

RESEARCH ARTICLE

*Control of Movement*

# Repetition effects reveal the subsequence representation of actions

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## Abstract

When a movement sequence is repeated, the second execution is faster than the first. This demonstrates that the brain retains some trace of the just-executed sequence, the earliest form of sequence memory. Currently, it is unclear whether this memory trace is represented at the level of 1) transitions between movements, 2) chunks of multiple movements, or 3) the entire sequence. To answer this question, we instructed human participants to generate sequences of 11 finger presses in a delayed response paradigm. From one trial to the next, segments of variable length (1, 2, 4, 6, or 11 digits) could be repeated from the previous trial. We observed that repetition benefits appeared when a segment of four consecutive finger presses or longer was repeated from the previous trial. This suggests that the benefit of repetition is not merely the sum of improvements in individual transitions, nor does it require the entire sequence to be repeated. The repetition benefit was small for the first transition of a repeated segment and increased with additional repetitions. This suggests that the memory supporting the repetition effect is mainly activated when a series of past movements matches the memory trace. Planned future movements had less of an effect on the repetition effect. Our results provide insight into the structure of the earliest memory traces for motor sequences.

**NEW & NOTEWORTHY** Many motor skills involve combining movements into sequences. After a single execution, humans retain a memory trace that speeds up repeated sequences. Consistent with previous work, our results show a repetition benefit even when only a small subsequence is repeated, suggesting that full sequence repetition is not necessary. This memory trace is activated when the last 2–3 movements match the current execution. Our work, therefore, sheds light on the structure of the earliest sequence memory.

*memory trace; repetition effects; sequential movements; skill learning*

## INTRODUCTION

The best way to improve a motor skill is through repeated practice. Even after a single trial, the human motor system shows some improvements. For example, the execution of a specific sequence causes the following execution of the same sequence to be faster, even if there is sufficient time to fully preplan each sequence. This benefit appears to depend on the motoric execution of the sequence and was not observed when the sequence was only preplanned but not executed (1). The representation remaining in the brain after a single execution is the very first memory trace of a skill and likely forms the seed for a longer-lasting memory representation. Understanding the structure of this initial memory trace,

therefore, may offer new insights into how sequence learning occurs.

The control of movement sequences itself has been shown to evoke a hierarchy of representation, ranging from elementary movements to the entire sequence (2–6). Sequence repetition must facilitate some level of this hierarchy (7), but whether repetition acts at the level of the entire sequence, small sequence components, or individual transitions remains unclear.

To address this question, we designed an experiment asking human participants to generate random sequences of 11 finger movements in a delayed response paradigm. From trial to trial, a variable number of digits (0, 4, 6, or 11) could be repeated. The repeated digits could occur consecutively



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within a segment or break down into single digits or pairs of digits. This allowed us to investigate whether repetition benefits occur by improving the execution of single digits, transitions between digits, some subcomponent of the sequence (subsequence), or the entire sequence, providing insights into how sequences are represented in the brain. For subsequences, we were also able to measure how long it took for the memory trace to be fully activated, thereby providing some insight into the temporal integration window of sequence representations.

## METHODS

### Participants

A total of 35 individuals (22 female, mean age =  $23 \pm 4$  yr) took part in the experiment. All participants were right-handed and reported no history of psychiatric or neurological disorders. Participants provided written informed consent for all procedures and data usage before the study started, and all the experimental procedures were approved by the Human Research Ethics Board at Western University. Five participants withdrew from the experiment, and their sessions were terminated before completion. Consequently, their data were excluded from successive analyses (final  $n = 30$ , 20 female, age =  $24 \pm 4$  yr).

### Apparatus

Finger presses were produced on a custom-made keyboard with five  $10.5 \times 2$  cm keys. Each key had an indentation to guide fingertip placement. Finger presses were isometric. Forces were measured by transducers (FSG-15N1A; Sensing and Control Honeywell; the dynamic range of 0–25 N; update rate 5 ms) located beneath the fingertip indentation of each key. Five white lines were displayed on a computer screen such that the vertical position of each line was proportional to the force exerted by each finger on the respective key. To register a key press, the applied force had to exceed a 1 N threshold, indicated by a horizontal white line in the middle of the screen (Fig. 1A).

### General Procedure

We used a discrete sequence production (DSP) task in which participants produced sequences of 11 keypresses with the 5 fingers of their right hand (Fig. 1A). Each trial was cued by a set of 11 numbers instructing which finger had to be pressed (e.g., 1 = thumb, 2 = index, ... 5 = little) in which order. The sequence had to be produced by pressing the fingers corresponding to the numbers, from left to right, as fast as possible. In the precue phase, participants were asked to prepare for the corresponding finger presses. After a random delay of 3–4 s, a go-cue marked the beginning of the movement phase. The go-cue was a green frame accompanied by a tone (Fig. 1A), indicating that participants had to perform the planned sequence of finger presses as quickly and accurately as possible.

Performance was evaluated in terms of both execution speed and press accuracy. Speed was defined in terms of total time (TT), which consisted of the reaction time (RT; from the onset of the sequence cue to the first keypress) plus the movement time (ET; from the onset of the first keypress

to the release of the last keypress). A single-press error invalidated the whole trial, so accuracy was calculated as the percent error rate per block of trials (number of trials with at least 1 error/number of total trials  $\times 100$ ). In a 500-ms feedback interval, participants were presented with performance points: –1 points for not completing the sequence within 10 s; 0 points for ET > 5 s or for pressing any wrong key; +1 points for correct execution below 5 s; and +3 points for correct execution below the current TT threshold. The TT threshold decreased by 2% from one block to the next if both the median TT in the current block was faster than the best median TT recorded hitherto and the error rate in the last block was below 20%. If either one of these criteria was not met, the thresholds for the next block remained unchanged. After each block of trials, the median TT, mean error rate, and points earned were displayed to the participants. From block to block, we instructed participants to try to go faster if their error rate was below 15% and to try to be more accurate if their error rate was above 15%.

### Experimental Design

The experiment consisted of two sessions conducted on two consecutive days. In the first session, participants were introduced to the task with 1 training block of 30 trials. Then, participants completed 8 blocks of 60 trials in the first session and 10 blocks of 60 trials in the second session. Each session took ~120 min.

On each trial, participants were presented with a random sequence of 11 numbers. Each number (1–5) was guaranteed to be included at least once but no more than four times in the sequence. Sequences were not allowed to have consecutive runs of three presses (e.g., 1–2–3) or repetitions of a press (e.g., 2–2).

In the next trial, 0, 4, 6, or all elements could repeat. Repeated elements could occur in isolation (1-digit), in pairs (2-digit), or in chunks of four (4-digit) or six (6-digit). Throughout the article, we use “element” to refer to numbers in the sequence, whereas “digit” represents the number of elements that were repeated in a consecutive group.

Moreover, partial repetitions could occur at the beginning, middle, or end of the sequence, resulting in a total of 12 partial repetition conditions (Fig. 1, B and C).

From trial to trial, there was a 20% probability for nonrepetition trials and a 20% probability for full repetition trials, with sampling done independently for each trial (i.e., the probability of each trial type was independent of previous trial types). This high proportion of nonrepetition and full repetition trials allowed us to estimate the baseline performance with high accuracy. Each of the 12 partial repetition conditions occurred with a 5% probability.

### Analysis of Reaction and Execution Times

Within each participant, error trials were removed, and the mean RT and ET were calculated for all 14 conditions across trials and two sessions.

To assess the effect of repetition on RT, we only considered conditions with repeated elements at the beginning of the sequence, such as conditions 4 or 11 (Fig. 1B). A two-tailed paired-sample *t* tests was used to compare repetition versus nonrepetition conditions.



B

## Analysis of Interpress Intervals

transition, “rep” if the transition was repeated, “post” if a non-repeated transition occurred after a repeated transition, and “nrep” otherwise. Furthermore, we grouped “rep” transitions into “first” if it was the initial transition within a repeated segment, “last” if it was the last one, and otherwise as “middle.” This grouping was conducted separately for 2-, 4-, and 6-digit conditions.

We used two-tailed paired-sample  $t$  tests to assess the repetition changes in IPI groups. Again, we reported uncorrected  $P$  values but applied a Bonferroni-corrected  $P$  threshold with  $P < 0.05/4$  to determine whether there was a repetition effect in the 1, 2, 4, or 6-digit condition. For other hypotheses, we conducted a single overall  $t$  test, averaged over 4- and 6-digit conditions.

## Modeling Repetition Changes

To characterize the repetition effects across all conditions, we tested a series of general linear models of the observed repetition in each of the 130 possible IPIs. The simplest model, termed the “current transition model” (or “curr” for short), included a single feature indicating whether the current transition was repeated or not. We compared the predictive power of this model with three more complex models. The “current + past transition model” (“curr + past” for short) contained three features: whether the current transition was repeated, whether the previous transition was repeated, and whether both were repeated (the interaction term). The “current + next transition model” (“curr + next”

for short) included features for the current and the upcoming transitions, as well as their interaction. Finally, the “current + past + next transition model” (“curr + past + next” for short) included features for the current, previous, and upcoming transitions, as well as all possible two-way interactions among these. All models also included an intercept term.

To compare the models, we estimated the predictive  $R^2$  using a 10-fold cross-validation scheme. We first concatenated the data of all subjects into a single data vector (130 samples/subject  $\times$  30 subjects) and then divided it into 10 random folds. For each model, we estimated the linear regression parameters using the ninefold and calculated the  $R^2$  on the 10-fold. We then computed the mean  $R^2$  over all 10 iterations. We used the same folds for all models.

We then compared each model to the “current transition model” by taking the difference in their predictive  $R^2$  term. To find a 95% confidence interval for this difference, we repeated the same process 15,000 times by bootstrapping over participants. If the lower bound of the interval was above zero, then that model was considered to have a greater predictive power than the current transition model.

## RESULTS

### Sequence Repetition Accelerates Performance over the Entire Training Period

Participants performed random sequences over two separate sessions. From session 1 to 2, the execution time improved from 4,137 ms ( $\pm 242$  ms standard error across participants) to 3,533 ms ( $\pm 209$  ms), a highly significant difference ( $t_{29} = 10.164$ ,  $P = 4.5e-11$ ). Based on our instructions (see METHODS), error rates are relatively stable with 20.1% ( $\pm 0.1\%$ ) in the first and 18.2% ( $\pm 0.1\%$ ) in the second session. Despite the overall improvement in performance, we found that when the entire sequence was repeated, the execution time was faster than in the nonrepetition condition. This was the case in both the first ( $98 \pm 17$  ms) and second ( $148 \pm 19$  ms) sessions. Therefore, we combined the data across the two sessions.

### Participants Benefit from Repeating a Subsequence in Long Movement Sequences

We then asked whether the sequence repetition benefit can arise when only part of the sequence is repeated and what length of repetition is necessary to observe this benefit. To do so, we varied the number of repeated digits, repeated transitions, and the length of repeated subsequences embedded in otherwise random sequences (Fig. 1, B and C). For partial repetitions, we grouped the conditions by the number of total elements repeated. We only found an overall effect on ET when participants repeated six consecutive digits from the previous trial (Fig. 1B, conditions 11, 12, and 13 averaged;  $51 \pm 14$  ms,  $t_{29} = 3.670$ ,  $P = 9.7e-4$ ). This partial repetition benefit did not depend on the placement of repeated elements—the repetition benefit did not vary whether it occurred at the beginning, middle, or end of the sequence (interaction term of the repeated-measures ANOVA:  $F_{2,58} = 0.492$ ,  $P = 0.6139$ ). In contrast, the repetition of four consecutive elements (conditions 4, 5, 6, and 7 averaged;  $t_{29} =$

$0.628$ ,  $P = 0.5347$ ), the repetition of six elements arranged in three 2-digit pairs (conditions 9 and 10 averaged;  $t_{29} = 1.275$ ,  $P = 0.2125$ ), the repetition of six isolated elements (condition 8;  $t_{29} = 0.512$ ,  $P = 0.6126$ ), and the repetition of four isolated elements (conditions 2 and 3 averaged;  $t_{29} = -0.649$ ,  $P = 0.5213$ ) did not lead to a significant overall effect on ET.

Together, these findings suggest that the repetition benefit does not require the entire sequence to be repeated but can occur with a subsequence of at least 6 digits in length. The repeated subsequence can be reused flexibly, independent of its location within the sequence.

In agreement with our previous report (1), we also found a small repetition effect on RT for a full repetition ( $10 \pm 3$  ms,  $t_{29} = 3.146$ ,  $P = 0.003$ ). No statistically significant effect was observed in any of the other conditions, even if we restricted the analyses to conditions in which the repeated digits were at the beginning of the sequence (Fig. 2B;  $t_{29} < 1.882$ ,  $P > 0.0699$ ).

### The Activation of a Memory Trace Depends on Both Current and Previous Transitions

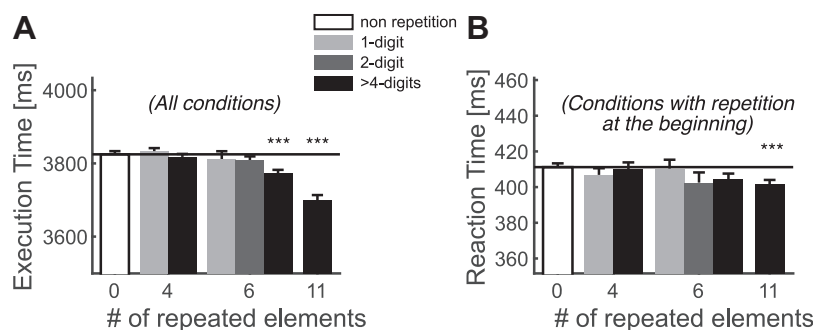
The overall execution time only improved following the repetition of 6 or 11 consecutive elements. The lack of a significant effect when 1, 2, or 4 consecutive finger presses were repeated, however, could reflect that the repetition both sped up and slowed down different parts of the sequence in such a way that the overall execution time did not statistically improve. To investigate this more closely, we performed a detailed analysis of the interpress intervals (IPIs).

We first analyzed the IPIs for full and nonrepetition conditions across the entire sequence (Fig. 3A). In a repetition  $\times$  IPI repeated-measures ANOVA, we found a significant effect of position ( $F_{9,261} = 23.536$ ,  $P < 2e-16$ ). In both conditions, the middle transitions were slower than the initial and final ones (IPI 1 vs. IPI 2–9:  $t_{29} = 5.106$ ,  $P = 1.8e-5$ , and IPI 10 vs. IPI 2–9:  $t_{29} = 7.228$ ,  $P = 5.8e-8$ ). This pattern is ubiquitous in DSP tasks and can be explained by the fact that the first few elements can be preplanned, enabling fast execution. In the middle of the sequence, participants have to plan the new actions on the fly (online planning), which slows their performance (8). Finally, in the end, more resources are available to plan the last elements, as no more future elements need to be taken into consideration, which again speeds up performance.

We also found a significant effect of repetition and a significant position  $\times$  repetition interaction ( $F_{9,261} = 4.900$ ,  $P = 4.4e-6$ ). Consistent with a previous report (1), the repetition benefit was smaller in the first transition and larger later in the sequence (IPI 1 vs. IPI 2–10:  $t_{29} = 5.364$ ,  $P = 9.2e-6$ ), suggesting that the repetition benefit arises from an acceleration of online planning.

To analyze this repetition benefit across the partial repetition conditions, we used the nonrepetition IPI for each sequential position as a baseline and subtracted it from the IPI data for each participant (Fig. 3B, see METHODS). We first asked whether there is a repetition benefit for any of the repeated IPIs. For 1-digit conditions, repeated IPI was not faster than the corresponding IPI in the nonrepetition conditions (data not shown;  $t_{29} = 1.962$ ,  $P = 0.0594$ ), suggesting that having an isolated digit at the same position as in the





**Figure 2.** Sequential nature of repetition improvement. **A:** group-averaged execution times for all conditions, categorized by the number of repeated digits, are presented. The contrasts indicate the length of the repeated subsequence (black: 4, 6, and 11-digit sequences; dark gray: 2-digit transitions; and light gray: isolated repeated digits). The solid black line represents the execution time for the condition with no repetition. Error bars represent the SE across participants. \*\*\* $P < 0.001$ , using two-tailed paired-sample  $t$  tests of each condition against the nonrepeated condition. **B:** group-averaged reaction times are shown in the same format as in **A** but for conditions with repetitions occurring at the beginning of the sequence.

last sequence is not sufficient for a repetition effect. For repeated transitions (2-digit conditions), we also did not find a repetition benefit (Fig. 3B, left;  $t_{29} = 0.725$ ,  $P = 0.4744$ ). For 4-digit conditions, however, a  $7 \pm 2$  ms repetition benefit was observed on repeated transitions (Fig. 3B, averaged over the first, middle, and last repeated transitions;  $t_{29} = 4.182$ ,  $P = 2.4 \times 10^{-4}$ ). A similar-sized repetition benefit of  $8 \pm 2$  ms was also found in the 6-digit conditions ( $t_{29} = 4.959$ ,  $P = 2.8 \times 10^{-5}$ ). The repetition effect for the 4- and 6-digit conditions was significant when applying Bonferroni correction for four tests.

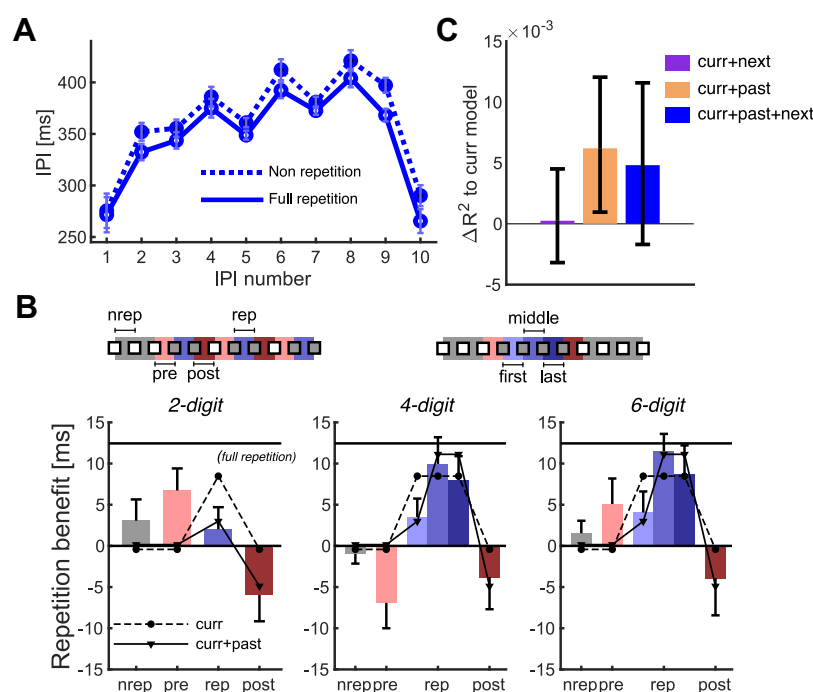
Interestingly, averaged across the 4- and 6-digit conditions, the speed-up in the first repeated transition was  $7 \pm 3$  ms smaller than in the middle transitions ( $t_{29} = 2.745$ ,  $P = 0.010$ ). In other words, the repetition effect was stronger when both the current and previous transitions matched the memory trace, suggesting the requirement of this matching for memory activation. This benefit for the middle transition was nearly the same size in the 4-digit ( $9 \pm 3$  ms) and 6-digit ( $11 \pm 2$  ms) conditions, and they both did not differ significantly from the repetition benefit in a fully repeated sequence ( $12 \pm 2$  ms): A repeated-measures ANOVA did not reveal a significant difference across these three situations

( $F_{2,58} = 0.478$ ,  $P = 0.6221$ ). Thus, a full repetition benefit occurs when the repeated segment is at least four digits long and does not seem to increase thereafter.

The repetition effect also did not seem to be sensitive to the next transition. For the last repeated transition in the repeated subsequence, the repetition benefit was as large as in the middle of the subsequence (averaged across 4- and 6-digit conditions,  $t_{29} = 0.795$ ,  $P = 0.4331$ ). Therefore, the influence of the memory trace does not seem to diminish, even when a future planned transition does not agree with the memory.

Finally, we asked whether the first nonrepeated transition after a repeated subsequence would be slower, which could indicate the interference between the activated memory trace for the last executed sequence and the incoming sensory information. Although we saw a small slowdown, the effect was not significant when averaged across the 4- and 6-digit conditions ( $t_{29} = -1.227$ ,  $P = 0.229$ ).

To systematically test for the contribution of the current, previous, and upcoming transitions to the repetition changes, we built four models incorporating different combinations of these factors (see METHODS). The baseline (“curr”) model only considered whether the current transition was



**Figure 3.** Repetition benefit is not solely an improvement in movement transitions. **A:** IPIs for full repetition (solid line) and nonrepetition (dotted line) conditions as a function of the position in the sequence. **B:** average repetition benefit on different transitions relative to the IPI at the same sequential position in the nonrepetition condition. The solid line represents the magnitude of the benefit in the full repetition condition. IPIs are grouped as “pre” (light red) if a nonrepeated IPI occurred before a repeated IPI, as “post” (dark red) if it occurred after, as “nrep” (gray) if it was not associated with repeated digits, and as “rep” (blue) if it was repeated. The repeated transitions were further grouped as “first,” “middle,” or “last,” depending on their position in the repeated subsequence. The dashed lines indicate the fit of the curr model, and the solid lines indicate the fit of the curr + past model. Error bars indicate the means  $\pm$  SE across participants. **C:** difference of  $R^2$  of curr + next (purple), curr + past (orange), and curr + past + next (blue) from the curr model. IPI, interpress interval.

repeated without any look-back or look-ahead window. Naturally, this model predicted equal benefits for all repeated IPIs (Fig. 3B, dashed line). The predictive  $R^2$  value of this model was 0.0127.

We then asked whether adding the information about the previous transition (curr + past model) resulted in a better prediction of repetition benefit. This model predicted smaller benefits for the first transition as well as post-repetition slowdown (Fig. 3C, solid lines). We found that the predictive  $R^2$  of this model was significantly larger than the baseline model by 95% confidence interval (CI) = (0.001, 0.012) (Fig. 3B).

The curr + past model did not predict the slight slowdown in the last transition compared with the middle one (Fig. 3C). Naturally, the model containing the information of the upcoming transition (curr + past + next model) was able to do that. However, adding information about the next transition to the curr and curr + past models did not result in a significant increase in predictive power. This suggests that the importance of the previous transition is more pronounced than that of the future one in activating the memory trace following sequence repetition.

## DISCUSSION

Our study investigated the structure of the first memory trace of a motor sequence, revealing key insights into how the brain processes and retains sequential information. Previous work has shown that, even after a single execution of a new sequence, the next execution of the same sequence is faster (1, 9). However, it remained unclear whether this improvement is due to the facilitation of individual movements (10), the transitions between them, chunks (or subsequences) of three or more movements, or the entire sequence.

In our study, we show that the repetition benefit does not only occur when the entire sequence is repeated. Even when only a subsequence of four consecutive movements was repeated from the preceding sequence, the execution of those finger presses was faster. A more recent study looking at the generalization of learning after a single trial (9) failed to find a benefit of a repeated subsequence of three presses. However, in our current paper, with careful counterbalancing of sequences and detailed analysis of different interpress intervals, we found that such benefits were present. The previous and current transitions (i.e., 3 presses in total) largely explained the repetition benefit (Fig. 3C).

Behavioral benefits when a learned chunk or subsequence (3 presses) is embedded in a random long sequence have also been observed in studies in which the learned sequence was trained over multiple days (5, 11–13). Thus, single-trial repetition and long-term motor skill learning appear similar in terms of behavioral generalization. This suggests that the initial sequential memory trace may have a similar structure to that of long-term memory. In addition, previous studies (1, 7) have shown that the repetition benefits decrease as long-term learning progresses, again suggesting that sequence repetition acts on the same representation that improves during multi-day learning.

In the current work, we cannot determine whether the specific position of the repeated subsequence within the

larger sequence is essential for repetition effects. Based on previous findings from sequence learning experiments (5), however, we would predict that the repetition benefit should be independent of where the subsequence is placed. Future work could test this by varying the relative location of repeated elements.

The neural mechanisms underlying this phenomenon likely involve the premotor and superior parietal areas of the brain. Notably, these regions have been shown to exhibit repetition suppression—reduced fMRI activity upon repeated sequence execution—even when the speed of execution is controlled (7). This suppression occurs in the same areas that are involved in long-term sequence learning, suggesting that the transient memory trace supporting repetition suppression shares a neural substrate with the stable memory trace that supports long-term skill retention (5, 14). This convergence of short-term and long-term memory processes highlights the role of these brain regions in both immediate and prolonged motor learning.

Our findings suggest that the nervous system breaks long sequences into manageable parts (15) rather than relying on a representation of the entire sequence. This insight is supported by our observation that increasing the length of the repeated segment beyond four movements did not provide any additional repetition benefit (Fig. 3B). However, it is still not clear whether the nervous system subdivides sequences discretely into fixed subsequences (i.e., chunks) or if it controls sequences using a finite temporal window, spanning both past and future targets. Dissociating the two possibilities is challenging because we do not know for certain how participants will break up a given sequence. First, the boundaries of chunks, indicated by slowdowns during sequence execution, differ among individuals and can change within the same participants during sequence learning (16). Second, slowdowns during sequence execution can also occur due to the biomechanical characteristics of the movements. Not knowing for certain where these chunk boundaries fall makes it harder to compare generalization within a chunk with generalization across chunk boundaries.

Our findings provide insight into the neural interactions between internal and external sequence representations (17–19). In our task, participants needed to read the numbers from the screen and convert these external cues into motor commands to execute the sequence. Previous studies have observed that a memory of a just-executed movement biases the motor cortex toward the execution of that movement (20). Such a bias might also exist for sequences but in higher-level brain areas, providing a memory trace that would cause a repetition benefit if it aligns with the externally cued subsequence.

One insight into the interaction between external stimuli and the memory trace comes from the finding that the repetition benefit was smaller at the beginning of the repeated segment and grew as more elements were repeated (Fig. 3B). This result suggests that, although the brain maintains an internal memory representation of all repeated finger presses, the memory is not fully activated until the memory and external cue match for a few finger presses. That is, memory activation appears to depend both on the present and the recent past.

Previous work has shown that the motor system plans a number of upcoming movements while controlling the current movement (8, 21, 22). Given this, it might be expected that participants slowdown once they detect a mismatch between a future stimulus and a future planned movement. This was not the case, as the last IPI of a repeated subsequence was not significantly slower than the one in the middle of the subsequence (Fig. 3B). Therefore, the influence of the lingering memory trace appears to be modulated only by the match with past (executed) movements but not on the match with future (planned) movements. This observation provides important constraints on the neural mechanisms that control the interactions between externally cued sequence execution and the earliest forms of sequence memory.

## DATA AVAILABILITY

Data will be made available upon reasonable request.

## GRANTS

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## AUTHOR CONTRIBUTIONS

M.S., J.A.P., and J.D. conceived and designed research; M.S. performed experiments; M.S. analyzed data; M.S. and J.D. interpreted results of experiments; M.S. prepared figures; M.S. drafted manuscript; M.S., J.A.P., and J.D. edited and revised manuscript; M.S., J.A.P., and J.D. approved final version of manuscript.

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