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RESEARCH ARTICLE

Serial practice impairs motor skill consolidation

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Abstract Recent reports have revealed that motor skill learning is impaired if two skills are practiced one after the other, that is before the first skill has had the time to become consolidated. This suggests that motor skills should be practiced in isolation from one another to minimize interference. At the moment, little is known about the effect of practice schedules high in contextual interference on motor skill consolidation. In Experiment 1, we investigated whether a serial practice schedule impairs motor skill consolidation. Participants had to learn two distinct sequences of finger movements (A and B) under either a blocked practice schedule or a serial practice schedule before being retested the following day. A control group also practiced Sequence A only. Our results revealed that a blocked practice schedule led to no interference between the sequences, whereas a serial practice schedule impaired the consolidation of Sequence B. In Experiment 2, we investigated the origin of the interference caused by a serial practice schedule by replacing the physical practice of Sequence A with either the observation of a model performing Sequence A or by asking participants to produce random finger movements. Our results revealed that both tasks interfered with the consolidation of Sequence B. Thus, we suggest that a serial practice schedule impairs motor skill consolidation through a conflict in the brain networks involved in the acquisition of the cognitive representation of the sequence and its execution.

Keywords Finger sequence task · Consolidation · Offline learning · Contextual interference · Serial practice · Observational learning

Introduction

Although physical practice has traditionally been seen as the most determinant factor for motor skill learning, recent experiments have challenged this position by showing that important neurophysiological processes also take place between the practice sessions (Walker et al. 2003; Krakauer and Shadmehr 2006; Stickgold and Walker 2007). More specifically, it has been shown that the acquisition of a new motor skill triggers various physiological changes in the brain, from gene expression to protein synthesis, which are essential to the long-term storage of the memory representation of the new skill. Convincing evidence for this idea has been obtained in rodent experiments in which the administration of a protein synthesis inhibitor had no impact on the rodents performance during the acquisition session but dramatically impaired the rodents' ability to demonstrate the acquired skill at a later time (McGaugh 2000). Thus, motor skill learning can be seen as a two-phase process in which the skill is first acquired during a practice session and then stored in long-term memory after the practice session. This second, "storage" phase is now referred to as consolidation, a process dependent on the passage of time (see Walker 2005; Krakauer and Shadmehr 2006; Trempe and Proteau 2012 for reviews).

Behaviorally, consolidation allows a newly practiced motor skill to be stored in long-term memory and to become resistant to different forms of interference (Robertson et al. 2004; Krakauer and Shadmehr 2006). For example, practicing two similar yet distinct sequences of movements

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immediately after one another impairs the retention of at least one of the two sequences, whereas no impairment occurs when the second sequence is learned several hours after the acquisition of the first one, i.e., after the first sequence has had the time to consolidate (see Trempe and Proteau 2012 for a description of similar results using a variety of other tasks and interfering agents). These results suggest that the memory representation emerging from the physical practice of a motor skill is initially labile and subject to interference before becoming stable and resistant to interference through consolidation (Brawn et al. 2010). The amount of interference between two skills depends on their intrinsic characteristics and the degree to which their representation conflict in working memory (Bays et al. 2005). For example, interference has been reported when the same brain networks were activated by the two skills (Shadmehr and Holcomb 1999), when participants wrote a few words in their native language after practicing a sequence of finger movements (Balas et al. 2007b), but not when the writing task was performed with the other hand (Balas et al. 2007a), and interference has also been observed when participants performed a semantic judging task after learning the finger sequence (Tibi et al. 2013). Together, these results demonstrate that the integrity of the consolidation process can be affected by the nature of the other tasks performed soon after acquisition.

Based on the aforementioned results, one could come to the conclusion that when a learner has to learn two distinct but similar motor skills, better long-term retention (or learning) would occur if the two skills are practiced in isolation from one another. Due to the initial fragility of the memory representation of the skills during and immediately following acquisition, allowing one motor skill to become consolidated before practicing the second skill would seem an optimal learning strategy as it would avoid any potential interference between the skills. Although this recommendation is intuitively appealing and finds support in several reports in the consolidation literature (Brashers-Krug et al. 1996; Krakauer et al. 1999; Walker et al. 2003), it nevertheless implies that it should be impossible to learn two motor skills in the same practice session (either alternately or in succession). As discussed in Robertson et al. (2004), this is not the case as several reports have demonstrated that two distinct procedural tasks can be learned at the same time. In addition, the conclusion that motor skills should only be practiced in isolation from one another is not supported by results stemming from contextual interference (CI) experiments (Shea and Morgan 1979) in which practice schedules that favor high interference between two tasks (e.g., when two tasks are learned alternately during a practice session or under a random schedule) lead to better learning compared to a practice schedule in which the interference between the tasks is minimized (e.g., when two motor skills are learned one after the other under a "blocked" schedule; Shea and Morgan 1979). Considering the recent literature on motor skill consolidation, the finding that a practice schedule which forces the learner to alternate between two skills during the same session can lead to better learning is puzzling as conditions that promote interference have usually been shown to be detrimental to the behavioral manifestations of consolidation. If a motor skill is initially labile and subject to interference, one could expect the high interference associated with an alternated practice schedule to result in impaired consolidation and poor learning. To our knowledge, very few studies have looked specifically at the effect of varying the level of contextual interference on the consolidation process. Using a repetitive transcranial magnetic stimulation (rTMS) following the acquisition of four different variations of a movement sequence, Kantak et al. (2010) reported that the brain structures engaged in the consolidation of the motor skill changes according to the practice schedule employed during acquisition (see also Wymbs and Grafton 2009; Song et al. 2012). The authors suggested that the modulation of the neural substrates involved in motor-memory consolidation may reflect a difference in the components of the task that were learned; variable practice (with random ordering) would favor the acquisition of the goal of the movements (i.e., the order of the elements in the sequence), whereas constant practice would favor the acquisition of the movement component of the sequence (i.e., how to produce the sequence; see Robertson 2009 for a description of this theoretical framework). This suggestion finds support in the results of Wilde et al. (2005) who reported that participants used different learning strategies based on the practice schedule they were exposed to when they attempted to learn three sequences of movements. Recently, Kim et al. (2016) conducted a series of experiment in which they assessed the consolidation of three sequences of finger movements learned under a random or blocked practice schedule. Since the authors assessed retention by averaging together the score of the three sequences, it was impossible to determine whether interference occurred between the sequences. Therefore, it remains unknown at this time whether a practice schedule associated with high contextual interference impairs motor skill consolidation.

To answer this question, we used a finger sequence task in which participants were asked to learn to type as fast and accurately as possible one or two 5-element sequences on a computer keyboard. Using this task, it has been repeatedly shown that consolidation not only leads to a more stable memory representation but can also trigger spontaneous performance gains (Robertson et al. 2004); when participants are retested following a consolidation interval lasting several hours, they demonstrate an increase in their typing speed (Fischer et al. 2002; Walker et al. 2002; Korman et al. 2003; Kuriyama et al. 2004) and a decrease in the number of erroneous key presses (Fischer et al. 2002; Korman et al. 2003; Kuriyama et al. 2004). No such improvement is observed if the retest session is conducted before the completion of the consolidation process. This spontaneous improvement, commonly referred to as "off-line learning", will be used in the following experiments as the indicator to assess the integrity of the consolidation process. Based on previous reports that have shown the sensitivity of the consolidation process to interference, we hypothesized that a practice schedule high in contextual interference should impair off-line learning in a finger sequence task.

Methods

Participants

Forty-seven undergraduate students (aged 19–26 years old, 19 males) from Bishop's University took part in the experiment. Participants were naïve to the purpose of the study and had no previous experience with the task. All participants except two were self-declared right-handed; since their performance was similar to that of their right-handed peers, their data were included in the analyses. None reported neurological disorder, and all had normal or corrected-to-normal vision. Five participants were excluded from the analyses because they either did not complete the entire experimental protocol or failed to follow the instructions. All participants gave their informed consent and the study was approved by the Ethics Review Committee for Student Research of Bishop's University.

Task

Participants performed a finger sequence task that consisted of learning to produce as fast and accurately as possible one or two 5-element sequences (Walker et al. 2002, 2003; Korman et al. 2003; Kuriyama et al. 2004). Using their non-dominant hand (except the two lefthanders, who also used their left hand), the sequences were typed on a QWERTY keyboard and each keystroke was recorded by a computer. Participants were asked to type the sequences using their index, middle, ring, and little fingers. Two different sequences were used: Sequence A, which consisted in typing F-A-E-W-F, and Sequence B, which consisted in typing W-E-A-F-W (see Fig. 1).

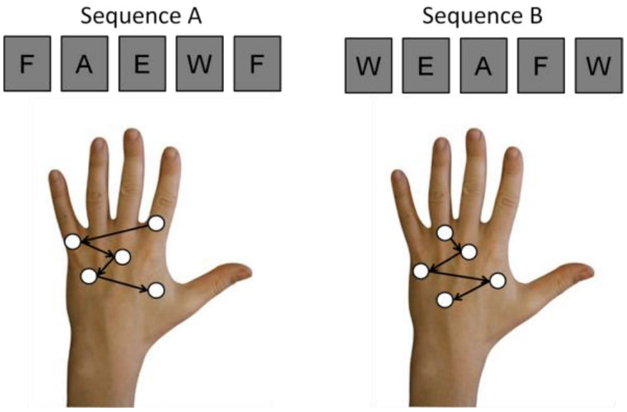

Fig. 1 Finger sequence task used in Experiments 1 and 2. Sequence A consisted in typing as fast and accurately as possible the *letters* F-A-E-W-F, whereas Sequence B consisted in typing W-E-A-F-W

Procedures

All participants took part in two practice sessions performed 24 h apart (see Fig. 2). Before the first session, they were randomly assigned to one of three groups which underwent experimental protocols with varying level interference between the tasks. In a typical experiment using the finger sequence task, participants are asked to produce as many sequences as possible during the blocks of 30 s. The performance of the participants is assessed by calculating the number of sequences typed during each block (speed), as well as the number of erroneous keys typed (accuracy). To be able to contrast our results with previous literature, we kept the 30 s block format and varied the level of interference by changing the schedule of the blocks. Participants assigned to a low CI schedule (hereafter referred to as the "Blocked Practice" group, $n = 14$, 4 males) performed 12 practice blocks of Sequence A followed by 12 practice blocks of Sequence B during the first session. Participants assigned to the high CI schedule practiced the two sequences in alternate order, i.e., performed one practice block of Sequence A followed by one practice block of Sequence B, until the end of the session. This group will be referred hereafter as the "Serial Practice" group ($n = 14$, 6 males) as this schedule allowed participants to repeat the sequence a certain number of times before moving on the next sequence (Lee and Magill 1983). In total, both groups performed 12 practice blocks of each sequence during the first session. In addition, participants of a third group experienced no interference and practiced only Sequence A (hereafter referred as the "Control group", $n = 14$, 6 males).

At the beginning of the first session (acquisition), participants were presented with the sequence(s) and were permitted to practice the sequence(s) three or four times prior to the data acquisition. This short warm-up served to ensure that participants understood what they had to do and could accurately type the sequence(s). The sequences (i.e., the letter that had to be typed) were initially presented on two

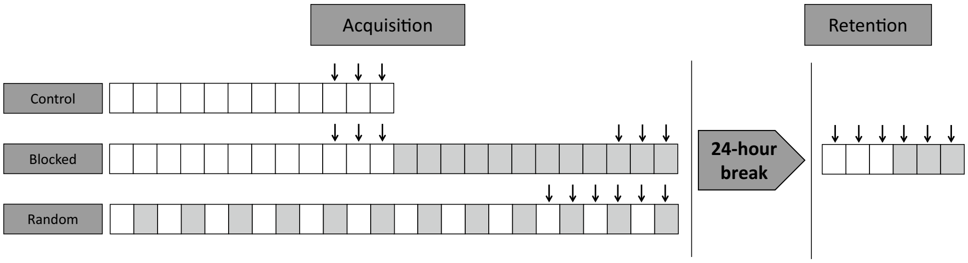

Fig. 2 Experimental protocol. Each *box* represents a 30-s block during which participants attempted to type as many sequences as possible (Sequence A *white boxes*, Sequence B *light gray boxes*). The *arrows* indicate the blocks that were used to calculate the participants' mean performance at the end of the acquisition session and during the retention test

8.5″ × 11″ sheets of paper and the letters were printed in 66 font size. Each sheet was positioned beside the computer keyboard until the completion of the third block of this particular sequence. After that, the sheet was removed from the participants' sight. Throughout the entire experiment, the sequence (i.e., the five letters that had to be typed) was presented on the computer screen at the same time as the signal prompting them to initiate the next block. Note that participants were told at the beginning of the acquisition session the order in which the practice blocks was organized. Thus, the presentation of the sequence on the computer screen served as a reminder, and not as a cueing signal indicating which sequence had to be typed. Participants were told to be as fast but also as accurate as possible. More specifically, they were told to maintain an accuracy score of at least 90% during each practice block (see below for the details regarding this calculation). If they obtained an accuracy score lower than 90%, they were asked to slow down during the following practice block. Additionally, they were instructed that if they made an error during the execution of one sequence, they should restart the sequence from the beginning.

All practice blocks lasted 30 s and were followed by a 30 s pause (Walker et al. 2003). During each block, the participants were asked to type as many sequences as possible. At the beginning of the blocks, the computer program prompted the participants to press any key, when ready, to initiate the start sequence. On the same screen, participants were also presented with their assigned sequence. The start sequence consisted in the words "Set", followed by "Go" being displayed on a computer screen located in front of the participants. The "Go" signal was accompanied simultaneously by a tone generated by the computer marking the beginning of the data recording. Thirty-seconds later, a second tone was generated by the computer and the word "Stop" was displayed on the screen to indicate the end of the practice block. Immediately after the termination of the practice block, the number of sequences accurately typed during the block as well as the accuracy score were displayed on the computer screen during the 30 s pause. If needed, participants were allowed to take a little more than 30 s of rest between two blocks (but not more than an additional 30 s), an opportunity very few participants took advantage of.

The second session (retention test) was performed 24 h after acquisition and was identical for all three groups. It consisted in three practice blocks of Sequence A immediately followed by three practice blocks of Sequence B. This second session served to assess the effects of the consolidation process taking place after acquisition.

Testing sessions were scheduled between 8:30 am and 6:00 pm, Monday through Friday. The various testing times were evenly distributed within all groups. Participants were invited to pursue their usual occupation between the sessions and were asked to not practice the sequence(s). They were also asked to avoid consuming alcoholic beverages or using recreational drugs and to sleep a minimum of 8 h between the sessions. Compliance with the instructions was confirmed verbally by the participants at the beginning of the second session. Moreover, participants filled out a written questionnaire to report hours of sleep and sleep disruptions, if any, during the night between the two practice sessions. Although participants slept on average 8.1 h (SD = 1.4) between the sessions, 14 reported sleeping less than 8 h (between 4.5 and 7.75 h), thus violating the study instructions. Since these participants were distributed randomly in all the groups and their behavior was not impaired, their data were kept in all the analyses. One participant was, however, removed from all analyses because the experimenter noticed clear sleep deprivation signs during the second experimental session.

Data analysis

For each 30 s block, we calculated the number of accurate sequences typed by each participant as well their accuracy. A sequence was considered accurate only when the five letters were typed successively. The participants' accuracy was calculated by dividing the number of key presses that were part of an accurate sequence (i.e., the number of accurate sequences × 5) by the total number of keys typed during each block. If a participant did not have the time to complete the last sequence of a practice block (i.e., if the stop signal occurred in the middle of a sequence), the last key presses were counted as accurate if they followed the appropriate sequence.

To determine whether the serial practice schedule affected the initial acquisition of the sequences compared to the Blocked schedule, we first computed separate 2 Groups (Blocked vs Serial) × 2 Sequences (A vs B) × 12 Blocks ANOVAs using the speed and accuracy data of acquisition. When necessary, we used the Greenhouse-Geisser correction to correct for a possible violation of sphericity assumption and pairwise comparisons with a Bonferroni adjustment were used to compute post hoc tests, when needed. To assess the integrity of the consolidation process, we relied on preplanned comparisons to look for evidence of off-line learning taking place between the sessions. This was done using separate *t* tests to compare the participants' speed (number of sequences typed per block) and accuracy (percentage of accurate key presses) before and after the 24-h rest interval (a statistical approach used by several before us; Walker et al. 2002, 2003, 2005; Kuriyama et al. 2004). For each sequence, the mean of the last three blocks of the acquisition session was compared to the mean of the three blocks performed in the retention test (Walker et al. 2003). Prior to the computation of all statistical tests, we assessed the normality of the distribution by calculating the *z*-score of the skewness and kurtosis values to ensure there was no inflation of a Type I error (Tabacknick and Fidell 2007). All significant effects are reported at $p < 0.05$.

Results

All three groups increased their typing speed during the acquisition session (see Fig. 3a, b). The 2 Groups (Blocked vs Serial) × 2 Sequences (A vs B) × 12 Blocks ANOVA comparing the participants' typing speed revealed a significant main effect of Block, $F(11, 286) = 54.6$, $p < 0.01$, $\eta_p^2 = 0.68$, which was superseded by a significant Block × Group interaction, $F(11, 286) = 2.7$, $p < 0.03$, $\eta_p^2 = 0.1$. Post hoc comparisons, however, revealed no significant differences between the groups for any of the blocks ($p > 0.17$). The ANOVA also revealed a significant main effect of Sequence, $F(1, 26) = 7.4$, $p = 0.01$, $\eta_p^2 = 0.22$, indicating that participants performed, on average, Sequence B faster than Sequence A ($M = 18.9 \pm 4.2$ and $M = 17.9 \pm 4.0$, respectively). The main effect of Group and all other interactions were not significant ($p > 0.38$). With regards to accuracy, the ANOVA revealed a significant effect of Block, $F(11, 286) = 5.5$, $p < 0.01$, $\eta_p^2 = 0.18$. Post hoc comparisons revealed that participants were significantly less accurate during Blocks 1 and 5 compared to Block 11 (see Fig. 3c, d). The main effect of Group approached significance, $F(1, 26) = 4.1$, $p = 0.053$, $\eta_p^2 = 0.14$. The main effect of sequence and all other interactions were not significant ($p > 0.35$).

To determine whether consolidation was affected by the different practice schedules, we computed paired-sample *t* tests to contrast the performance of the participants at the end of the acquisition session with their performance during the 24-h retention test. Participants

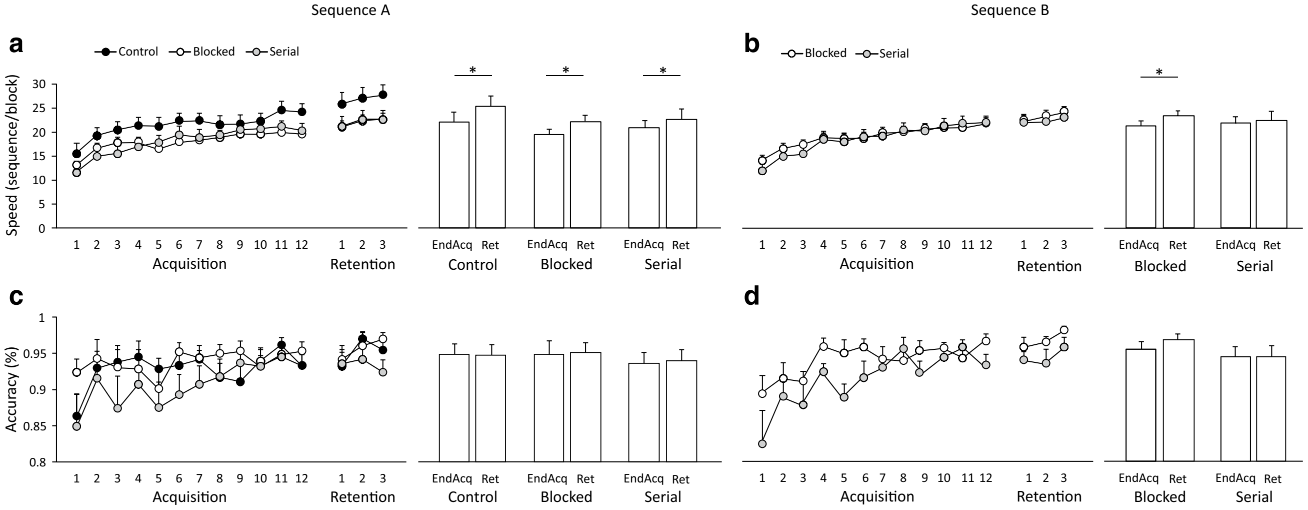

Fig. 3 Participants' mean speed for sequence A (Panel **a**) and B (Panel **b**) during acquisition and retention. The columns illustrate, for each group, the mean performance during the last three blocks of the acquisition session and the retention test. The symbol *asterisk* indicates a significant difference between the groups and the error bars illustrate the standard error of the mean. The participant's mean accuracy for Sequence A and B is illustrated on Panels **c** and **d**, respectively

of the Control group demonstrated a significant between-session improvement in speed for Sequence A, $t(13) = 5.39$, $p < 0.001$ $d = 0.44$, but no significant gain in accuracy $t(13) = 1.977$, $p > 0.071$, $d = 0.19$. Participants of the Blocked Practice group also significantly improved their typing speed of both sequences, $t(13) = 2.84$, $p < 0.014$, $d = 0.43$ and $t(13) = 3.32$, $p < 0.005$, $d = 0.49$, for Sequences A and B, respectively. In contrast, participants of the Serial Practice group demonstrated a significant speed gain for Sequence A, $t(13) = 2.91$, $p < 0.012$, $d = 0.33$, but not for Sequence B, $t(13) = 1.18$, $p > 0.261$, $d = 0.12$. Participants of both the Blocked Practice and Serial Practice groups demonstrated no accuracy gain for any of the sequences ($p > 0.07$).

Discussion

The main objective of this experiment was to assess how varying the level of interference between two finger sequences affects motor skill consolidation. Three groups of participants learned to type as fast and accurately as possible either one or two distinct sequences of finger movements under a blocked or serial practice schedule. Our results revealed that when participants learned only one sequence during the acquisition session, they demonstrated a significant increase in speed when retested 24 h later, an “off-line learning” effect that has previously been identified as a hallmark of the consolidation process with the finger sequence task (Korman et al. 2003; Walker et al. 2003; Kuriyama et al. 2004). Participants who learned the two distinct sequences under a blocked practice schedule also demonstrated a significant off-line learning effect for both sequences, whereas participants who learned the two sequences under a serial practice schedule demonstrated off-line learning only for Sequence A. This result is coherent with our prediction that practicing alternately two distinct sequences when their memory representation is still labile and subject to interference impairs consolidation.

At first glance, our results appear to differ slightly from seminal works on motor skill consolidation as we observed that participants of the Blocked Practice group demonstrated intact consolidation even if Sequence B was practiced immediately following Sequence A, that is when the memory representation of Sequence A was still labile and subject to interference. In previous reports, this practice schedule has been associated with impaired consolidation. For example, when participants practiced Sequence A and B under a blocked practice session (i.e., without a consolidation interval in-between the sequences), Walker et al. (2003) reported no between-session improvement in accuracy for Sequence A, a sign that Sequence B interfered with the consolidation of Sequence A. It is noteworthy that participants nevertheless demonstrated a modest, yet significant between-session improvement in speed for Sequence A. Thus, in Walker et al. (2003) experiment, interference mostly affected the accuracy of Sequence A. In our experiment, participants were specifically instructed to maintain a high level of accuracy during the initial practice session and they were invited to slow down if their accuracy fell below 90%. Based on this instruction, the participants’ accuracy remained high throughout the sessions, thus minimizing the potential for change between the sessions. Still, participants of the Blocked Practice group improved Sequence A speed off-line by 13%, a result closely aligned with that of Walker et al. (2003). Thus, results of our blocked practice condition are coherent with those reported before under a similar condition.

Our results also reproduced, at least in part, some of the main contextual interference effects. More specifically, while high CI schedules are usually associated with impaired performance during acquisition, a serial practice schedule in which the learner has the opportunity to repeat a certain number of times the motor skills before moving on to the next skill, has usually been shown to temper the negative aspects of a truly random schedule (Schmidt and Lee 2005). Thus, observing no performance difference in acquisition between the Serial Practice and Blocked Practice groups could be expected. Furthermore, while our blocked practice schedule did not result in impaired retention, it should be noted that our retention test was performed under a blocked schedule, a condition that has been shown to diminish the retention impairment associated with blocked practice (Lee 2012).

Nevertheless, the observation that a serial practice schedule impaired consolidation is intriguing in the light of the plethora of previous reports showing a learning advantage for the high contextual interference schedules over blocked practice. How can serial practice favor learning when consolidation is impaired? This apparent discrepancy can perhaps be reconciled when considering the brain processes benefiting from high CI schedules and those engaged in the finger sequence task. High CI schedules are believed to enhance learning as they allow the learner to contrast two (or more) tasks during practice (Shea and Morgan 1979) and/or to reconstruct more frequently the action plan required to execute the action (Lee and Magill 1983). According to both hypotheses (elaboration and reconstruction, respectively), high CI schedules favor the movement planning process, which is then reflected in better movement execution. In contrast, the finger sequence task consists of learning to perform as many sequences as possible during 30 s. Performance is linked to the learner’s knowledge of the sequence and to the discovery of strategies to accelerate its execution. When practicing the finger sequence task, participants develop both a spatial representation of the sequence and a motor representation (Verwey et al. 2016). This echoes Robertson's (2009) framework suggesting that sequence production tasks involve learning the goal-based component (i.e., the sequence elements and their order) as well as the movement-based component (i.e., how to produce the sequence). Both components have been shown to benefit from a consolidation interval when participants had to learn a long (12-element) sequence (Cohen et al. 2005). In our experiment, while we cannot rule out the possibility that learning the cognitive representation of the task (or the goal-based component) contributed to the participant's performance increase, it seems safe to assume that most of the improvement came from acquiring the movement-based component as the sequences were rather short (5-element) and disclosed in advance. Movement execution, therefore, represents the crux of the task and only minimal movement planning is required; once the motor plan has been uploaded in working memory, it only has to be repeatedly replayed, and thus requires minimal reconstruction. In addition, it seems unlikely that providing the participants with the opportunity to contrast the sequences frequently using a serial practice schedule could provide a learning advantage as the sequences were quite distinct from one another. Thus, the brain process(es) that benefits from a high CI schedule seems to contribute minimally to the performance improvement in the finger sequence task. In contrast, the process(es) involves in this task seems to be particularly sensitive to interference, a finding coherent with the observation that learning short sequences requires a stabilization period (Robertson et al. 2004). This would explain why our serial practice schedule impaired consolidation, as evidenced by the impaired off-line learning gains. It is noteworthy, however, that contrary to Robertson et al.'s suggestion, our serial practice schedule did not produce a stable memory trace. One possibility to account for this discrepancy is that the protective role provided by a high CI schedule may only occur with longer sequences or with adaptation tasks. More investigations will be needed.

It also important to note that while our serial practice schedule impaired one of the behavioral manifestations of consolidation (i.e., off-line learning), it nevertheless did not impair learning per se as participants of the Serial Practice group demonstrated good retention of the initial performance gains they made for Sequence B. Thus, in our experiment, the serial practice schedule seems to have interfered with the process leading to off-line gains while leaving other memory storage process intact. This result is coherent with previous reports in which interference impaired off-line gains without decreasing performance (Walker et al. 2003; Balas et al. 2007b). However, this observation differs from what is usually observed using visuomotor and dynamic adaptation tasks. In these tasks, participants are asked to perform rapid and linear goal-oriented movements while a mechanical or visual perturbation is applied to their arm or to its visual representation, respectively. The participant's objective is to adjust his/her movements using a feed-forward process to compensate for the deviation. When a second and opposed perturbation is experienced immediately after the first one (i.e., under a blocked schedule), performance returns to a naïve level when retention of the first perturbation is assessed in a delayed retention test (Krakauer et al. 1999; Hinder et al. 2007). Interestingly, it has been demonstrated that only a random practice schedule allows participants to learn two opposed force fields (dynamic adaptation) during the same practice session (Osu et al. 2004). It should be noted though that a dynamic adaptation task is believed to require the learning of a new internal model (Shadmehr et al. 2010), a process driven by the sensory prediction errors experienced during practice (Shadmehr et al. 2010; Izawa et al. 2012). When multiple internal models have to be learned at the same time, creating an association between the internal models with the sensory cues becomes primordial. This markedly contrasts with the acquisition of a new sequence of movements which requires the learning of the order of the elements as well as the movement-based component. Neurophysiologically, these two tasks are known to activate different brain networks (Doyon and Benali 2005), thus reinforcing the idea that different processes may be at play. It, therefore, seems possible that a high interference and unpredictable schedule may be necessary to fully differentiate the two internal models and their associated sensory cues while the same practice schedule may cause interference in the process(es) underlying sequence learning.

The reason why interference occurs and its underlying mechanism remains poorly understood. The most widely accepted view states that interference depends on the degree to which the memory representation of the two skills conflicts in working memory (Bays et al. 2005) and/or if the memory representations overlap in certain networks (Shadmehr and Holcomb 1999). This competition/overlap can be caused by the tasks sharing the same visuomotor plan (Hirashima and Nozaki 2012), the same effector (Balas et al. 2007a) or by the context in which the tasks are practiced (for example, practicing two tasks in isolation or one after the other, Walker et al. 2003). In our experiment, the Serial Practice group and the Blocked Practice group differed only by their practice schedule (i.e., the context) with which the two sequences were acquired. As mentioned above, serial practice is associated with a higher CI compared to blocked practice. It is, therefore, not surprising to realize that consolidation, a process sensitive to interference, is impaired when using a serial practice schedule. Since the two sequences were similar and involved the usage of the same finger digits, it seems plausible that practicing them interchangeably has exacerbated the overlap between the memory representations of the two sequences and made it more difficult for the central nervous system to dissociate between the two. The reason why Sequence A interfered with Sequence B and not vice versa remains, however, unknown and will require further experiments.

If interference occurs when the memory representation of two tasks overlap in certain brain networks (Shadmehr and Holcomb 1999), one could wonder where the locus of interference was when the two sequences were acquired under serial practice. While we argued that the movement execution process may have been impaired, it remains nevertheless possible that the interference originated from a conflict in the network engaged in the acquisition of the cognitive representation of the sequences. Experiment 2 was designed to investigate the locus of interference reported in Experiment 1.

Experiment 2

We used an experimental protocol similar to that experienced by the participants of the Serial Practice group but replaced all the practice blocks of Sequence A with two different tasks. Our objective was to isolate the cognitive and execution processes from one another to determine which of the two caused interference under the serial practice schedule. To investigate whether interference occurred because of an overlap in the networks responsible for the cognitive processes associated with the acquisition of the sequences, the physical practice blocks of Sequence A were replaced with an equivalent number of blocks during which participants of a first group observed a novice model performing Sequence A. It has been demonstrated that observation allows the learner to gain a cognitive representation of the task observed (Badets and Blandin 2010; Rohbanfard and Proteau 2011), to learn the sequences elements in visuo-spatial coordinates (Gruetzmacher et al. 2011), and to develop error-detection capability (Blandin and Proteau 2000). Thus, by observing a model practice Sequence A, participants should engage the networks involved in acquiring a cognitive representation of the sequence without engaging the brain networks involved in its execution. If the observation of Sequence A leads to interference similar to that reported in Experiments 1, we will conclude that a serial practice schedule leads to interference in the network involved in acquiring the cognitive representation of the sequence.

Alternatively, it is possible that interference in Experiment 1 may have arisen due to a conflict in the networks involved in the execution of the sequences. Consequently, for a second group of participants, we replaced the physical practice blocks of Sequence A with a task consisting of producing random finger movements, thus soliciting the brain networks engaged in the production of finger movements without engaging the structures involved the acquisition of a cognitive representation. If performing blocks of random movements interferes with the consolidation of the sequence physically practiced (Sequence B), we will conclude that interference occurred in the networks engaged in the physical production of the sequences.

Methods

Twenty-three new participants were recruited for this experiment (mean age = 22.7 ± 2.5, 11 males). They were all right-handed, naïve to the purpose of the study, and none of them took part in the first experiment. Participants were randomly assigned to one of two groups and they all underwent an experimental protocol similar to the Serial Practice group in Experiment 1. To determine whether the interference observed in Experiment 1 originated from an overlap in the network involved in learning the cognitive representation of the sequences, for one group of participants, all the practice blocks of Sequence A were replaced by 30-s blocks of observation during acquisition. This group will be referred to as the Observation group ($n = 11$, 5 males). More specifically, instead of physically practicing Sequence A, participants in the Observation group watched 30-s video segments of a novice model learning Sequence A. Participants of the Observation group, therefore, alternated between observation blocks and physical practice blocks of Sequence B (see Fig. 4). The model featured in the video was right-handed and had never practiced Sequence A before the video session. Using her left hand, the model performed 12 30-s blocks of practice during which she attempted to type Sequence A as fast and accurately as possible. Her performance was recorded using an HD camera located above her left shoulder with a focus on her left hand. The model's mean performance across the 12 acquisition blocks (average number of sequences typed per block) was similar to the mean performance of the participants in the Serial Practice group of Experiment 1 ($M = 24.4$ and $M = 24.09 \pm 5.7$, respectively) and her performance improvement during acquisition was representative of a good participant performing this task for the first time (she typed 20 and 25 accurate sequences during the first and last practice blocks, respectively). The 12 unique 30-s video segments of the model were presented to the participants of the Observation group on a computer screen located beside the main computer used for the experiment. After each 30-s video segment, the model's performance was displayed on the screen during 5 s (number of correctly typed sequences and percentage of accuracy), thus

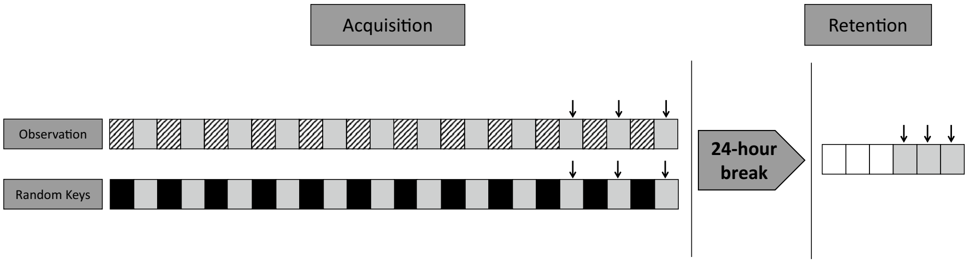

Fig. 4 Experimental protocol of Experiment 2. Each *box* represents a 30-s block during which participants either observed a novice model practicing Sequence A (*striped boxes*), typed random key presses (*dark gray boxes*), or typed as many times as possible Sequence B (*light gray boxes*). In the retention test, participants also performed blocks of Sequence A (*white boxes*). The *arrows* indicate the blocks that were used to calculate the participants' mean performance at the end of the acquisition session and during the retention test

giving the participants an opportunity to realize the model was improving. At the beginning of the experimental session on Day 1, participants were told that their objective was to learn to type as fast and accurately as possible both Sequences A and B and that there were going to be retested on both sequences the following day. To ensure that participants remained attentive to the video segments, participants were also asked to identify two-letter words briefly presented during each 30-s video segment. Participants were told that the first letter of the word would appear at any time during the first half of the video segment and the second letter would appear during the second half. Letters were black, bold, 0.8 cm high, and were displayed around the left hand knuckle of the middle finger during 0.3 ms. To confirm they remained attentive, participants were instructed to verbally state the two-letter word at the end of each 30-s video clip. None of the participants failed to identify more than one two-letter word.

To determine whether the interference observed in Experiment 1 was caused by an overlap of the networks involved in the execution of the sequences, a second group of participants underwent an experimental protocol identical to the one performed by the Observation group. However, the observation blocks were replaced by blocks during which participants typed random key presses. This group will be referred to as the Random Key Presses group ($n = 12$, 6 males). Participants in the Random Key Presses group were presented strings of letters ordered randomly on $8.5'' \times 11''$ cardboards (one cardboard per block, each cardboard containing all the letters to be typed in the block) and were asked to type them as quickly and accurately as possible on a computer keyboard. The cardboards were positioned in front of the participants at eye-level. The letters presented were identical to those used for Sequences A and B (i.e., A, W, E, and F) and participants were asked to use the same four fingers that had been associated with each letter in Experiment 1. Given that the purpose of this group was to replicate the motor activation resulting from the physical practice of Sequence A, the length of the letter strings presented to the participants in each block corresponded to the mean number of key presses performed by the participants of the Serial Practice Group in Experiment 1. Thus, the length of the letter strings increased from 58 (Block 1) to 117 (Block 12). The letter strings had been generated randomly by a computer program and the same letter strings were presented to all participants of the Random Key Presses group. As illustrated on Fig. 4, participants of the Random Key Presses group alternated between blocks of random key presses with 30-s blocks of physical practice of sequence B (with a 30-s rest in between).

All participants performed a retest session 24 h later consisting of three practice blocks of Sequence A followed by three practice blocks of Sequence B. All other procedures and analyses were identical to those pertaining to the participants of the Serial Practice group of Experiment 1. Participants slept on average 8.0 h (SD = 1.0) between the two sessions (9 participants slept less than 8 h; they were all maintained in the analyses).

Results

In Experiment 1, interference was inferred when no significant off-line learning was observed when comparing the mean performance of the last three practice blocks of the acquisition session with the mean performance of the three practice blocks performed the following day. In the current experiment, the same statistical comparisons were performed. If observation and/or typing random keys compete for shared resources in the brain, participants should demonstrate no off-line learning of Sequence B, as in Experiment 1. Participants of the Observation group demonstrated no between-session gain in speed and accuracy [$t(10) = -0.181$, $p > 0.860$, $d = 0.05$, and $t(10) = -0.871$, $p > 0.404$, $d = 0.02$, respectively], thus indicating that the observation of a model performing Sequence A impaired the consolidation of Sequence B (see Fig. 5). In addition, participants of the Random Key

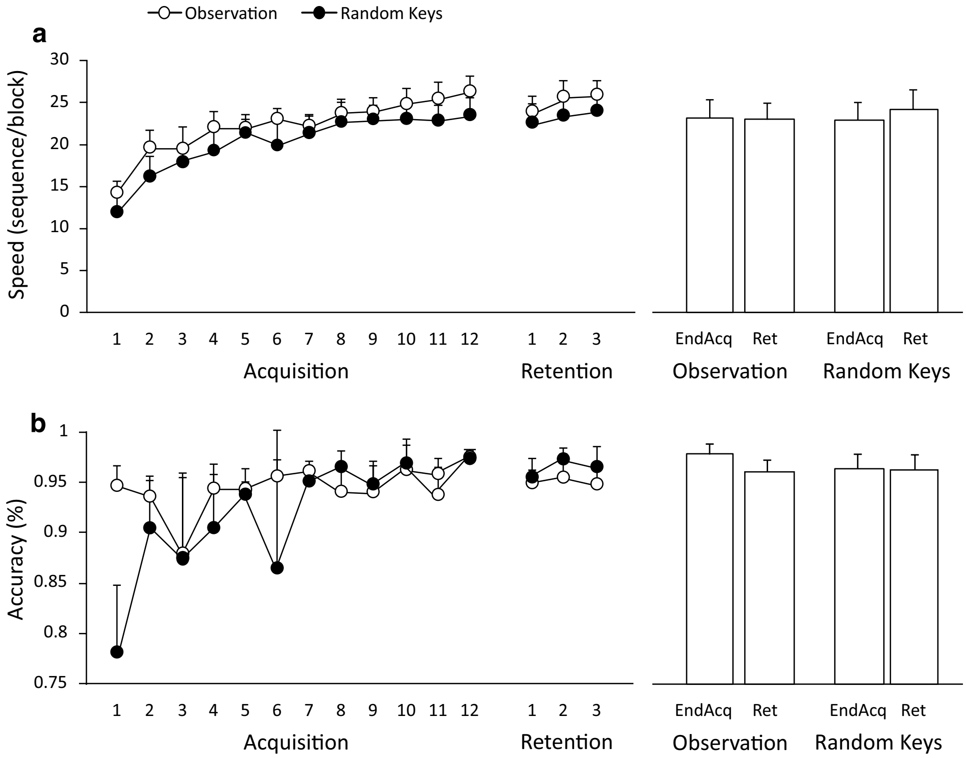

Fig. 5 The participants' mean speed (**a**) and accuracy (**b**) for Sequence B during acquisition and retention. The columns illustrate, for each group, the mean performance during the last three blocks of the acquisition session and the retention test. The *error bars* illustrate the standard error of the mean

Presses group also demonstrated no between-session gain in speed, nor accuracy [$t(11) = 1.20$, $p > 0.255$, $d = 0.12$, and $t(11) = -0.219$, $p > 0.831$, $d = 0.07$, respectively], thus indicating that producing random finger movements also impaired the consolidation of Sequence B.

Discussion

Experiment 2 was designed to investigate the locus of interference when participants practiced two different sequences of finger movements under a serial practice schedule. We hypothesized that the interference could originate from a conflict between the cognitive representation of the two tasks or from an overlap in the network involved in the production of the finger movements. To assess these two possibilities, we designed an experimental protocol similar to the one experienced by participants of the Serial Practice group in Experiment 1. However, the physical practice blocks of Sequence A were replaced with either the observation of a novice model practicing Sequence A or with the typing of random key presses using the fingers associated with Sequence A.

To our surprise, our results revealed that both observation and the production of random finger movements impaired consolidation. Participants of the Observation and Random Key Presses groups demonstrated no offline learning of Sequence B, a result similar to the one we observed in Experiment 1 when participants physically practiced two different sequences under a serial practice schedule. This suggests that both observation and the production of random finger movements interfered with the consolidation of Sequence B.

The finding that the production of random key presses interfered with the consolidation of the sequence physically practiced is coherent with our understanding of the role of motor networks for sequence learning. Because the letter strings did not contain any repetitive sequence, participants only needed to identify the letter presented, select the appropriate finger, and execute the movement. Typing a string of random letters and/or a sequence, therefore, both recruit the networks involved in movement execution. Of interest to the present discussion is the extensive body of literature demonstrating the role of M1 for sequence learning. Repeated practice and performance increases have been associated with an enlargement of the motor maps in M1 devoted to the control of the fingers in humans (Pascual-Leone et al. 1994; Karni et al. 1995) and rodents (Kleim et al. 2004), and with increased activation of M1 following consolidation (Doyon and Benali 2005; Walker et al. 2005; Lohse et al. 2014). Furthermore, the integrity of M1 has been demonstrated to be crucial to the consolidation of finger sequences, as evidenced by experiments in which a transcranial magnetic stimulation applied to M1 impaired consolidation (Muellbacher et al. 2002; Robertson et al. 2005; Kantak et al. 2010). Together, these results all suggest that M1 may be involved in the long-term storage of the memory representation of the skill (Karni et al. 1995; Sanes and Donoghue 2000; Penhune and Steele 2012), and perhaps more specifically in the storage of the movement-based presentation (Kantak et al. 2010). Combined with the observation that M1's excitability increases during a high CI schedule (i.e., random practice; Wright et al. 2016), it seems plausible that the locus of interference in Experiments 1 (Serial Practice group) and 2 (Random Key Presses group) may have been in M1.

The finding that observing a novice model practicing a sequence of finger movements interfered with the consolidation of a sequence physically practiced is, to our knowledge, novel. In a study conducted by Larssen et al. (2012), the authors tested a similar idea using a visuomotor adaptation task in which participants had to adjust their reaching movements to compensate for a rotation of the visual representation of their hand. In this task, it has repeatedly been reported that participants are unable to consolidate the memory representations of two different rotations (e.g., a 30° clockwise rotation followed by a 30° counter clockwise rotation) when practiced one after the other because the memory representation of one rotation interferes with the consolidation of the other (Krakauer et al. 1999, 2005; Caithness et al. 2004). In their experiment, Larssen et al. (2012) reported no interference when the second rotation was acquired by observing a model, a result implying that physical practice and observation may not consolidate in the same brain networks. A similar conclusion has also been reported when participants performed a sequence production task consisting in knocking three wooden barriers in a prescribed movement time (Trempe et al. 2011). It is important to note that these two tasks involved a more procedural/implicit form of learning than the finger sequences used in the current experiments. Visuomotor adaptation requires a remapping of the relation between the movements produced and their sensory consequences (van Beers et al. 2002). Although explicit strategies can be used early in practice to initiate the movement in the right direction, complete adaptation ultimately requires a low level, implicit remapping (Mazzoni and Krakauer 2006). The most convincing evidence for this remapping is the presence of aftereffects when the rotation is removed (i.e., a bias in the direction previously imposed by the rotation), even if the learner is aware that there is no longer a rotation applied to the visual feedback. Similarly, the timing task used by (Trempe et al. 2011) required participants to learn the correct timing of four movements, something that can only be "felt" and is thus difficult to describe explicitly. In the current experiments, although the finger sequence task has an implicit component to it, it also involves an explicit component, something we referred to earlier as learning the cognitive representation of the task, or the goal-based component (Robertson 2009). Since observation has been shown to allow one to learn the cognitive representation of a skill, our result demonstrating that the observation of Sequence A interfered with the consolidation of Sequence B can be interpreted as a sign of interference in the brain networks responsible for acquiring the goal-based component.

Although it seems plausible to speculate that the random key presses and the observation blocks both interfered with the consolidation of Sequence B through a conflict in different brain networks, it is still possible that the overlap may have been in the same network. More specifically, a substantial body of evidence demonstrated the existence of an action-observation network (AON) made of neurons that respond both to the observation of a motor task and to its execution (see Rizzolatti and Craighero 2004 for a review). These "mirror" neurons are believed to allow us to understand the actions of others as well as their intent. In humans, mirror neurons have been located in the supplementary motor area, lateral premotor cortex (Caspers et al. 2010), and M1 (Dushanova and Donoghue 2010), three important structures for sequence learning (Doyon and Benali 2005; Penhune and Steele 2012; Wright et al. 2016). Thus, a possibility is that our observation and random key presses tasks both solicited the AON, which may have been the locus of interference. However, the many results demonstrating a qualitative difference in the learning process during observation and physical practice argue against this possibility (Ong and Hodges 2010; Trempe et al. 2011; Ong et al. 2012; Larssen et al. 2012). For example, Ong and Hodges (2010) reported that while observation allowed their participants to adapt to a visuomotor rotation, only physical practice resulted in aftereffects, a finding suggesting that learners may acquire different components of the tasks based on the acquisition modality (observation or physical practice). In addition, Trempe et al. (2011) reported that observational learning and physical practice led to distinct behavioral outcomes following consolidation, a sign that observation and physical practice may consolidate in different networks. Similarly, Larssen et al. (2012) reported interference between two tasks learned through observation as opposed to a condition in which only one task was observed, an indication there can be observation-specific interference. Together, these results indicate that while observation and physical practice share common neural networks, they both lead to distinct patterns of interference. It, therefore, seems likely that our observation and random key presses tasks interfered with the consolidation of Sequence B through a conflict in different networks.

General discussion

The main objective of this research project was to investigate whether varying levels of interference affects motor skill consolidation, and more specifically the off-line learning gain usually observed when practicing a sequence of finger movements. In Experiment 1, our results demonstrated that a serial practice schedule led to significant interference between the two sequences. In Experiment 2, we expanded this result by showing that observation and the production of random movements both led to a similar pattern of interference.

Together, our results support the idea that the practice schedule employed during acquisition has a profound influence on how the brain processes the tasks (Kantak et al. 2010; Song et al. 2012; Wright et al. 2016) More specifically, under high contextual interference practice schedules, a broad network of brain structures is activated to support the acquisition of sequence specific elements (Wymbs and Grafton 2009), structures that have been shown to be essential for long-term memory storage (Doyon and Benali 2005). In addition, the scheduling of the practice session also affects the excitability of certain structures and the speed at which the memory representation of the tasks migrate to areas of long-term storage (Wright et al. 2016). While these changes are usually seen positively, results of both our experiments, however, suggest there is a price to pay. While certain cognitive processes may benefit from this enhanced activation pattern, as CI experiments have repeatedly demonstrated over the years, it also seems to make other processes more vulnerable to interference. If interference occurs when two tasks share common neural substrates, one could speculate that the broader the brain activation, the higher the risk of interference. This would explain why in Experiment 1 our serial practice schedule increased the interference between the two sequences and why two seemingly different tasks both interfered with the consolidation of Sequence B in Experiment 2.

Together, the result of both experiments suggest that when one learns to produce as quickly as possible a sequence of finger movements, the brain processes improved off-line through consolidation differ from those that are favored by high CI practice schedules. It is also of interest to note that the largest off-line learning effect for Sequence A in Experiment 1 was observed when participants were initially exposed to only one sequence (mean off-line learning of 2.9 ± 2.0 sequences for participants of the Control group), and that progressively more contextual interference led to smaller off-line learning (mean off-line learning of 2.4 ± 2.4 and 1.8 ± 2.3 for participants of the Blocked practice and Serial practice groups, respectively). Although this difference did not reach statistical significance, it nevertheless reinforces the idea that an increase in the between-task interference has an adverse effect on motor skill consolidation. Based on our results, the acquisition of two finger sequences seem to be optimized, at least early in practice, by practicing the two tasks in low CI schedule or in isolation from one another.

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