 0.027). 529 With training, participants then moved closer to the aligned chunk structure, as indicated 530 by a significant change in the difference between the distance to the aligned and

531 misaligned chunk structure across days ($F_{(12,84)} = 5.303$, p < 1e-16). The control group 532 also showed clear crystallization over time (see Figure 6d&e). Compared to the 533 experimental groups, control participants showed a higher day-to-day and trial-by-trial 534 change in the beginning of training, which then reduced more quickly (Group x Day 535 interaction; day-to-day: $F_{(11,330)} = 3.780$, p = 4.003e-05; trial-by-trial: $F_{(12,456)} = 4.254$, p =536 2.167e-06). In summary, the control group showed similar behavioral patterns to the 537 experimental participants, indicating that similar processes of habit formation are also at 538 play in the absence of explicit instructions.

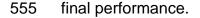
539 Idiosyncratic chunk structures at the end of training and their importance to

540 performance

541 Finally, we analyzed how the final chunk structure that participants adopted for each 542 sequence influenced their performance after 3 weeks of training. We visualized this 543 relationship by plotting the chunk structure for each sequence and participant in the 2-544 dimensional space defined in earlier Fig. 6a, with the corresponding average MT 545 indicated by the size of the symbol (Fig. 7).

546 The first insight is that participants used quite diverse chunk structures. To show 547 that this is not due to within-subject variability of performance, we compared 548 participants' within-subject variation in IPI patterns for each sequence across even and 549 odd trials (in the last three days of training) to the between-subject variation in IPI 550 patterns for each sequence. We found that the between-subject variability was much 551 higher than the within-subject variability ($t_{(31)} = 36.130$, p < 1e-16). This clearly shows 552 that participants developed their own, idiosyncratic way of chunking each sequence. 553 which is not fully dictated by the biomechanical requirements of the sequence. With this

result in mind, we asked whether these individual differences relate to differences in



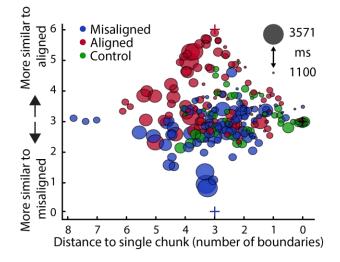


Figure 7. Relationship between chunking and speed (days 11-14). The x-axis indicates the distance to a single chunk and the y-axis the relative distance to the two instructed chunk structures. Each data point indicates the average chunk structure and MT of a single sequence and participant in the last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

556

Figure 7 suggests, that performance was better for sequences that were closer to the aligned chunk structure. To statistically test whether this finding holds true within each individual, we regressed the MT for 6 sequences (last 4 days & excluding the control sequence) for each participant in the last four days of training against the corresponding distance to the aligned chunk structure. On average the individual slopes were

significantly greater than 0, both for the experimental (Fig. 8a; $t_{(31)} = 2.220$, p = 0.017), 562 563 and control group (Fig. 8b, $t_{(7)} = 2.720$, p = 0.015). Thus, finding a better way of 564 chunking (for the same number of chunk boundaries) improved performance. 565 Secondly, Fig. 7 also suggests, that performing the sequence with a reduced 566 number of chunks is beneficial for performance. We regressed the MT for 6 sequences 567 (last 4 days & excluding the control sequence) against the corresponding distance to 568 the single chunk structure to (Fig. 8c). The majority of the participants showed a positive 569 relationship between the number of chunks and MT: a one-sample t-test indicated that 570 the individual slopes were significantly greater than 0 ($t_{(31)} = 6.104$, p = 4.560e-07). This 571 relationship was also found for the control participants (Fig. 8d, $t_{(7)} = 3.429$, p = 0.006). 572 Thus, performing the sequences with fewer chunks led to better performance. Note that 573 for both analyses, the chunk structure can be determined independently from the overall 574 performance criterion (MT, see Methods).

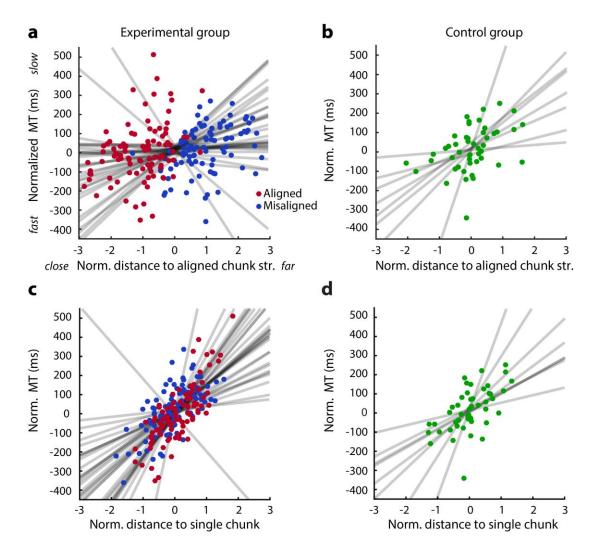


Figure 8. Relationship between the distance to the aligned/single chunk structure and MT. (a) Scatterplot between the normalized (per subj.) distance to the aligned chunk structure and normalized MT in the last four days of practice. A separate regression line is fitted to the 6 sequences for each participant. 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 a single chunk.

575 Overall, these results suggest that the two optimization processes - joining 576 chunks and aligning the remaining chunk boundaries with biomechanical constraints -

577 positively influenced participants' ultimate performance. Sequences for which

578 participants could not develop a better way of chunking were performed substantially

579 slower.

580

Discussion

581 In this study, we utilized chunking as a tool to investigate the role of motor habits in skill 582 learning. We influenced the structure of the initial declarative sequence representation 583 by manipulating how participants memorized them (Park, Wilde, & Shea, 2004). By 584 experimentally imposing two different chunk structures on the same physical sequence, 585 we could make causal inferences about the effects of cognitive chunking on motor skill 586 development. This is an important advance over previous observational studies (Wright 587 et al., 2010; Wymbs et al., 2012; Ramkumar et al., 2016), which did not experimentally 588 control how participants chose to chunk sequences.

589 We report three main results. First, consistent with previous studies (de Kleine & 590 Verwey, 2009; Verwey et al., 2010, 2009; Verwey & Dronkert, 1996), our data 591 demonstrate that a stable chunking pattern can be induced through cognitive 592 manipulations during the initial stages of sequence learning. Importantly, participants did not completely overcome this imposed chunk structure, even after 2 weeks of 593 594 additional training. Participants' chunk structure crystallized towards the end of training, 595 making it unlikely that the influence of the initial instruction would disappear completely 596 with longer practice. Finally, the chunking structure remained stable, even when the 597 task changed from a memory-guided to a stimulus-guided task. Thus, the initial 598 instruction led to the formation of specific motor patterns that were still clearly 599 measurable after three weeks of training.

600 Second, we tested whether this stable pattern of chunking could be considered a 601 motor habit. To do so, we designed two different ways of instructing the sequence, one 602 aligned and the other misaligned with biomechanical influences. This manipulation 603 either facilitated or impeded performance in the first two weeks of practice. We showed 604 that participants did not overcome the misaligned structure completely, even though it 605 was detrimental to their performance. Thus, the stable chunking pattern meets the 606 requirements (as laid out in our definition) for being called a motor habit. Therefore, we 607 believe that studying sequential chunking can provide valuable insights into the neural 608 systems underlying motor habits. Indeed, it has recently been suggested that chunking 609 plays an integral role in the formation and expression of habits (Dezfouli, Lingawi, & 610 Balleine, 2014; Graybiel, 2008) and is neurally represented in the dorsal lateral striatum 611 as action "start and stop signals" (Barnes, Kubota, Hu, Jin, & Graybiel, 2005; Graybiel, 612 1998; Jin, Tecuapetla, & Costa, 2014; Smith & Graybiel, 2013a, 2014).

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

We identified two ways in which participants overcame the limitation induced by the bad habit. After initially breaking up the instructed sequences into 5 chunks on average, participants then joined chunks together, and by doing so, decreasing the amount of additional time spent on chunk boundaries. While previous research has suggested that the size of chunks increases with training, these findings were usually

623 conflated with the overall speed of the action (Wymbs et al., 2012; Song and Cohen, 624 2014; Solopchuk et al., 2016). Using a Bayesian model to assess chunk structure 625 independent of performance, we demonstrated a positive relationship between chunk 626 concatenation and execution speed, both in the experimental as well as in the control 627 group that developed a chunking strategy without explicit instructions. However, our 628 results also indicate that participants did not merge all sequences into a single chunk 629 after 3 weeks of training, but on average subdivided each sequence into 3-4 chunks. 630 This suggests that the number of motor actions that can be joined in a single chunk may 631 be limited (Verwey et al., 2002; Verwey and Eikelboom, 2003; Langan and Seidler, 632 2011; Ramkumar et al., 2016).

We found that participants also optimized performance by rearranging chunk boundaries in a biomechanically efficient manner. Consistent with our prediction based on the difficulty of individual digit transitions, placing chunk boundaries at digit transitions that take more time to execute and combining finger presses that are adjacent resulted in faster performance for the full sequence. This optimization process was also observable in the control group that memorized and practiced sequences on their own terms.

640 Conversely, we observed that sequences that were not chunked in line with
641 these strategies were performed slower. Therefore, if a more beneficial way of chunking
642 was not found, participants still produced sequences using longer movement times,
643 suggesting that other learning mechanisms did not fully make up for a persistent motor
644 habit. Considering that participants' behavior became highly invariant in the last week of

practice, we predict that some motor habit will remain and continue to influenceparticipants' performance even after prolonged training.

647 In many motor tasks, there are numerous strategies and processes that can lead 648 to excellent performance (Verwey et al., 2010; Verstynen et al., 2012). Examining 649 Figure 7, one can observe that the shortest MTs were achieved anywhere in the space 650 between the aligned and single chunk structure. Occasionally, good performance was 651 also reached in other locations in chunk space. Our analysis showed that participants 652 adopted guite idiosyncratic chunk structures for each sequence at the end of training. 653 This suggests that there is considerable inter-individual variability in which technique 654 works best for reaching a high level of performance. Part of these differences may 655 reflect biomechanical variation across participants, leading to slightly different optimal 656 solutions. Alternatively, these differences may be learning-related. A number of ways of 657 chunking may work approximately equally well, such that the cost of changing an 658 established habit may outweigh the small benefit that could be gained from changing 659 the structure. A similar observation can be made in sports, where even top-ranked 660 athletes use slightly different techniques to reach similar levels of performance.

The establishment of a novel experimental paradigm to study motor habit formation will allow us to explore ways to encourage learners to abandon or change a current habit. While our attempt at accelerating this process by changing the task from a memory-based to a stimulus-based task was ultimately not successful, there are many other techniques that would be possible. In many disciplines, teachers have developed ways to help students overcome habits. For instance, the Hanon piano exercise helps students play difficult passages of a musical piece by breaking up learned phrases into

668 new chunks to explore different rhythms. Playing a passage slower than intended has 669 also been suggested to break habits (Chang, 2016). Overall, the general advice from 670 the diverse literature on learning piano is to diversify training and to practice with careful 671 awareness to prevent habits from forming (Sadnicka et al., 2017). This suggests that 672 changes in context and the exploration of novel ways of moving can aid performance 673 and the abandonment of habits.

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

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

686

687	References
688 689 690	Abrahamse EL, Ruitenberg MFL, de Kleine E, Verwey WB (2013) Control of automated behavior: insights from the discrete sequence production task. Front Hum Neurosci 7:1–16.
691 692 693	Acuna DE, Wymbs NF, Reynolds CA, Picard N, Turner RS, Strick PL, Grafton ST, Kording KP (2014) Multifaceted aspects of chunking enable robust algorithms. J Neurophysiol 112:1849–1856.
694 695	Adams CD (1982) Variations in the sensitivity of instrumental responding to reinforcer devaluation. Q J Exp Psychol Sect B 34:77–98.
696 697	Ashby FG, Ell SW, Waldron EM (2003) Procedural learning in perceptual categorization. Mem Cogn 31:1114–1125.
698 699 700	Barnes TD, Kubota Y, Hu D, Jin DZ, Graybiel AM (2005) Activity of striatal neurons reflects dynamic encoding and recoding of procedural memories. Nature 437:1158–1161.
701 702	Bo J, Seidler RD (2009) Visuospatial working memory capacity predicts the organization of acquired explicit motor sequences. J Neurophysiol 101:3116–3125.
703 704	Brainard MS, Doupe AJ (2002) What songbirds teach us about learning. Nature 417:351–358.
705 706	Chang CC (2016) Fundamentals of Piano Practice, 3rd ed. CreateSpace Independent Publishing Platform.
707 708	Dempster AP, Laird NM, Rubin DB (1977) Maximum likelihood from incomplete data via the EM algorithm. J R Stat Soc Ser B Methodol 39:1–38.
709 710	Dezfouli A, Balleine BW (2012) Habits, action sequences and reinforcement learning. Eur J Neurosci 35:1036–1051.
711 712	Dezfouli A, Lingawi NW, Balleine BW (2014) Habits as action sequences: hierarchical action control and changes in outcome value. Philos Trans R Soc B Biol Sci

713 369:20130482–20130482.

- 714 Dickinson A (1985) Actions and Habits: The Development of Behavioural Autonomy.
 715 Philos Trans R Soc B Biol Sci 308:67–78.
- 716 Diedrichsen J, Kornysheva K (2015) Motor skill learning between selection and
- 717 execution. Trends Cogn Sci 19:227–233.
- Diedrichsen J, White O, Newman D, Lally N (2010) Use-Dependent and Error-Based
 Learning of Motor Behaviors. J Neurosci 30:5159–5166.
- Fricsson KA et al. (1993) The role of deliberate practice in the acquisition of expert
 performance. Psychol Rev 100:363–406.
- Graybiel AM (1998) The basal ganglia and chunking of action repertoires. Neurobiol
 Learn Mem 70:119–136.
- Graybiel AM (2008) Habits, Rituals, and the Evaluative Brain. Annu Rev Neurosci31:359–387.
- Graybiel AM, Grafton ST (2015) The Striatum: Where Skills and Habits Meet. ColdSpring Harb Perspect Biol 7:a021691.
- Haith AM, Krakauer JW (2018) The multiple effects of practice: skill, habit and reduced
 cognitive load. Curr Opin Behav Sci 20:196–201.
- 730 Halford GS, Wilson WH, Phillips S (1998) Processing capacity defined by relational
- complexity: implications for comparative, developmental, and cognitive psychology.
 Behav Brain Sci 21:803–864.
- 733 Hardwick RM, Forrence AD, Krakauer JW, Haith AM (2019) Time-dependent
- 734 competition between goal-directed and habitual response preparation. Nat Hum735 Behav 3:1252–1262.
- 736 Hayes JR (2013) The Complete Problem Solver. Taylor & Francis.
- 737 Hélie S, Waldschmidt JG, Ashby FG (2010) Automaticity in rule-based and information-

738	integration categorization. Attention, Perception, Psychophys 72:1013–1031.
739 740 741 742	Jager W (2003) Breaking ' bad habits ': a dynamical perspective on habit. Hum Decis Mak Environ Percept Underst Assist Hum Decis Mak Real-Life Settings (L Hendrickx, W Jager, L Steg, eds), Lib Amicorum Charles Vlek, Univ Groningen, Groningen, Netherlands:149–160.
743 744	Jin X, Tecuapetla F, Costa RM (2014) Basal ganglia subcircuits distinctively encode the parsing and concatenation of action sequences. Nat Neurosci 17:423–430.
745 746	Jog MS, Kubota Y, Connolly CI, Hillegaart V, Graybiel AM (1999) Building Neural Representations of Habits. Science (80-) 286:1745–1749.
747 748 749	Kleine E De, Verwey WB (2009) Representations underlying skill in the discrete sequence production task: effect of hand used and hand position. Psychol Res Psychol Forsch 73:685–694.
750 751	Kuriyama K, Stickgold R, Walker MP (2004) Sleep-dependent learning and motor-skill complexity. Learn Mem 11:705–713.
752 753	Langan J, Seidler RD (2011) Age differences in spatial working memory contributions to visuomotor adaptation and transfer. Behav Brain Res 225:160–168.
754 755	Miller GA (1956) The magical number seven, plus or minus two: some limits on our capacity for processing information. Psychol Rev 63:81–97.
756 757	Moors A, De Houwer J (2006) Automaticity: A Theoretical and Conceptual Analysis. Psychol Bull 132:297–326.
758 759	Park J-H, Wilde H, Shea CH (2004) Part-Whole Practice of Movement Sequences. J Mot Behav 36:51–61.
760 761	Park S-W, Dijkstra TMH, Sternad D (2013) Learning to never forget—time scales and specificity of long-term memory of a motor skill. Front Comput Neurosci 7:1–13.
762 763	Ramkumar P, Acuna DE, Berniker M, Grafton ST, Turner RS, Kording KP (2016) Chunking as the result of an efficiency computation trade-off. Nat Commun
	43

- 764 7:12176.
- 765 Robbins TW, Costa RM (2017) Habits. Curr Biol 27:R1200–R1206.
- Sadnicka A, Kornysheva K, Rothwell JC, Edwards MJ (2017) A unifying motor control
 framework for task-specific dystonia. Nat Rev Neurol 14:116–124.
- Sakai K, Kitaguchi K, Hikosaka O (2003) Chunking during human visuomotor sequence
 learning. Exp Brain Res 152:229–242.
- Seger CA, Spiering BJ (2011) A critical review of habit learning and the Basal Ganglia.
 Front Syst Neurosci 5:1–9.
- Seidler RD, Bo J, Anguera JA (2012) Neurocognitive contributions to motor skill

learning: The role of working memory. J Mot Behav 44:445–453.

- Smith KS, Graybiel AM (2013a) Using optogenetics to study habits. Brain Res
 1511:102–114.
- Smith KS, Graybiel AM (2013b) A dual operator view of habitual behavior reflecting
 cortical and striatal dynamics. Neuron 79:361–374.
- Smith KS, Graybiel AM (2014) Investigating habits: strategies, technologies and
 models. Front Behav Neurosci 8:1–17.
- Smith KS, Graybiel AM (2016) Habit formation coincides with shifts in reinforcement
 representations in the sensorimotor striatum. J Neurophysiol 115:1487–1498.
- Solopchuk O, Alamia A, Olivier E, Ze A, Zénon A (2016) Chunking improves symbolic
 sequence processing and relies on working memory gating mechanisms. Learn
 Mem 23:108–112.
- Song S, Cohen L (2014) Impact of conscious intent on chunking during motor learning.
 Learn Mem 21:449–451.
- Verstynen T, Phillips J, Braun E, Workman B, Schunn C, Schneider W (2012) Dynamic
 Sensorimotor Planning during Long-Term Sequence Learning: The Role of

Variability, Response Chunking and Planning Errors Balasubramaniam R, ed.
PLoS One 7:e47336.

- Verwey WB (1996) Buffer loading and chunking in sequential keypressing. J Exp
 Psychol Hum Percept Perform 22:544–562.
- 793 Verwey WB (1999) Evidence for a multistage model of practice in a sequential
- movement task. J Exp Psychol Hum Percept Perform 25:1693–1708.
- Verwey WB (2001) Concatenating familiar movement sequences: The versatile
 cognitive processor. Acta Psychol (Amst) 106:69–95.
- 797 Verwey WB, Abrahamse EL, de Kleine E (2010) Cognitive processing in new and
 798 practiced discrete keying sequences. Front Psychol 1:32.
- 799 Verwey WB, Abrahamse EL, Jiménez L (2009) Segmentation of short keying
- 800 sequences does not spontaneously transfer to other sequences. Hum Mov Sci801 28:348–361.
- 802 Verwey WB, Dronkert Y (1996) Practicing a Structured Continuous Key-Pressing Task:
 803 Motor Chunking or Rhythm Consolidation? J Mot Behav 28:71–79.
- Verwey WB, Eikelboom T (2003) Evidence for Lasting Sequence Segmentation in the
 Discrete Sequence-Production Task. J Mot Behav 35:171–181.
- 806 Verwey WB, Lammens R, Honk J Van (2002) On the role of the SMA in the discrete
 807 sequence production task: a TMS study. Neuropsychologia 40:1268–1276.
- 808 Verwey WB, Wright DL (2014) Learning a keying sequence you never executed:
- 809 Evidence for independent associative and motor chunk learning. Acta Psychol810 (Amst) 151:24–31.
- Welch LR (2003) Hidden Markov Models and the Baum-Welch Algorithm. IEEE Inf
 Theory Soc Newsl 53:1,10-13.
- Wickens JR, Horvitz JC, Costa RM, Killcross S (2007) Dopaminergic Mechanisms in
 Actions and Habits. J Neurosci 27:8181–8183.

- Wiestler T, Diedrichsen J (2013) Skill learning strengthens cortical representations of
 motor sequences. Elife 2:1–20.
- 817 Wiestler T, Waters-Metenier S, Diedrichsen J (2014) Effector-Independent Motor
- 818 Sequence Representations Exist in Extrinsic and Intrinsic Reference Frames. J
- 819 Neurosci 34:5054–5064.
- Wong AL, Lindquist MA, Haith AM, Krakauer JW (2015) Explicit knowledge enhances
 motor vigor and performance: motivation versus practice in sequence tasks. J
 Neurophysiol 114:219–232.
- 823 Wright DL, Rhee J-H, Vaculin A (2010) Offline Improvement during Motor Sequence
- Learning Is Not Restricted to Developing Motor Chunks. J Mot Behav 42:317–324.
- 825 Wymbs NF, Bassett DS, Mucha PJ, Porter MA, Grafton ST (2012) Differential
- Recruitment of the Sensorimotor Putamen and Frontoparietal Cortex during MotorChunking in Humans. Neuron 74:936–946.
- 828 Yokoi A, Bai W, Diedrichsen J, Yokoi XA, Bai W, Diedrichsen XJ (2017) Restricted
- 829 transfer of learning between unimanual and bimanual finger sequences. J
- 830 Neurophysiol 117:1043–1051.