The planning horizon for movement sequences

Running title: The horizon of sequence planning

Giacomo Ariani[1, 2, §, *], Neda Kordjazi[1, §], Jörn Diedrichsen[1, 2, 3]

[1]The Brain and Mind Institute, [2]Department of Computer Science, [3]Department of Statistical and Actuarial Sciences, Western University, London, Ontario N6A 3K7, Canada.

[§]Denotes equal contribution.

*Correspondence. Address correspondence to Giacomo Ariani at gariani@uwo.ca, The Brain and Mind Institute, Western University, Western Interdisciplinary Research Building, London, ON N6A 3K7, Canada.

Word count. Abstract: 220; Introduction: 603; Discussion: 1460. 24 pages, 6 figures, 0 tables.

Author contributions. N.K. and J.D. designed research; N.K. performed research; G.A. and N.K. analyzed data; G.A. drafted the manuscript; G.A. and J.D. edited the manuscript.

Acknowledgements. This work was supported by a James S. McDonnell Foundation Scholar award, an NSERC Discovery Grant (RGPIN-2016-04890), and the Canada First Research Excellence Fund (BrainsCAN). We thank Eva Berlot and J. Andrew Pruszynski for comments on earlier versions of the manuscript.

Disclosures. The authors declare no conflicts of interest.

Abstract

When performing a long chain of actions in rapid sequence, future movements need to be planned concurrently with ongoing action. However, how far ahead we plan, and whether this ability improves with practice, is currently unknown. Here we designed an experiment in which healthy volunteers were asked to produce 14-item sequences of finger movements quickly and accurately in response to numerical stimuli. On every trial, participants were only shown a fixed number of stimuli ahead of the current keypress. The size of this viewing window varied between 1 (next digit revealed with pressing of current key) and 14 (full view of the sequence). Participants practiced the task for 5 days and their performance was continuously assessed on random sequences. Our results clearly indicate that participants used the available visual information to plan multiple actions into the future, but that the planning horizon was limited: receiving more information than 3 movements ahead did not result in faster sequence production. Over the course of practice, we found larger performance improvements for larger viewing windows. Additionally, we show that the improved planning was accompanied by an expansion of the planning horizon with practice. Together, these findings show that one important aspect of sequential motor skills is the ability of the motor system to exploit visual information for planning multiple responses into the future.

Key words

Motor planning; Sequence production; Practice effects; Hand function.

Introduction

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

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

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

Here we asked 1) how far the benefit of planning ahead extends beyond current execution, and 2) whether this planning horizon can be improved with practice. To answer these questions, we used a

discrete sequence production (DSP) task, in which participants performed random sequences of 14 keypresses with their right hand in response to numerical cues. We manipulated how many digits participants could see ahead of the current keypress. Viewing window size ranged from 1 (only the next movement is cued, as in the serial reaction time task, SRTT) to 14 (the entire sequence shown at once, as in the DSP task). Participants practiced producing varying sequences over 5 days. This design allowed us to examine both the horizon of motor planning in sequence production and the influence of practice on the planning horizon.

Methods

Participants

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

Apparatus

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

Procedure

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

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

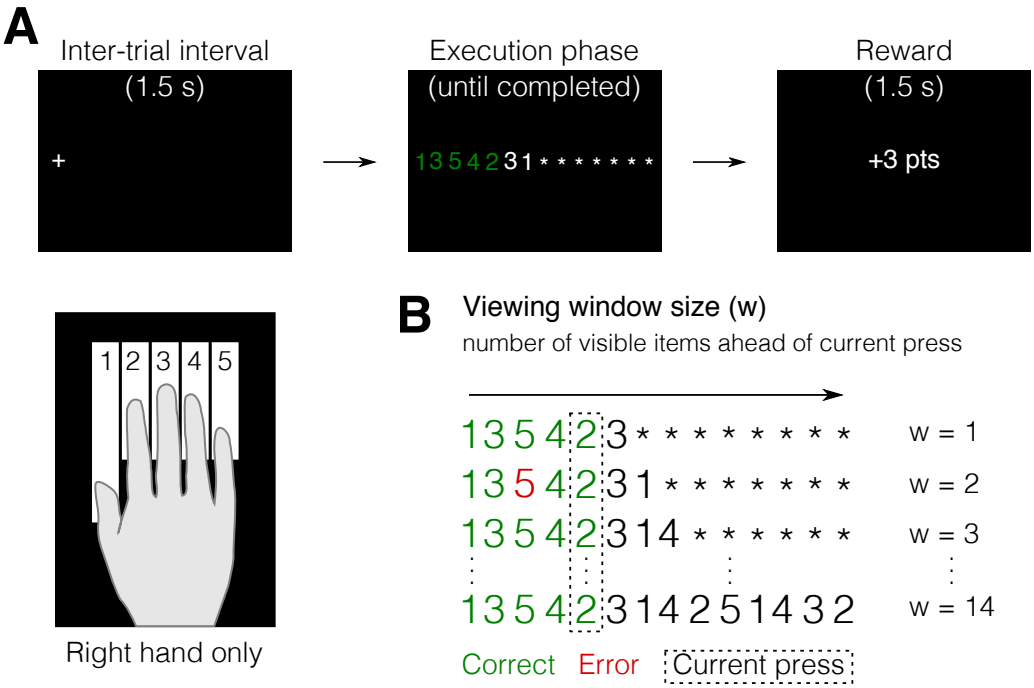

Figure 1 | Varying viewing window in a discrete sequence production (DSP) task. A. *Example trial in a DSP task with viewing 2 items ahead of the current keypress, while the remaining items are masked by asterisks.* ***B.*** *Viewing window size (w) manipulation, from w = 1 (equivalent to a simple reaction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

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

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

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

Data analysis

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

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

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

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

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

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

Results

Preplanning future movements speeds up sequence production

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

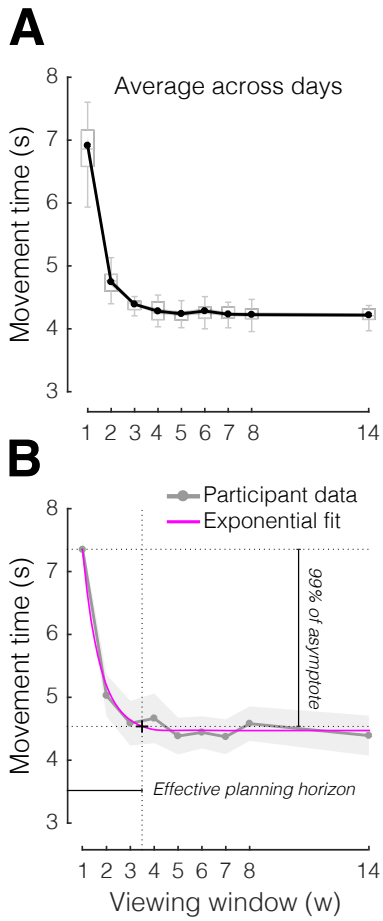

Figure 2 | The benefit of planning ahead on sequential performance. A. *Average movement time as a function of viewing window, across the 5 days of*

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

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

Practice expands the planning horizon

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

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

determined the effective planning horizon for each participant and day (Fig. 2B) using an exponential fit (see Methods), we found that the planning horizon expanded from 3.20 to 3.88 digits ahead of current action between day 1 and day 5 (paired-samples *t*-test, t_{13} = 2.840, p = 0.014, Fig. 3C). Thus, participants not only became more efficient in planning but planned sequential actions further into the future.

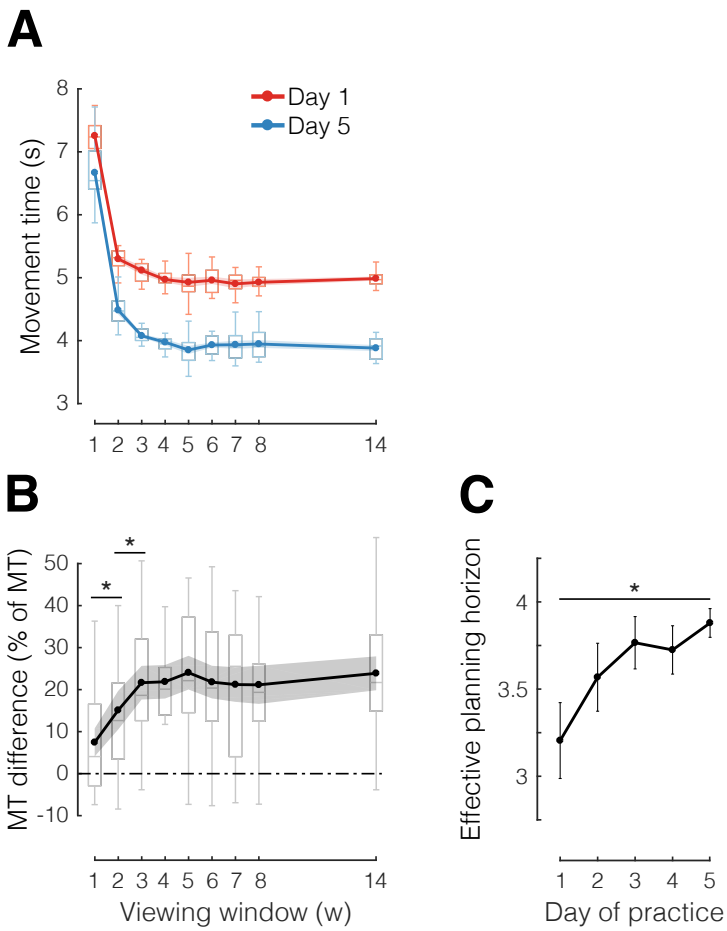

Figure 3 | The effective planning horizon increases with practice. A. *Average movement time (MT) as a function of viewing window (w), separately for early (day 1, red) and late (day 5, blue) stages of sequence practice.* ***B.*** *Difference in performance (sequence MT) between early and late practice (data in A), normalized by average MT, as a function of w.* ***C.*** *Mean effective planning horizon (estimated as shown in Fig. 2B) for each day of practice. Box plots show the median and whole range of individual data points (one per participant). Shaded areas (or error bars) reflect standard error of the mean. *p < 0.05, two-tailed paired-samples t-tests.*

Note that faster MTs for larger window sizes did not occur at the expense of reduced accuracy in performance. On average, the percent accuracy of presses remained roughly constant around 85-90%

across all viewing window conditions. We found no significant main effect of window size ($F_{8,104}$ = 1.182, p = 0.317), practice stage ($F_{1,13}$ = 0.325, p = 0.578), or interaction between the two factors ($F_{8,104}$ = 0.548, p = 0.818).

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

Reaction times increase with the amount of preplanning

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

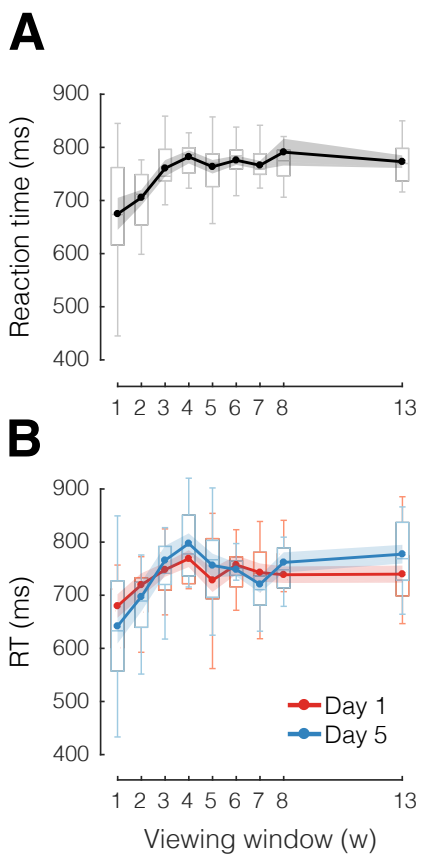

Figure 4 | Longer reaction times for larger viewing windows. ***A.*** *Average reaction time as a function of viewing window.* ***B.*** *Subset of data in A, separating between early (day 1, red) and late (day 5, blue) stages of practice. Box plots show the median and whole range of individual data points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

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

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

Planning ahead continues during sequence production

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

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

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

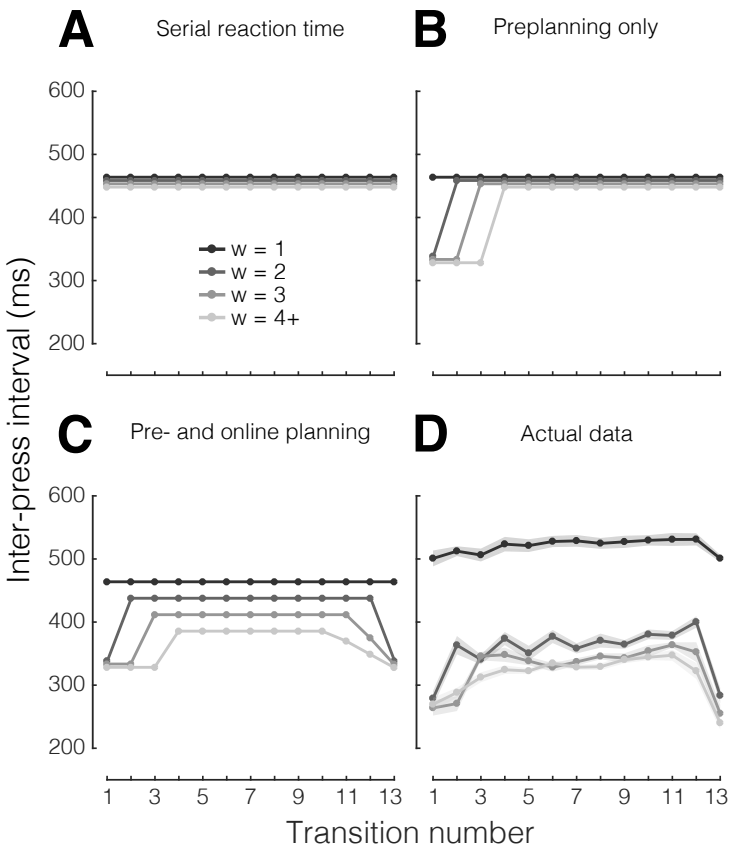

Figure 5 | Predictions and analysis of inter-press intervals (IPIs). *Average inter-press interval (IPI) as a function of transition number within each sequence, separately for viewing window size (w, different shades of gray). 4+ indicates w ≥ 4.* ***A.*** *Prediction 1 (null hypothesis): no effect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

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

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

Both pre- and online planning improve with practice

Finally, we asked whether practice effects on MT are more likely related to improvements in preplanning, online planning, or both. From day 1 to day 5 (Fig. 6A), we observed significant main effects of practice stage on IPI duration on both early (IPI 1-3: $F_{1,13}$ = 17.623, p = 0.001) and middle IPIs (IPI 5-12: $F_{1,13}$ = 15.988, p = 0.002). To quantify the relative contributions of preplanning and online planning, we carried a separate analysis (Fig. 6B) averaging across IPIs that were more likely preplanned (IPI 1 for w = 2, IPI 1-2 for w = 3, and IPI 1-3 for w ≥ 4), or not (the remaining IPIs for each viewing window condition, which had to be planned online). For w = 1, only the first press, but not the first IPI, can be preplanned. Therefore, we cannot attribute any of the observed improvements to either sequence preplanning or online planning. Instead, eventual improvements need to arise from improved visual identification, S-R mapping, or execution. We computed the IPI difference between day 1 and day 5 for these three categories, normalized it by the average IPI duration across days (separately for each category), and plotted it against viewing window size (Fig. 6B). This analysis confirmed that IPIs

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

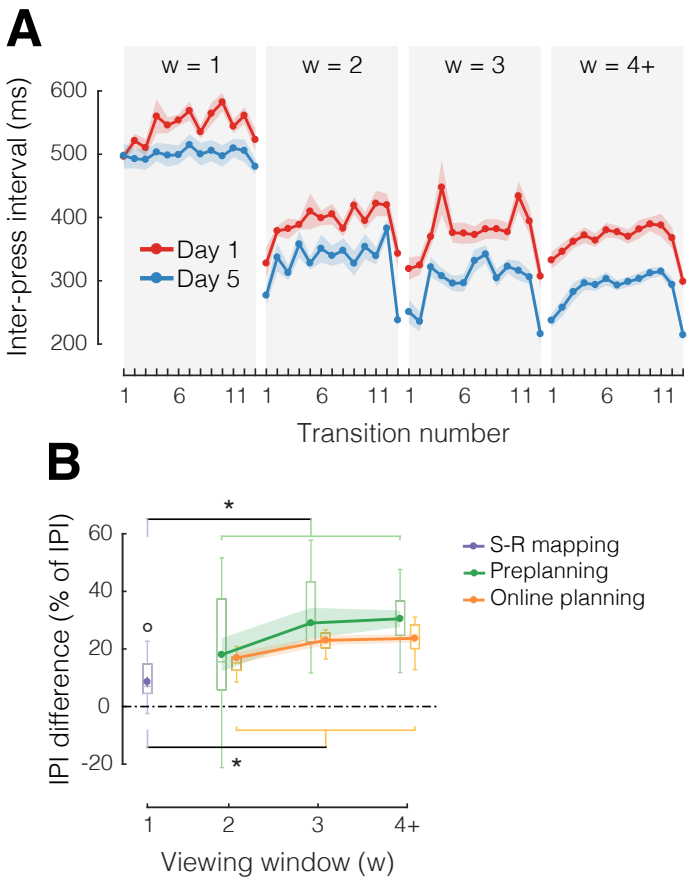

Figure 6 | Improvements in pre- and online planning with practice. A. *Mean IPI as a function of transition number, separately for practice stage (day 1, red; day 5, blue) and viewing window size (w = 1, 2, 3, 4+ in separate plots).* ***B.*** *Average IPI difference between day 1 and day 5, normalized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

Discussion

The ability to plan ahead for future actions while executing current ones is a fundamental yet underappreciated faculty of the human brain. In this study, we manipulated the amount of visual information available for motor planning while performing a discrete sequence production task. Our results provide evidence that participants planned multiple sequential actions (at least 3) into the future (Fig. 2-4). Furthermore, we show larger practice-induced benefits in speed for larger window sizes (MT difference, Fig. 3), as well as increases in the horizon of sequence planning (based on the exponential fit, Fig. 3). In-depth analysis of the inter-press intervals (Fig. 5-6) revealed that the enhanced planning of future actions was present both before (preplanning) and during (online planning) sequence production.

Fast sequence production depends on the speed of online planning

Before a voluntary movement can be performed, it needs to be planned (Keele, 1968; Keele and Summers, 1976; Kerr, 1978; Rosenbaum, 1980; Bock and Arnold, 1992; Crammond and Kalaska, 1994, 2000; Cisek and Kalaska, 2002, 2004), at least to some degree (Cisek and Kalaska, 2010; Ames et al., 2014). However, many real-life motor skills require quick sequences of movements that are not always predictable. Proficiency in such skills depends on our ability to select and plan future movements both before sequence onset and during sequence production. To shed light on this ability, we used a viewing window paradigm that varied the amount of information available for planning the next finger movements. We replicate previous work showing evidence for anticipatory planning in the context of movement sequences (Rosenbaum et al., 1987; Rhodes et al., 2004; Herbort and Butz, 2009), and longer reaction times when more elements are available for planning ahead (Henry and Rogers, 1960). Furthermore, we show that, once preplanning reaches capacity, the execution of later elements in the sequence slows down, which we interpret as evidence that successive movements need to be planned online. In a previous paper (Ariani and Diedrichsen, 2019), we have reported that this is the case even when participants execute relatively short (e.g., 5-item) and well-known (e.g., trained) sequences. By varying the time available for preplanning a sequence, we could show that only the first 3 sequence elements were planned prior to execution. Further evidence for online planning across a range of activities comes from studies investigating how visual information is used for motor planning. For example, it has been shown that participants move their eyes to future targets in reading (Rayner, 1978), sequential reaching (Säfström et al., 2014), and object manipulation (Johansson et al., 2001). More directly, a recent unpublished study revealed the horizon of online planning by restricting the viewing window in a continuous manual tracking task (Bashford et al., 2018). Together, these studies support our view that the ability of the motor system to deal with a stream of incoming stimuli while

437 producing motor responses (i.e., the speed of online planning) enables skillful performance for
438 unpredictable movement sequences.
439
440 *Motor planning has a limited capacity*
441 Despite its importance, our ability to plan future movements is somewhat limited. We found the span
442 of the planning horizon (~3-4 movements) to be smaller than the typical amount of information that
443 can be stored in short-term memory (Miller, 1956; Cowan, 2010). However, according to a more recent
444 theory, short-term memory capacity is not dictated by a fixed number of items, but rather should be
445 viewed as a finite resource that can be allocated flexibly across multiple items via selective attention
446 (Luck and Vogel, 1997; Bays and Husain, 2008). Similarly, characterizing the planning horizon as having
447 a hard, discrete limit (i.e., a specific number of movements) may not be the best description. A more
448 realistic model may be that planning capacity has a soft horizon that depends on the amount of
449 cognitive resources available for planning. In accordance with the competitive queueing hypothesis
450 (Averbeck et al., 2002, 2006; Rhodes et al., 2004; Kornysheva et al., 2019; Mantziara et al., 2020), this
451 idea predicts that more planning resources are allocated to the immediately upcoming actions, and
452 decreasing amount of attention is paid to future actions. Eventually subjects run out of resources and
453 start executing responses. Completing preceding movements frees up new resources that can be
454 allocated to plan successive movements online. Thus, the discrepancy between the short-term memory
455 span and planning horizon may reflect the fact that planning a movement takes up more central
456 resources than remembering a digit.
457
458 *The horizon of motor planning can be expanded with practice*
459 Conceptualizing the capacity of motor planning as a limited resource makes it interesting to ask
460 whether the planning horizon can be improved with practice. Indeed, in agreement with a previous
461 unpublished study (Bashford et al., 2018), we found that practice had expanded the span of the
462 planning horizon. Our conclusion was based on two key observations: 1) the benefit of seeing further
463 ahead was greater late than early in practice (significant interaction between w and day on MT); 2) the
464 influence of window size on MT can be described with an exponential function whose decay rate
465 decreased with practice (change in the slope of the exponential). Speed improvements that are
466 independent of the amount of available information can be attributed to improved stimulus
467 identification, S-R mapping, or implementation of single responses (Haith et al., 2016; Ariani and
468 Diedrichsen, 2019; Hardwick et al., 2019). As participants become more fluent at translating numbers
469 on the screen into finger movements, each individual press is executed more quickly, thus contributing
470 to faster sequence production across all window sizes. The greater performance benefits for larger

window sizes, together with the expansion of the effective planning horizon, however, clearly indicate that participants improved their ability to make use of advance information. Importantly, we show that these improvements occur not only for preplanning (i.e., before movement onset) but also for online planning (i.e., after movement onset). Unlike previous studies that examined sequence-specific effects in sequence production (Verwey, 2001; Verwey and Wright, 2004; Wiestler and Diedrichsen, 2013; Ariani and Diedrichsen, 2019; Berlot et al., 2020), here we focused on random sequences. Note that, because of this, the observed practice effects cannot be explained by the formation of specific chunking structures previously proposed as a way to deal with the complexity of planning long movement sequences (Ramkumar et al., 2016; Popp et al., 2020). Instead, we found that even when people have no prior experience with a sequence, they can over time improve in the motor planning processes that underlie sequence production. In other words, practice effects are not only about learning *what* sequence to produce, but also about learning *how* to coordinate execution and planning efficiently.

Do pre- and online planning rely on the same neural process?

Our results revealed notable similarities between preplanning and online planning. Both processes contributed to faster sequential performance when participants had a chance to see at least 3 upcoming sequence elements, with diminishing gains for larger window sizes. Moreover, practice-related improvements on the relevant IPIs (early IPIs for preplanning, late IPIs for online planning) were comparable between the two processes. These similarities suggest that preplanning and online planning may rely on the same process, i.e., motor planning, either happening in isolation before movement initiation, or in parallel, simultaneous with execution. This raises questions about the neuronal implementation of pre- and online planning. Previous research has shown that movement planning is also reflected in brain structures responsible for movement execution, such as the primary motor cortex (M1), and the dorsal premotor cortex (PMd, Crammond and Kalaska, 2000; Ames et al., 2014, 2019; Elsayed et al., 2016; Ariani et al., 2018; Lara et al., 2018). A recent study (Ames et al., 2019) also shows that *re*-planning of an ongoing movement engages similar neuronal population dynamics as preplanning it. The authors recorded M1 and PMd activity in two monkeys performing a delayed reaching task with occasional target jumps (20% of trials) that could occur during the RT (before movement onset) and would require mid-reach corrections. They found that neuronal population activity related to the target jump played out in both the neural state-spaces defined by preparatory and movement activity recorded on non-jump trials. However, it remains unclear which neuronal populations are engaged when online planning is not related to the ongoing movement, but rather to future and possibly different movements. Since the neuronal state of the main sensorimotor regions is likely occupied by execution processes related to the ongoing movement, do online planning processes

shift to other structures? Or do they engage separate state-space dimensions within the same region? Our study lays the behavioral foundation for this investigation, showing that humans are able to plan multiple movements into the future while simultaneously controlling an ongoing movement. This ability of online planning improves with practice and is a key determinant of any skilled sequence production.

References

Ames KC, Ryu SI, Shenoy K V. (2014) Neural dynamics of reaching following incorrect or absent motor preparation. Neuron 81:438–451.

Ames KC, Ryu SI, Shenoy K V. (2019) Simultaneous motor preparation and execution in a last-moment reach correction task. Nature Communications 10:2718.

Ariani G, Diedrichsen J (2019) Sequence learning is driven by improvements in motor planning. Journal of Neurophysiology 121:2088–2100.

Ariani G, Kwon YH, Diedrichsen J (2020) Repetita iuvant: repetition facilitates online planning of sequential movements. Journal of Neurophysiology 123:1727–1738.

Ariani G, Oosterhof NN, Lingnau A (2018) Time-resolved decoding of planned delayed and immediate prehension movements. Cortex 99.

Averbeck BB, Chafee M V., Crowe DA, Georgopoulos AP (2002) Parallel processing of serial movements in prefrontal cortex. Proceedings of the National Academy of Sciences 99:13172–13177.

Averbeck BB, Sohn JW, Lee D (2006) Activity in prefrontal cortex during dynamic selection of action sequences. Nature Neuroscience 9:276–282.

Bashford L, Kobak DD, Diedrichsen J, Mehring C (2018) Motor skill learning leads to the increase of planning horizon. bioRxiv c:505198.

Bays PM, Husain M (2008) Dynamic Shifts of Limited Working Memory Resources in Human Vision. Science 321:851–854.

Berlot E, Popp NJ, Diedrichsen J (2020) A critical re-evaluation of fMRI signatures of motor sequence learning. eLife 9:2020.01.08.899229.

Bock O, Arnold K (1992) Motor control prior to movement onset: preparatory mechanisms for pointing at visual targets. Experimental Brain Research 90:209–216.

Churchland MM, Cunningham JP, Kaufman MT, Ryu SI, Shenoy K V. (2010) Cortical Preparatory Activity: Representation of Movement or First Cog in a Dynamical Machine? Neuron 68:387–400.

Cisek P, Kalaska JF (2002) Simultaneous Encoding of Multiple Potential Reach Directions in Dorsal Premotor Cortex. Journal of Neurophysiology 87:1149–1154.

Cisek P, Kalaska JF (2004) Neural correlates of mental rehearsal in dorsal premotor cortex. Nature 431:993–996.

Cisek P, Kalaska JF (2010) Neural mechanisms for interacting with a world full of action choices. Annual review of neuroscience 33:269–298.

Cohen A, Ivry RB, Keele SW (1990) Attention and structure in sequence learning.

JExpPsychol[LearnMemCogn] 16:17–30.
Cowan N (2010) The Magical Mystery Four. Current Directions in Psychological Science 19:51–57.
Crammond DJ, Kalaska JF (1994) Modulation of preparatory neuronal activity in dorsal premotor cortex due to stimulus-response compatibility. Journal of Neurophysiology 71:1281–1284.
Crammond DJ, Kalaska JF (2000) Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity. Journal of neurophysiology 84:986–1005.
Diedrichsen J, Kornysheva K (2015) Motor skill learning between selection and execution. Trends in Cognitive Sciences 19:227–233.
Elsayed GF, Lara AH, Kaufman MT, Churchland MM, Cunningham JP (2016) Reorganization between preparatory and movement population responses in motor cortex. Nature Communications:13239.
Ericsson KA, Krampe RT, Tesch-Römer C (1993) The role of deliberate practice in the acquisition of expert performance. Psychological Review 100:363–406.
Haith AM, Pakpoor J, Krakauer JW (2016) Independence of Movement Preparation and Movement Initiation. Journal of Neuroscience 36:3007–3015.
Hardwick RM, Forrence AD, Krakauer JW, Haith AM (2019) Time-dependent competition between goal-directed and habitual response preparation. Nature Human Behaviour 3:1252–1262.
Henry FM, Rogers DE (1960) Increased Response Latency for Complicated Movements and A "Memory Drum" Theory of Neuromotor Reaction. Research Quarterly American Association for Health, Physical Education and Recreation 31:448–458.
Herbort O, Butz M V. (2009) Anticipatory planning of sequential hand and finger movements. Journal of Motor Behavior 41:561–569.
Johansson RS, Westling G, Bäckström A, Flanagan JR (2001) Eye–Hand Coordination in Object Manipulation. The Journal of Neuroscience 21:6917–6932.
Kaufman MT, Churchland MM, Ryu SI, Shenoy K V (2014) Cortical activity in the null space: permitting preparation without movement. Nature Publishing Group 17.
Keele SW (1968) Movement control in skilled motor performance. Psychological Bulletin 70:387–403.
Keele SW, Summers JJ (1976) The Structure of Motor Programs. In: Motor Control, pp 109–142. Elsevier.
Kerr B (1978) Task Factors That Influence Selection and Preparation for Voluntary Movements. In: Information Processing in Motor Control and Learning, pp 55–69. Elsevier.
Kornysheva K, Bush D, Meyer SS, Sadnicka A, Barnes G, Burgess N (2019) Neural Competitive Queuing of Ordinal Structure Underlies Skilled Sequential Action. Neuron 101:1166-1180.e3.
Kornysheva K, Sierk A, Diedrichsen J (2013) Interaction of temporal and ordinal representations in

movement sequences. Journal of Neurophysiology 109:1416–1424.
Krakauer JW, Hadjiosif AM, Xu J, Wong AL, Haith AM (2019) Motor learning. Comprehensive Physiology 9:613–663.
Lara AH, Elsayed GF, Zimnik AJ, Cunningham JP, Churchland MM (2018) Conservation of preparatory neural events in monkey motor cortex regardless of how movement is initiated. eLife 7.
Lashley K (1951) The problem of serial order in behavior. Cerebral Mechanisms in Behavior Edited by:112–147.
Luck SJ, Vogel EK (1997) The capacity of visual working memory for features and conjunctions. Nature 390:279–284.
Mantziara M, Ivanov T, Houghton G, Kornysheva K (2020) Competitive state of actions during planning predicts sequence execution accuracy. bioRxiv:2020.05.08.085068.
Miller GA (1956) The magical number seven, plus or minus two: some limits on our capacity for processing information. Psychological Review 63:81–97.
Popp NJ, Yokoi A, Gribble PL, Diedrichsen J (2020) The effects of habits on motor skill learning. bioRxiv:338749.
Ramkumar P, Acuna DE, Berniker M, Grafton ST, Turner RS, Kording KP (2016) Chunking as the result of an efficiency computation trade-off. Nature Communications 7:1–11.
Rayner K (1978) Eye movements in reading and information processing. Psychological Bulletin 85:618–660.
Rayner K (1998) Eye movements in reading and information processing: 20 years of research. Psychological Bulletin 124:372–422.
Rayner K (2014) The gaze-contingent moving window in reading: Development and review. Visual Cognition 22:242–258.
Rayner K, Reingold EM (2015) Evidence for direct cognitive control of fixation durations during reading. Current Opinion in Behavioral Sciences 1:107–112.
Rhodes BJ, Bullock D, Verwey WB, Averbeck BB, Page MPA (2004) Learning and production of movement sequences: Behavioral, neurophysiological, and modeling perspectives. Human Movement Science 23:699–746.
Rosenbaum DA (1980) Human movement initiation: Specification of arm, direction, and extent. Journal of Experimental Psychology: General 109:444–474.
Rosenbaum DA, Cohen RG, Jax SA, Weiss DJ, van der Wel R (2007) The problem of serial order in behavior: Lashley's legacy. Human Movement Science 26:525–554.
Rosenbaum DA, Hindorff V, Munro EM (1987) Scheduling and Programming of Rapid Finger Sequences: Tests and Elaborations of the Hierarchical Editor Model. Journal of Experimental

Psychology: Human Perception and Performance 13:193–203.
Säfström D, Flanagan JR, Johansson RS (2013) Skill learning involves optimizing the linking of action phases. Journal of Neurophysiology 110:1291–1300.
Säfström D, Johansson RS, Flanagan JR (2014) Gaze behavior when learning to link sequential action phases in a manual task. Journal of Vision 14:1–15.
Van Galen GP, Smyth MM, Meulenbroek RGJ, Hylkema H (1989) The role of short-term memory and the motor buffer in handwriting under visual and non-vidual guidance. Computer Recognition and Human Production of Handwriting:253–271.
Verwey WB (1994) Mechanisms of skill in sequential motor behavior.
Verwey WB (2001) Concatenating familiar movement sequences: The versatile cognitive processor. Acta Psychologica 106:69–95.
Verwey WB, Abrahamse EL (2012) Distinct modes of executing movement sequences: Reacting, associating, and chunking. Acta Psychologica 140:274–282.
Verwey WB, Shea CH, Wright DL (2014) A cognitive framework for explaining serial processing and sequence execution strategies. Psychonomic Bulletin and Review 22:54–77.
Verwey WB, Wright DL (2004) Effector-independent and effector-dependent learning in the discrete sequence production task. Psychological Research.
Waters-Metenier S, Husain M, Wiestler T, Diedrichsen J (2014) Bihemispheric Transcranial Direct Current Stimulation Enhances Effector-Independent Representations of Motor Synergy and Sequence Learning. The Journal of Neuroscience 34:1037–1050.
Wiestler T, Diedrichsen J (2013) Skill learning strengthens cortical representations of motor sequences. eLife 2:e00801.
Wiestler T, Waters-Metenier S, Diedrichsen J (2014) Effector-independent motor sequence representations exist in extrinsic and intrinsic reference frames. Journal of Neuroscience 34:5054–5064.
Willingham DB (1999) Implicit motor sequence learning is not purely perceptual. Memory and Cognition 27:561–572.
Wong AL, Haith AM, Krakauer JW (2015a) Motor Planning. The Neuroscientist 21:385–398.
Wong AL, Lindquist MA, Haith AM, Krakauer JW (2015b) Explicit knowledge enhances motor vigor and performance: motivation versus practice in sequence tasks. Journal of Neurophysiology 114:219–232.
Yarrow K, Brown P, Krakauer JW (2009) Inside the brain of an elite athlete: the neural processes that support high achievement in sports. Nature reviews Neuroscience 10:585–596.