Research report

Offline consolidation in implicit sequence learning

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ABSTRACT

The goal of this study was to investigate offline memory consolidation with regard to general motor skill learning and implicit sequence-specific learning. We trained young adults on a serial reaction time task with a retention interval of either 24 h (Experiment 1) or 1 week (Experiment 2) between two sessions. We manipulated sequence complexity (deterministic *vs* probabilistic) and motor responses (unimanual or *vs* bimanual). We found no evidence of offline memory consolidation for sequence-specific learning with either interval (in the sense of no deterioration over the interval but no further improvement either). However, we did find evidence of offline enhancement of general motor skill learning with both intervals, independent of kind of sequence or kind of response. These results suggest that general motor skill learning, but not sequence-specific learning, appears to be enhanced during offline intervals in implicit sequence learning.

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1. Introduction

There have been a vast number of studies on sequence learning, but only recently has there been much interest in how it relates to memory consolidation. The term consolidation usually refers to the *stabilization*, and even *enhancement*, of memory traces after their initial acquisition. For example, it has been demonstrated that the performance of some procedures can be significantly improved after a "silent" or *offline* interval subsequent to training. During this interval, there is no further practice, or even mention, of the procedure, and learning remains largely tacit or *implicit* (Brown & Robertson, 2007; Hallgato, Gyori-Dani, Pekar, Janacsek, & Nemeth, 2013; Krakauer & Shadmehr, 2006; Németh et al., 2010). Consolidation is also sometimes referred to as *resistance* to interference and forgetting (Ghilardi, Moisello, Silvestri, Ghez, & Krakauer, 2009; Goedert & Willingham, 2002; Stephan, Meier, Orosz,

Cattapan-Ludewig, & Kaelin-Lang, 2009). In the present study, we use the first definition (i.e., further improvement or enhancement). For related reviews see Doyon et al. (2009), Robertson (2009), Siengsukon and Boyd (2009), and Song (2009).

Offline consolidation of sequence learning may depend on a variety of factors, such as training session intervals (Albouy et al., 2008; Press, Casement, Pascual-Leone, & Robertson, 2005; Walker, Brakefield, Hobson, & Stickgold, 2003), practice (Korman, Raz, Flash, & Karni, 2003; Shanks & Cameron, 2000; Steele & Penhune, 2010), sleep versus wakefulness and time of day (Brawn, Fenn, Nusbaum, & Margoliash, 2010; Cajochen et al., 2004; Della-Maggiore, 2005; Doyon et al., 2009; Fischer, Hallschmid, Elsner, & Born, 2002; Keisler, Ashe, & Willingham, 2007; Kuriyama, Stickgold, & Walker, 2004; Manoach et al., 2004; Maquet, Schwartz, Passingham, & Frith, 2003; Peigneux et al., 2003; Spencer, Sunm, & Ivry, 2006), and degree of explicit awareness (Ghilardi et al., 2009; Hotermans, Peigneux,

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Maertens de Noordhout, Moonen, & Maquet, 2006; Robertson, Pascual-Leone, & Press, 2004). It is not yet clear how sequence learning *per se* changes from a labile state to a more stable one, although there is a large body of work on motor memory consolidation (see Krakauer & Shadmehr, 2006, for a review).

The purpose of the present study was to investigate the separate contributions of general motor skill learning and sequence-specific memory consolidation in *implicit* sequence learning. General motor skill learning refers to faster responses as a result of practice. Sequence-specific learning refers to faster responses as a result of the acquisition of sequence-specific knowledge. Many serial reaction time task (SRTT) studies to date have not distinguished between these two components of performance (but see Hallgato et al., 2013; Németh et al., 2010; Song, Howard, & Howard, 2007, for exceptions).

Evidence of offline motor memory consolidation in conjunction with *explicit* sequence learning was found when participants performed a finger-tapping task with two training sessions (Doyon et al., 2009; Walker, Brakefield, Morgan, Hobson, & Stickgold, 2002; Walker, Brakefield, Seidman, et al., 2003). Specifically, after one night's sleep, with no further practice between sessions, participants showed marked improvements in speed and accuracy. However, there is a difference between motor skill learning in a finger-tapping task of this kind, with short, simple response sequences, and implicit sequence learning in a SRTT, with longer, more complex sequences. In the former, measures of performance relate to the speed at which the movements are carried out, that is, general motor skill. In the latter, measures of performance relate to both the speed of the movements, but also to sequence-specific learning. Beneficial changes in performance that occur during training are taken as evidence of *online learning* of both motor skill learning and sequence-specific learning. Additional improvements, that develop during intervals between sessions, in the absence of further physical practice, are taken as evidence of *offline consolidation* (Krakauer & Shadmehr, 2006; Robertson et al., 2004). The terms are sometimes confused as well as confounded.

Research into motor memory consolidation suggests that implicit sequence learning might be stabilized during the hours immediately after learning, which would be compatible with the time course of synaptic change (Morris, 2006). However, there is, as yet, no firm evidence of an offline consolidation process for *implicit* sequence-specific learning. In contrast, this occurrence has been well documented for *explicit* sequence learning (Press et al., 2005; Walker et al., 2002). It may well be that whereas sleep is helpful towards the consolidation of explicit memory traces (i.e., *passive* offline processing), sufficient practice (i.e., *active* online training) is all that is useful for the consolidation of implicit memory traces (Della-Maggiore, 2005; Press et al., 2005; Robertson et al., 2004; Walker, Brakefield, Hobson, et al., 2003). In fact, offline consolidation, in the sense of "silent" improvement, may play no role at all in implicit sequence-specific learning (Hallgato et al., 2013; Németh & Janacsek, 2011; Németh et al., 2010; Siengsukon & Boyd, 2009; Song et al., 2007; Spencer, Gouw, & Ivry, 2007).

For example, when learning was assessed in young adults across three sessions with equivalent intervals of wakefulness or sleep, Song et al. (2007) found offline improvement in motor

skill learning after wakefulness but not sleep. Further, when Németh et al. (2010) used an alternating serial reaction time task (ASRTT, see Howard & Howard, 1997; Romano, Howard, & Howard, 2010), they found no sequence-specific improvements from an a.m. to p.m. session or a p.m. to a.m. session. Similarly, when Németh and Janacsek (2011) tested participants on *probabilistic* sequence learning, before and after a 12-h, 24-h, or a 1-week interval, they found an improvement in general motor skill (i.e., motor learning regardless of sequencing) in young adults after all three intervals (older adults only showed improvement after the 12-h interval). Importantly, Németh and Janaseck found no improvement in *sequence-specific learning* in either age group after any of the intervals.

The purpose of this study was to investigate offline consolidation of motor skill learning and sequence-specific learning in the sense of improvements in learning rather than just stabilization or lack of deterioration. We report two experiments, in which an SRTT was used. In Experiment 1, consolidation was tested after an interval of 24 h and in Experiment 2, consolidation was tested after one week. In both experiments, one half of the participants were exposed to a *deterministic* sequence and the other half to a *probabilistic* sequence. To test probabilistic sequence learning we used an ASRTT in which every alternate component is sequenced according to a predictable rule with pseudorandom trials in between (see Howard & Howard, 1997; Németh et al., 2010; Romano et al., 2010). The main reason for using a *probabilistic* sequence was to avoid the emergence of explicit knowledge, which might alter performance (Cleeremans & Jiménez, 1998; Destrebecqz & Cleeremans, 2001; Perruchet, Bigand, & Benoit-Gonin, 1997; Remillard, 2008; Remillard & Clark, 2001; Song et al., 2007). We tested whether consolidation would differ for the learning of probabilistic and deterministic sequences, in particular, whether it might be stronger for deterministic sequences (see Deroost, Zeeuws, & Soetens, 2006; Destrebecqz & Cleeremans, 2001; Wilkinson & Jahanshahi, 2007). In fact, it has been shown that when sequence structure is complex, as it is for probabilistic sequences, offline consolidation of sequence learning may not occur (Goedert & Willingham, 2002), or at least not unless the sequence is explicit and not without an interval including sleep (see Cohen & Robertson, 2007; Song, 2009).

In both experiments presented here, responses were either *bimanual*, with half of the participants in each condition using the index and ring fingers of both hands, or *unimanual* with the other half of the participants using all four fingers of the dominant hand. We reasoned that, as information would be integrated across the left and right brain hemispheres, consolidation of bimanual learning might be enhanced compared to unimanual. Indeed, after an interval of 24 h, Kuriyama et al. (2004) found enhanced consolidation in *bimanual* compared to *unimanual* finger-tapping performance, but this was only when the sequence was complex. A number of fMRI (functional magnetic resonance imaging) studies have shown that bimanual and unimanual tasks recruit somewhat different neural systems in the early stages of motor training, but it is not yet clear if this has any lasting effect on memory consolidation in sequence-specific learning (Bapi, Doya, & Harner, 2000; Gerloff & Andres, 2002; Sun, Miller, Rao, & D'Esposito, 2007).

In Experiment 1, with an interval of 24 h between the two training sessions, we expected to find offline improvement in general motor skill learning (i.e., faster responses at the beginning of the second session). We also tested whether there would be offline sequence-specific consolidation, in the sense of *enhancement* (i.e., additional improvement) of implicit sequence knowledge at the beginning of the second session compared to the end of the first. Similarly, in Experiment 2, with a one-week interval, we expected to find offline improvement in general motor skill learning, and we tested whether there would also be offline *enhancement* of sequence-specific learning.

Online sequence learning (probabilistic as well as deterministic sequences) was assessed by inserting *crucial new sequence blocks* at two points. These were near the beginning and end of each of the two training sessions. We compared mean response times (RTs) for the crucial blocks to those of surrounding blocks (providing *sequence learning scores*). *Offline consolidation of sequence-specific learning* was assessed by comparing *sequence learning scores* for the first crucial block of the second session with those for the second crucial block of the first session. *Offline consolidation of general motor skill learning* was assessed by comparing RTs in the first block of the second session with those in the last block of the first session.

2.   Experiment 1

2.1.   Method

2.1.1.   Participants and design
Eighty undergraduate students from the University of Bern (50 women and 30 men, mean age 23 years, SD = 3, age range 18–34 years) were assigned at random to one of four experimental conditions. Kind of sequence (*deterministic* vs *probabilistic*) and kind of responding (*unimanual vs bimanual*) were manipulated between subjects, whilst block was manipulated within subjects, resulting in a mixed design. Participants carried out two identical sequence learning sessions separated by 24 h.

2.1.2.   Materials and apparatus
Four small rectangles, each 2 cm × 3 cm, were permanently displayed on the computer screen. They were horizontally aligned, approximately 10 cm above the bottom edge of the screen and separated from one another by 3 cm gaps. On any given trial, one of the rectangles (and only one) was shown filled in black. This served as the stimulus to which participants responded by pressing the appropriate key (one out of four). The arrangement of the keys was isomorphic to the arrangement of the rectangles. Consequently, upon each correct key press, the stimulus appeared to move to a different location. Unbeknownst to participants, the location change was sequenced. In the *deterministic condition*, two statistically identical sequences were used in a counterbalanced way between subjects, with a sequence changeover at blocks 3 and 9 (*counterbalancing sequence* blocks). The 12-element sequences were 342312413214 and 213243142341 (referred to as A and B), where the numbers 1 to 4 represent the four stimulus locations from left to right. In the *probabilistic* condition, the same

two counterbalanced sequences were used but not in their entirety because each alternate trial varied between two possibilities. For example, where the *deterministic* sequence was 342312413214, the *probabilistic* sequence was 3(4 or 1) 2(3 or 4)1(2 or 3)4, etc. We did not permit consecutive location repetitions in the *probabilistic* sequences because interspersed pseudorandom trials were restricted to locations that were not the same as the previous or the following trial (cf., Keisler & Willingham, 2007). Thus, our *probabilistic* sequences featured no immediate predictability from one trial to the next (first order sequencing) or from a preceding trial to a subsequent trial (second order sequencing; see Remillard, 2003, for a different set-up).

Viewing distance was approximately 40 cm and the same four response keys were used for both conditions. The designated response keys were in the same horizontal row and were spaced out to match the stimulus locations on the screen. On each trial, the stimulus (filled rectangle) remained on screen until the appropriate key was pressed. The response to next stimulus interval was 200 msec. The experiment was programmed in E-Prime 1.1 software (Psychology Software Tools, www.pstnet.com).

2.1.3.   Procedure
Participants were tested individually, during the late morning or early afternoon, with the two training sessions taking place at the same time of day. Instructions were given on paper. Participants were told that the experiment concerned the effects of practice on speed of response and would comprise two *sessions* separated by an interval of 24 h, during which time they should not discuss the experiment with others. At the beginning of *session 1*, participants were instructed to respond as quickly and as accurately as possible to the changing location of the filled rectangle that appeared on the screen, by pressing the designated keys one after another. An initial practice block (block 1, 96 trials, pseudorandom order) was followed by nine experimental blocks (96 trials each, sequenced order). With the exception of blocks 1, 3 and 9, participants received the same sequenced ordering of trials throughout. In blocks 3 and 9, they received the counterbalanced sequence, which was new to them. Each sequenced block began with 3 random trials. At the end of each block, a message on the screen advised participants to take a short break. No feedback on performance was given and the presence of sequences was not mentioned.

After exactly 24 h, *session 2* was conducted (blocks 11–20) using the same procedure as *session 1*, the same counterbalanced arrangement of unimanual versus bimanual responding (between subjects) and the same *deterministic* versus *probabilistic* sequences (between subjects) as in Experiment 1. Finally a brief interview was conducted to assess explicit knowledge. Participants were asked if they had noticed anything in particular about the stimulus locations and responses. The existence of sequenced ordering was then explained and participants were asked to report the main sequence, either by guessing or from memory.

2.1.4.   Data analysis
Trials on which errors were made, trials immediately following an error, as well as the first three random trials of

each block, were excluded from the analysis. RT data were aggregated and mean RTs per block were computed separately for each participant. An alpha level of .05 was used for the analyses. Degrees of freedom and *MSE* values were Green-house–Geisser adjusted where appropriate. Effect sizes are partial η^2 values. For *session 1, sequence learning scores for block 9* were calculated in milliseconds as the mean RT difference between block 9 and the average of surrounding blocks 8 and 10. For *session 2*, the same procedure was used, that is *sequence learning scores for block 13* were calculated as the mean RT difference between block 13 and the average of surrounding blocks 12 and 14, and *sequence learning scores for block 19* were calculated as the mean RT difference between block 19 and the average of surrounding blocks 18 and 20. *Consolidation of general motor skill learning* was assessed by comparing RTs at block 11 (beginning of session 2) with RTs at block 10 (end of session 1). *Consolidation of sequence-specific learning* was assessed by comparing *sequence learning scores* at block 13 (session 2) with *sequence learning scores* at block 9 (session 1). *Explicit knowledge* was taken to have been acquired if, after the experiment, the participant correctly reported 6 or more elements of the 12-element training sequence. We used this strict criterion because, with no adjacent repeats and a starting point anywhere in the sequence, an average of 4 out of 12 correct could easily be reported purely by guessing. The first 2 elements would inevitably count as correct and subsequent elements could only be 1 out of 3 possibilities each time.

2.2. Results

Mean overall error rates, averaged over all blocks of trials, were generally low, on average 5% (*SE* = .42) and are not presented further. A preliminary two factorial analysis of variance (ANOVA) on the RT data revealed a significant main effect of *block* across sessions 1 and 2 combined (20 blocks), $F(19, 1482) = 82.64$, $MSE = 1304$, $p < .001$, $\eta^2 = .51$, but no effect of *sequence counterbalancing* (*sequence A vs sequence B*), $F(1, 78) = .17$, $MSE = 87,016$, $p = .68$, $\eta^2 = .002$, and no significant *blocks × counterbalancing* interaction, $F(19, 1482) = .39$, $p = .99$, $\eta^2 = .005$. Hence, for all other analyses, data were collapsed across the A versus B sequence counterbalancing factor. RT data are presented in Fig. 1. Sequence learning scores are summarized in Table 1 (top line).

2.2.1. Session 1
At block 9, mean *sequence learning scores* (RTs at block 9 minus average of blocks 8 and 10 combined) for the *kind of sequence* factor were 36 msec (*SE* = 5) for *deterministic* and 6 msec (*SE* = 4) for *probabilistic*, with single-sample one-tailed *t*-tests against zero giving $t(39) = 7.65$, $p < .001$ for *deterministic* and $t(39) = 1.52$, $p = .07$ for *probabilistic*. For the *kind of responding* factor, the mean for *unimanual* was 25 msec (*SE* = 5), with a single-sample one-tailed *t*-test against zero giving $t(38) = 4.64$, $p < .001$, and for *bimanual*, the mean was 17 msec (*SE* = 4), with a single-sample one-tailed *t*-test against zero giving $t(39) = 3.85$, $p < .001$. A mixed three-factorial ANOVA was conducted, with RTs at block 9 compared to the average of blocks 8 and 10 as a within subjects factor, and with *kind of responding* and *kind of sequence* as between subjects factors. This revealed a significant main effect of *block* (sequence
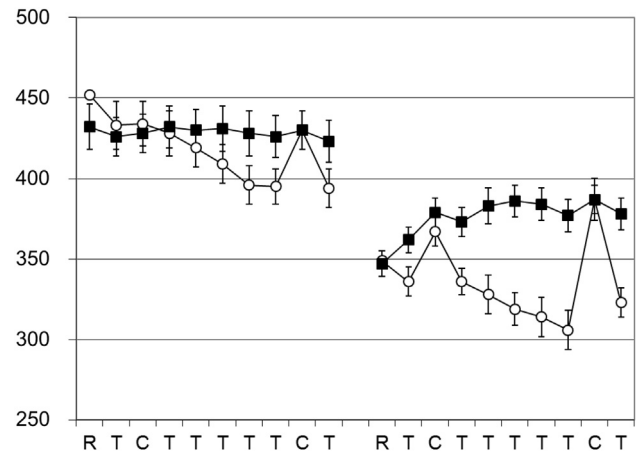
Fig. 1 – **Mean response times, combined for unimanual and bimanual groups as a function of blocks (R: random; T: training sequence; C: counterbalanced sequence), shown separately for deterministic (white circles) and probabilistic (black squares) sequence conditions, indicating session 1 (left) and session 2 (right) with an interval of 24 h between sessions. Error bars represent standard errors.**

learning effect), $F(1, 76) = 46.85$, $MSE = 370$, $p < .001$, $\eta^2 = .38$, but no significant main effect of *kind of sequence* $F(1, 76) = .84$, $MSE = 11,384$, $p = .36$, $\eta^2 = .01$, no significant main effect of *kind of responding* $F(1, 76) = 1.26$, $MSE = 11,384$, $p = .27$, $\eta^2 = .02$. The *blocks × kind of sequence* interaction was significant $F(1, 76) = 23.47$, $MSE = 370$, $p < .001$, $\eta^2 = .24$. None of the other possible interactions reached significance (all *F*s < 2). In other words, by block 9, overall, sequence learning occurred, in particular for *deterministic* sequences. Whether responding was *unimanual* or *bimanual* made no difference to the sequence learning.

Table 1 – **Summary of sequence learning scores (in msec) for Experiment 1 and Experiment 2, and pooled across Experiments 1 and 2 for kind of responding and kind of sequence. Standard errors in parentheses.**

	Session 1		Session 2	
	B3	B9	B13	B19
24 h interval (Exp 1)	1 (3)	20 (3)[a]	22 (3)[a]	40 (6)[a]
1-week interval (Exp 2)	6 (3)[b]	24 (4)[a]	19 (3)[a]	42 (6)[a]
Unimanual	3 (3)	25 (4)[a]	21 (4)[a]	43 (6)[a]
Bimanual	4 (3)	20 (4)[a]	19 (3)[a]	41 (5)[a]
Deterministic	5 (3)	38 (4)[a]	32 (4)[a]	72 (6)[a]
Probabilistic	1 (2)	7 (3)[a]	8 (2)[a]	10 (3)[a]

Note. B3, B9, B13, and B13 refer to the learning score at this particular random block compared to the mean of the adjacent sequenced blocks.

[a] Learning scores greater than zero (all *p*s < .05).

[b] In contrast to Experiment 1, in Experiment 2, the learning score at B3 was significantly different from zero, $t(79) = 2.25$, $p = .03$. However, this is a spurious effect because the experiments did not differ in design or procedure until after block 10.

2.2.2. Session 2

At block 13, mean *sequence learning scores* (RTs at block 13 minus average of blocks 12 and 14) for the *kind of sequence* factor were 31 msec ($SE = 6$) for *deterministic* and 12 msec ($SE = 3$) for *probabilistic*, with single-sample one-tailed *t*-tests against zero giving $t(39) = 5.62$, $p < .001$ for *deterministic* and $t(39) = 3.57$, $p < .001$ for *probabilistic*. For the *kind of responding* factor, the mean for *unimanual* was 24 msec ($SE = 6$), with a single-sample one-tailed *t*-test against zero giving $t(38) = 4.11$, $p < .001$, and the mean for *bimanual* was 19 msec ($SE = 4$), with a single-sample one-tailed *t*-test against zero giving $t(40) = 5.18$, $p < .001$. A mixed three-factorial ANOVA was conducted, with RTs at block 13 compared to the average of blocks 12 and 14 as a within subjects factor, and with *kind of responding* and *kind of sequence* as between subjects factors. This revealed a significant main effect of *block* (sequence learning effect), $F(1, 76) = 43.66$, $MSE = 428$, $p < .001$, $\eta^2 = .37$, an almost significant effect of *kind of sequence* $F(1, 76) = 3.62$, $MSE = 5657$, $p = .06$, $\eta^2 = .05$ (*deterministic* slightly faster than *probabilistic*), and a significant main effect of *kind of responding*, $F(1, 76) = 7.01$, $MSE = 5657$, $p < .01$, $\eta^2 = .08$ (*bimanual* responses being generally faster than *unimanual*). The *blocks × kind of sequence* interaction was significant, $F(1, 76) = 8.38$, $MSE = 428$, $p < .01$, $\eta^2 = .10$ (stronger learning effect for *deterministic* than *probabilistic*), but none of the other possible interactions reached significance (Fs < 3). In brief, in session 2, participants showed a significant sequence learning effect as early as the third block (block 13), with the effect being stronger for *deterministic* sequences and comparable for *unimanual* and *bimanual* responding.

At block 19, mean *sequence learning scores* (RTs at block 19 minus average of blocks 18 and 20) for the *kind of sequence* factor were 71 msec ($SE = 8$) for *deterministic* and 9 msec ($SE = 4$) for *probabilistic*, with single-sample one-tailed *t*-tests against zero giving $t(39) = 8.62$, $p < .001$ for *deterministic* and $t(39) = 2.10$, $p < .02$ for *probabilistic*. For the *kind of responding* factor, the mean for *unimanual* was 45 msec ($SE = 10$) with a single-sample one-tailed *t*-test against zero giving $t(38) = 4.72$, $p < .001$ and the mean for *bimanual* was 36 msec ($SE = 7$) with a single-sample one-tailed *t*-test against zero giving $t(40) = 5.20$, $p < .001$. A mixed three-factorial ANOVA was conducted, with RTs at block 19 compared to the average of blocks 18 and 20 as a within subjects factor, and with *kind of responding* and *kind of sequence* as between subjects factors. This revealed a significant main effect of *block* (sequence learning effect), $F(1, 76) = 73.32$, $MSE = 885$, $p < .001$, $\eta^2 = .49$, a significant effect of *kind of sequence* $F(1, 76) = 5.74$, $MSE = 7007$, $p \leq .02$, $\eta^2 = .07$ (*deterministic* being generally faster than *probabilistic*), and an almost significant main effect of *kind of responding* $F(1, 76) = 3.64$, $MSE = 7007$, $p = .06$, $\eta^2 = .05$ (*bimanual* generally somewhat faster than *unimanual*). Of all the possible interactions, only the *blocks × kind of sequence* interaction reached significance (all other Fs < 1), $F(1, 76) = 43.58$, $MSE = 885$, $p < .001$, $\eta^2 = .36$ (*deterministic* showing greater sequence learning than *probabilistic*). In other words, participants showed a significant sequence learning effect at block 19, but it was greater for *deterministic* than *probabilistic* sequences. In fact, for *deterministic* sequences, the sequence learning effect at block 19 was more than twice the size of the effect at block 13. For *probabilistic* sequences the size of the effect remained unchanged.

2.2.3. Consolidation of general motor skill learning

A mixed three-factorial ANOVA was conducted, with RTs at block 10 (session 1) compared to those at block 11 (session 2) as a within subjects factor, and with *kind of responding* (unimanual vs bimanual) and *kind of sequence* (deterministic vs probabilistic) as between subjects factors. This revealed a significant main effect of *block* $F(1, 76) = 134.24$, $MSE = 1079$, $p < .001$, $\eta^2 = .64$ (RTs at block 11 being notably faster than those at block 10) but no main effect of *kind of sequence*, $F(1, 76) = 1.00$, $MSE = 7951$, $p = .32$, $\eta^2 = .01$ (RTs for *deterministic* and *probabilistic* being generally similar on these two blocks) and no main effect of *kind of responding*, $F(1, 76) = 1.79$, $MSE = 7951$, $p = .19$, $\eta^2 = .02$ (no difference between *unimanual* and *bimanual* on these two blocks). The *blocks × kind of sequence* interaction was significant, $F(1, 76) = 8.38$, $MSE = 1079$, $p < .01$, $\eta^2 = .09$ (stronger decrease for *probabilistic* than *deterministic*), as was the *blocks × kind of responding* interaction, $F(1, 76) = 4.76$, $MSE = 1079$, $p < .05$, $\eta^2 = .06$ (slightly stronger decrease for *bimanual* than *unimanual*). Neither the *kind of sequence × kind of responding* interaction nor the *blocks × kind of sequence × kind of responding* interaction reached significance (both Fs < 1). These results indicate significant offline improvement in general motor skill learning between sessions 1 and 2, with the effect being slightly stronger for *bimanual* responding, and for participants who trained on a *probabilistic* rather than *deterministic* sequence in session 1.

2.2.4. Consolidation of sequence-specific learning

A mixed three-factorial ANOVA was conducted, with *sequence learning scores* at block 9 (session 1) compared to those at block 13 (session 2) as a within subjects factor, and with *kind of responding* (unimanual vs bimanual) and *kind of sequence* (deterministic vs probabilistic) as between subjects factors. This revealed a significant main effect of *kind of sequence*, $F(1, 76) = 19.72$, $MSE = 1188$, $p < .001$, $\eta^2 = .21$ (*deterministic* showing generally higher scores than *probabilistic*) but no main effect of *kind of responding*, $F(1, 76) = 1.13$, $MSE = 1188$, $p = .29$, $\eta^2 = .02$ (no difference between *unimanual* and *bimanual*) and, more importantly, no main effect of *sequence learning scores*, $F(1, 76) = .06$, $MSE = 407$, $p = .80$, $\eta^2 = .001$. None of the four possible interactions reached significance (all Fs < 1). Hence, these results give no indication of offline enhancement of sequence-specific learning between sessions 1 and 2.

2.2.5. Explicit knowledge

At the end of *session 2*, one participant, who trained on a *deterministic* sequence, correctly reported all 12 elements of the sequence. Without this participant, the mean for the deterministic sequence was 3.72 elements correct out of 12 ($SD = 1.11$, $n = 79$), which we take as chance level. Her individual *sequence learning score* was 49 msec at the end of session 1 (block 9 vs surrounding blocks) compared to 92 msec at the beginning of session 2 (block 13 vs surrounding blocks). This difference suggests that sequence-specific enhancement (offline consolidation between sessions) had occurred for this particular participant. Group mean sequence learning scores are shown in Table 1. None of the participants who trained on a *probabilistic* sequence correctly reported as much as half (or more than half) of the alternating sequence elements. We take this to be chance level only.

In order to follow-up a potential relationship between explicit knowledge and sequence-specific consolidation, we conducted additional correlational analyses. If explicit knowledge played a significant role, we hypothesized that the correlations between explicit knowledge and the individual sequence learning score would be higher at the beginning of session 2 (B13) compared to the end of session 1 (B9). For *deterministic* sequence learning, the correlations were $r = .12$, $p = .46$, and $r = .31$, $p = .052$. Importantly, testing the statistical significance of the difference between these dependent correlations (Hoerger, 2013) showed no statistical differences, $Z_H(37) = -1.35$, $p = .174$. For *probabilistic* sequence learning, the correlations between explicit knowledge and individual sequence learning scores were $r = -.16$, $p = .34$, and $r = -.16$, $p = .33$. Again, these correlations were not statistically different, $Z_H(37) = .02$, $p = .98$. These results are in line with the group-mean analyses and they suggest that explicit knowledge did not play a significant role in the present experiment.

2.3. Discussion

In session 1, there was evidence of significant sequence learning by block 9. This was indicated by slower responses when a new sequence was introduced. Despite unimanual responding being slower than bimanual, there was no difference between them with regard to sequence learning. In session 2, a significant sequence learning effect emerged as early as the third block (block 13), with the effect being stronger for *deterministic* sequences, and again much the same for unimanual and bimanual responding. The sequence learning effect at block 19 was even greater for *deterministic* sequences, and more than twice the size of the effect at block 13. For *probabilistic* sequences the size of the effect remained unchanged across session 2.

As expected, there was significant offline improvement in general motor skill learning between session 1 and session 2, with a slightly stronger effect for bimanual compared to unimanual responding. This confirms that consolidation, in the sense of further motor skill improvement in the absence of further physical practice (i.e., during the 24 h interval), had occurred. However, there was no indication at all of any offline enhancement of implicit sequence-specific learning, which is contrary to what might be expected based on the findings of explicit learning of finger tapping sequences (e.g., Kuriyama et al., 2004).

However, our results are in agreement with the findings of Németh et al. (2010), who also used the ASRTT, and who found no sequence-specific improvements from an a.m. to p.m. session or from a p.m. to a.m. session, in young and older adults alike. They concluded that consolidation of implicit sequence learning may be unaffected by sleep between training sessions, that is, implicit sequence learning may always need active, online processing for improvements to be observed. In fact, inter-session enhancement of what has been learned implicitly may not occur at all, such that performance at the start of a new session simply continues where it left off at the end of the last session.

Although Genzel et al. (2012) found that participants who slept immediately after motor sequence training showed better sequence-specific *retention* (i.e., "savings" rather than

"enhancement") than participants who stayed awake for a comparable length of time, the difference evened out once the awake group had their normal night's sleep. The finding suggests that even if sleep does not play a role in the further enhancement of sequence-specific learning, it may help stabilize memory traces – in other words, it may ward off forgetting. Genzel et al. (2012) also found that general motor skill learning showed improvement, after an interval, that was independent of sleep.

However, when Song et al. (2007) examined off-learning in young adults (three sessions with equivalent periods of wakefulness or sleep in between), their results showed evidence of offline improvement of general motor skill learning *only* after a period of wakefulness – that is, *not* after sleep. Importantly for us, Song et al.'s results showed *no improvement in implicit sequence-specific learning*, following either wakefulness or sleep. It may just be, of course, that participants needed more time for the consolidation of implicit sequence-specific learning (see Press et al., 2005).

Walker, Brakefield, Seidman, et al. (2003) found increasingly stronger sequence-specific consolidation with longer intervals, however, in their study sequence knowledge was essentially explicit. Hence, in Experiment 2, we investigated whether the consolidation of implicit sequence learning might benefit from more time by using a one-week interval between sessions. As before, we expected to find offline improvement in general motor skill learning, and we tested whether there would be any additional offline enhancement of sequence-specific learning.

3. Experiment 2

3.1. Method

3.1.1. Participants and design
Eighty undergraduate students from the University of Bern, who had not taken part in Experiment 1, participated in return for course credit (46 women and 34 men, mean age 25 years, SD = 5, age range 20–40 years). As in Experiment 1, *kind of sequence* (*deterministic vs probabilistic*) and *kind of responding* (*unimanual vs bimanual*) were manipulated between subjects whilst block was manipulated within subjects, resulting in a mixed design and participants were assigned at random to one of the four conditions.

3.1.2. Materials, procedure and data analysis
These were exactly as in Experiment 1, apart from the fact that the second session was administered after one week instead of after 24 h. Again, testing took place at the same time of day for both sessions.

3.2. Results

Mean overall error rates, averaged over all blocks of trials, were generally low, on average 6% (SE = .54) and are not presented further. A preliminary two factorial ANOVA revealed a significant main effect of *block* across sessions 1 and 2 combined (20 blocks), $F(19, 1482) = 91.22$, $MSE = 1067$, $p < .001$, $\eta^2 = .54$, but no effect of *sequence counterbalancing* (*sequence A*

vs sequence B), $F(1, 78) = .41$, $MSE = 92,874$, $p = .52$, $\eta^2 = .006$, and no *blocks × counterbalancing* interaction, $F(19, 1482) = .96$, $p = .51$, $\eta^2 = .01$. Hence, for all other analyses, data were collapsed across the A versus B sequence counterbalancing factor. RT data are presented in Fig. 2. Sequence learning scores are summarized in Table 1 (second line).

3.2.1. Session 1

At block 9, mean *sequence learning scores* (RTs at block 9 minus average of blocks 8 and 10) for the *kind of sequence* factor were 40 msec ($SE = 6$) for *deterministic*, with a single-sample one-tailed *t*-test against zero giving $t(39) = 6.84$, $p < .001$, and 8 msec ($SE = 3.5$) for *probabilistic*, with a single-sample one-tailed *t*-test against zero giving $t(39) = 2.19$, $p < .02$. For participants who made *unimanual* responses, the mean *sequence learning* score was 24 msec ($SE = 5$), with a single-sample one-tailed *t*-test against zero giving $t(39) = 4.71$, $p < .001$. For those who made *bimanual* responses, the mean was also 24 msec ($SE = 6$), with a single-sample one-tailed *t*-test against zero giving $t(39) = 4$, $p < .001$. A mixed three-factorial ANOVA was conducted with RTs at block 9 compared to the average of blocks 8 and 10 as a within subjects factor, and with *kind of responding* and *kind of sequence* as between subjects factors. This revealed a significant main effect of *block* (sequence learning effect), $F(1, 76) = 48.46$, $MSE = 473$, $p = .001$, $\eta^2 = .39$, and a significant main effect of *kind of responding* (i.e., *bimanual* generally faster than *unimanual*), $F(1, 76) = 10.93$, $MSE = 8664$, $p < .001$, $\eta^2 = .13$, but no significant main effect of *kind of sequence* $F(1, 76) = 1.51$, $MSE = 8664$, $p = .22$, $\eta^2 = .02$. Only the *blocks × kind of sequence* interaction (stronger learning effect for *deterministic* than *probabilistic*) reached significance, $F(1, 76) = 22.31$, $MSE = 473$, $p = .001$, $\eta^2 = .23$ (all other *Fs* < 2). In other words, by block 9, there was evidence of sequence learning for *unimanual* as well as *bimanual* responding, and for both kinds of sequence, but with the effect being stronger for *deterministic* than *probabilistic* sequences.

3.2.2. Session 2

At block 13, mean *sequence learning scores* (RTs at block 13 minus average of blocks 12 and 14) for the *kind of sequence* factor were 32 msec ($SE = 5$) for *deterministic* and 5 msec ($SE = 3$) for *probabilistic*, with single-sample one-tailed *t*-tests against zero giving $t(39) = 6.94$, $p < .001$ for *deterministic*, and $t(39) = 1.50$, $p = .16$ for *probabilistic*. For the *kind of responding* factor, the mean for *unimanual* was 19 msec ($SE = 5$), with a single-sample one-tailed *t*-test against zero giving $t(39) = 3.83$, $p < .001$. The mean for *bimanual* was 18 msec ($SE = 4$), with a single-sample one-tailed *t*-test against zero giving $t(39) = 4.39$, $p < .001$. A mixed three-factorial ANOVA was conducted with RTs at block 13 compared to the average of blocks 12 and 14 as a within subjects factor, and with *kind of responding* and *kind of sequence* as between subjects factors. This revealed a significant main effect of *block* (sequence learning effect), $F(1, 76) = 43.04$, $MSE = 318$, $p = .001$, $\eta^2 = .36$, a significant main effect of *kind of responding*, $F(1, 76) = 15.87$, $MSE = 7030$, $p < .001$, $\eta^2 = .17$ (*bimanual* generally faster than *unimanual*), but no significant effect of *kind of sequence* $F(1, 76) = .32$, $MSE = 7030$, $p = .57$, $\eta^2 = .004$, and no significant *blocks × kind of responding* interaction, $F(1, 76) = .001$, $MSE = 318$, $p = .98$, $\eta^2 = 0$. There was a significant *blocks × kind of sequence* interaction, $F(1,$
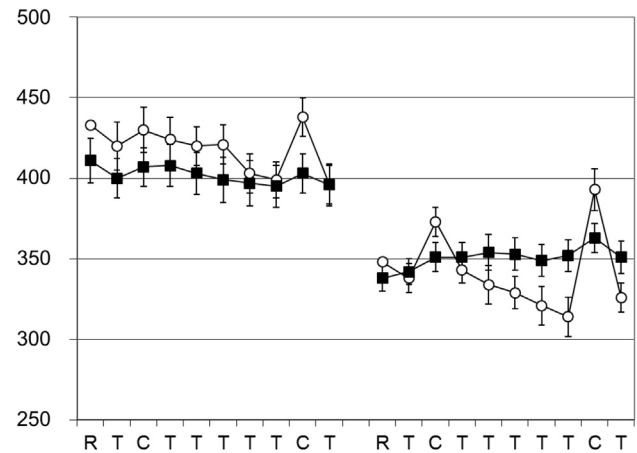
Fig. 2 – Mean response times, combined for unimanual and bimanual groups as a function of blocks (R: random; T: training sequence; C: counterbalanced sequence), shown separately for deterministic (white circles) and probabilistic (black squares) sequence conditions, indicating session 1 (left) and session 2 (right) with an interval of 1 week between sessions. Error bars represent standard errors.

$76) = 24.50$, $MSE = 318$, $p < .001$, $\eta^2 = .24$ (stronger sequence learning effect for *deterministic* than *probabilistic*), a marginally significant *kind of responding × kind of sequence* interaction, $F(1, 76) = 3.21$, $MSE = 7030$, $p < .08$, $\eta^2 = .04$, but no *blocks × kind of sequence × kind of responding* interaction, $F(1, 76) = .25$, $MSE = 318$, $p = .62$, $\eta^2 = .003$. In other words, by block 13, *deterministic* sequences showed a strong sequence learning effect but *probabilistic* did not, and *unimanual* versus *bimanual* responding made no difference to sequence learning.

At block 19, mean *sequence learning scores* (RTs at block 19 minus average of blocks 18 and 20) for the *kind of sequence* factor were 73 msec ($SE = 8$) for *deterministic* and 12 msec ($SE = 3$) for *probabilistic*, with single-sample one-tailed *t*-tests against zero giving $t(39) = 8.68$, $p < .001$ for *deterministic*, and $t(39) = 4.27$, $p < .001$ for *probabilistic*. For the *kind of responding* factor, the mean for *unimanual* was 40 msec ($SE = 7$), with a single-sample one-tailed *t*-test against zero giving $t(39) = 5.38$, $p < .001$. For *bimanual* it was 45 msec ($SE = 8$), with a single-sample one-tailed *t*-test against zero giving $t(39) = 5.29$, $p < .001$. A mixed three-factorial ANOVA was conducted, with RTs at block 19 compared to the average of blocks 18 and 20 as a within subjects factor, and with *kind of responding* and *kind of sequence* as between subjects factors. This revealed a significant main effect of *block* (sequence learning effect), $F(1, 76) = 89.21$, $MSE = 808$, $p < .001$, $\eta^2 = .54$, a significant main effect of *kind of responding* (*bimanual* still generally faster than *unimanual*), $F(1, 76) = 16.44$, $MSE = 8198$, $p < .001$, $\eta^2 = .18$, but no significant effect of *kind of sequence* $F(1, 76) = .005$, $MSE = 8198$, $p = .94$, $\eta^2 = 0$. There was no significant *blocks × kind of responding* interaction, $F(1, 76) = .24$, $MSE = 808$, $p = .63$, $\eta^2 = .003$, but a significant *blocks × kind of sequence* interaction, $F(1, 76) = 46.67$, $MSE = 808$, $p < .001$, $\eta^2 = .38$ (a stronger learning effect for *deterministic* than *probabilistic*), and an almost significant *kind of responding × kind of sequence*

interaction, $F(1, 76) = 3.40$, $MSE = 8198$, $p < .07$, $\eta^2 = .04$. Finally, there was no blocks × kind of sequence × kind of responding interaction, $F(1, 76) = .136$, $MSE = 808$, $p = .71$, $\eta^2 = .002$. In other words, by block 19, participants showed a greater sequence learning effect for deterministic sequences compared to probabilistic, in fact more than twice the size of the effect at block 13. The mean sequence learning score for deterministic sequences at the end of session 2 was also considerably larger than that at the end of session 1. Whereas learning of probabilistic sequences did not reach significance at block 13, it did at block 19. By block 19, kind of responding (unimanual vs bimanual) still made no difference to the sequence learning effects.

3.2.3. Consolidation of general motor skill learning

A mixed three-factorial ANOVA was conducted, with RTs at block 10 (session 1) compared to those at block 11 (session 2) as a within subjects factor, and with kind of responding (unimanual vs bimanual) and kind of sequence (deterministic vs probabilistic) as between subjects factors. This revealed a significant main effect of block $F(1, 76) = 106.94$, $MSE = 1060$, $p < .001$, $\eta^2 = .59$ (RTs at block 11 being notably faster than those at block 10), a significant main effect of kind of responding, $F(1, 76) = 14.38$, $MSE = 8042$, $p < .001$, $\eta^2 = .16$ (unimanual generally slower on these two blocks than bimanual) but no main effect of kind of sequence, $F(1, 76) = .12$, $MSE = 8042$, $p = .73$, $\eta^2 = .002$ (deterministic and probabilistic being generally similar). None of the four possible interactions reached significance. Thus, offline improvement in general motor skill learning occurred between sessions 1 and 2, for unimanual as well as bimanual responding, and for participants trained on either probabilistic or deterministic sequences.

3.2.4. Consolidation of sequence-specific learning

A mixed three-factorial ANOVA was conducted, with sequence learning scores at block 9 (session 1) compared to those at block 13 (session 2) as a within subjects factor, and with kind of responding (unimanual vs bimanual) and kind of sequence (deterministic vs probabilistic) as between subjects factors. This revealed a significant main effect of kind of sequence, $F(1, 76) = 33.52$, $MSE = 1089$, $p < .001$, $\eta^2 = .31$ (deterministic showing generally higher scores than probabilistic) but no main effect of kind of responding, $F(1, 76) < .001$, $MSE = 1089$, $p = .995$, $\eta^2 < .001$ (no difference between unimanual and bimanual) and, more importantly, no main effect of sequence learning scores, $F(1, 76) = 2.40$, $MSE = 494$, $p = .13$, $\eta^2 = .03$. None of the four possible interactions reached significance. These results give no indication of offline improvement in sequence-specific learning between sessions 1 and 2. This pertains to deterministic and probabilistic sequences alike, and to unimanual and bimanual responding alike.

3.2.5. Explicit knowledge

At the end of session 2, none of the participants were able to report the whole sequence. None of the participants who trained on a probabilistic sequence correctly reported more than half of the alternating sequence elements, which was equivalent to chance level. However, in order to follow-up a potential relationship between explicit knowledge and sequence-specific consolidation, we conducted additional correlational analyses as in Experiment 1, by comparing the correlations between explicit knowledge and the individual sequence learning score at the end of session 1 (B9) and at the beginning of session 2 (B13). For deterministic sequence learning, the correlations were $r = .15$, $p = .35$, and $r = .22$, $p = .17$. Importantly, testing the statistical significance of the difference between these dependent correlations (Hoerger, 2013) showed no statistical differences, $Z_H(37) = -.41$, $p = .68$. For probabilistic sequence learning, the correlations between explicit knowledge and individual sequence learning scores were $r = -.13$, $p = .42$, and $r = .08$, $p = .64$. Again, these correlations were not statistically different, $Z_H(37) = .26$, $p = .79$. These results replicate those of Experiment 1.

3.3. Discussion

The pattern of results of Experiment 2 was very similar to that of Experiment 1. There was evidence of sequence learning, for unimanual and bimanual responding alike, and for both kinds of sequence, and with the effect being stronger for deterministic than probabilistic sequences. These results are summarized in Table 1. As expected, there was a significant offline improvement (i.e., consolidation) in general motor skill learning between sessions, for unimanual and bimanual responding alike and with training on probabilistic and deterministic sequences alike. However, whereas Walker, Brakefield, Seidman, et al. (2003) found that additional nights of sleep led to even greater improvements in offline consolidation, we did not even find numerically greater enhancement of general motor skill learning in Experiment 2 compared to Experiment 1. The reason for the difference may lie in the fact that the finger-tapping motor task in the Walker et al. study was associated with explicit sequence knowledge. More importantly, as in Experiment 1, there was no indication of any offline improvement (i.e., no consolidation) in sequence-specific learning between sessions, for either deterministic or probabilistic sequences, or for unimanual or bimanual responding (see Table 1).

4. General discussion

The purpose of this study was to investigate the contributions of general motor skill learning and sequence-specific memory consolidation in implicit sequence learning. We investigated offline consolidation effects, in motor skill learning as well as in implicit sequence-specific learning, by assessing performance improvements (i.e., faster RTs) between training sessions. Evidence of offline consolidation of general motor skill learning was found in Experiment 1, with an interval of 24 h between sessions, as well as in Experiment 2, with an interval of one week.

Assessment of offline general skill learning was conservative because we compared the last block of session 1, which was sequenced, with the first block of session 2, which was not. In other words, even if performance at the end of session 1 was faster because of sequence-specific learning (in addition to general motor skill training effects), performance on the first block of session 2 was faster still — when the order of trials in that block was random. Thus, if anything, the

extent of general motor skill consolidation may have been underestimated.

In neither case was there any indication of offline enhancement of implicit sequence learning *per se*. That is, there was no suggestion that sequence-specific memory traces had been consolidated, in the sense of improved, during the interval. This result contrasts with the consolidation effects for more general motor skill learning. In both experiments, offline periods included sleep as well as wakefulness and neither appeared to have led to improved sequence-specific learning. This result is consistent with studies in the literature showing that sleep usually enhances explicit but not implicit sequence learning (see Robertson et al., 2004).

It must, of course, be borne in mind that, in the present study, we did not manipulate periods of sleep or wakefulness with a view to examining their effect on memory consolidation in implicit sequence learning. Hence, our comments on this particular topic are only speculative. All we are saying is that, given our present results, it would appear that offline consolidation does not play a major role in implicit sequence learning, at least not in the sense of further "silent" improvement (Hallgato et al., 2013; Németh & Janacsek, 2011; Németh et al., 2010; Siengsukon & Boyd, 2009; Spencer et al., 2007).

It is still possible, of course, that other activities interfered with offline processing of sequence-specific knowledge during the interval between training sessions. For example, Brown and Robertson (2007) have argued that offline consolidation of a procedural memory trace can be blocked by declarative learning, particularly across intervals involving wakefulness (i.e., rather than sleep). As the opposite situation can also be found, with offline processing of a declarative memory being blocked by an episode of procedural learning, Brown and Robertson have suggested a dynamic declarative–procedural relation (i.e., equivalent to the explicit–implicit distinction), in which the balance is modulated by when the consolidation takes place, and which allows for reciprocal interaction between the two memory systems (Brown & Robertson, 2007; Cohen & Robertson, 2011).

Hence, a lack of offline consolidation of sequence-specific learning after 24 h, or one week, as found in the present study, might be explained in terms of participants having been "preoccupied" during much of the interval with other, more declarative forms of learning. One way to test our explanation might be to compare performance of, say, students during an intense learning period (i.e., prior to examinations) and students at a more relaxed time (i.e., at the end of term). However, as evidence for and against the effects of sleep on sequence learning are still up for debate, we do not expect to see the question of mental state being raised just yet, but we thank an anonymous reviewer of an earlier draft of our manuscript for suggesting the idea.

In contrast to the above, we suggest that offline consolidation of the general motor skill learning component of the SRTT was less likely to have been blocked during the interval between training sessions. Although this component was very largely *procedural*, it was at least partly *declarative* in the sense that participants were aware of pressing the keys and their motor performance was deliberate (i.e., they had an explicit mental representation of the task requirements). This might

have helped with consolidation of motor skill learning during the interval. In contrast, the implication is that implicit sequence-specific learning *per se* benefits more from active online practice than from passive offline waiting.

It should also be noted that, in order to test implicit learning of the specific training sequence, we used a counterbalanced arrangement whereby the new sequence in the crucial transfer blocks was an almost perfect reversal of the training sequence, for example, 342312413214 and 213243142341, respectively, depending on the starting point. Thus, theoretically, it might be argued, especially in the case of deterministic sequences, that at least some learning of the training sequence could have been transferred to the test sequence by means of "reversed recognition". We thank an anonymous reviewer for this subtle suggestion. If so, then the method we used to assess sequence-specific consolidation effects could have been compromised, that is, the effect would have been weakened and the result misleading. While, so far, there is no evidence for reversed transfer of this kind in implicit sequence learning, there are a few studies that have addressed the idea in explicit sequence learning (e.g., Albouy et al., 2013; Witt, Margraf, Bieber, Born, & Deuschl, 2010). We agree that, in such a situation, the recognition of fragments of a familiar sequence that have been reversed (during an offline interval) might indeed encourage faster learning of a new sequence (after the interval), and thereby mask any offline consolidation of an already familiar sequence. However, we think such a scenario would be very unlikely in the case of implicit sequence learning, which rests more on familiarity with the underlying statistical structure of the sequence, namely element and transition frequencies and associated chains of *one-way* transitions. It is hard to see how element reversals would have any impact without awareness.

Another point to mention is that when we compared sequence learning and consolidation for unimanual versus bimanual responding, we found consistent results across both experimental settings and no interactions in either experiment. This is an interesting result because typically in experimental psychology, bimanual performance is involved, whereas in neuropsychological studies, particularly those involving neuroimaging, it is unimanual. Thus, our results suggest that findings from these different subdisciplines are likely to generalize across different experimental settings and that this is true for both implicit sequence learning and consolidation.

To conclude, we acknowledge that sequence learning results of any kind can be affected by specific stimulus materials, mode of presentation, response requirements, or sequence complexity. Indeed, it has been argued that only one or two of these components (e.g., visuo-spatial and motor) usually drive performance (Bapi et al., 2000; Cock & Meier, 2013; Deroost et al., 2006; Goschke & Bolte, 2012; Hallgato et al., 2013; Meier, Weiermann, & Cock, 2012). However, although we cannot predict that exactly the same memory consolidation results would be found with, say, auditory stimuli or verbal responses, we are inclined to think that our present results will generalize given the findings of other studies in the literature. In fact, one of our current projects is to test whether the present findings will generalize to implicit *task sequence* learning (Meier & Cock, 2010; Meier et al., 2013;

Weiermann, Cock, & Meier, 2010). A further promising avenue is to investigate the neural basis of sequence-specific learning and consolidation as well as the possibility to improve sequence learning and consolidation, for example, by transcranial electrical stimulation methods.

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REFERENCES

Albouy, G., Sterpenich, V., Balteau, E., Vandewalle, G., Desseilles, M., Dang-Vu, T., et al. (2008). Both the hippocampus and striatum are involved in consolidation of motor sequence memory. *Neuron, 58,* 261–272.

Albouy, G., Sterpenich, V., Vandewalle, G., Darsaud, A., Gais, S., Rauchs, G., et al. (2013). Interaction between hippocampal and striatal systems predicts subsequent consolidation of motor sequence memory. *PLoS One, 8*(3), e59490.

Bapi, R. S., Doya, K., & Harner, A. M. (2000). Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. *Experimental Brain Research, 132*(2), 149–162. http://dx.doi.org/10.1007/s002219900332.

Brawn, T. P., Fenn, K. M., Nusbaum, H. C., & Margoliash, D. (2010). Consolidating the effects of waking and sleep on motor-sequence learning. *Journal of Neuroscience, 30,* 13977–13982. http://dx.doi.org/10.1523/Jneurosci.3295-10.2010.

Brown, R. M., & Robertson, E. M. (2007). Off-line processing: reciprocal interactions between declarative and procedural memories. *Journal of Neuroscience, 27,* 10468–10475.

Cajochen, C., Knoblauch, V., Wirz-Justice, A., Krauchi, K., Graw, P., & Wallach, D. (2004). Circadian modulation of sequence learning under high and low sleep pressure conditions. *Behavioural Brain Research, 151,* 167–176.

Cleeremans, A., & Jiménez, L. (1998). Implicit sequence learning: the truth is in details. In M. A. Stadler, & P. A. Frensch (Eds.), *Handbook of implicit learning* (pp. 323–364). Thousand Oaks: SAGE Publications.

Cock, J., & Meier, B. (2013). Correlation and response relevance in sequence learning. *Psychological Research, 77*(4), 449–462. http://dx.doi.org/10.1007/s00426-012-0444-x.

Cohen, D. A., & Robertson, E. M. (2007). Motor sequence consolidation: constrained by critical time windows or competing components. *Experimental Brain Research, 177,* 440–446.

Cohen, D. A., & Robertson, E. M. (2011). Preventing interference between different memory tasks. *Nature Neuroscience, 14*(8), 953–955. http://dx.doi.org/10.1038/nn.2840.

Della-Maggiore, V. (2005). Motor memory consolidation, night and day. *Journal of Neuroscience, 25,* 9067–9068.

Deroost, N., Zeeuws, I., & Soetens, E. (2006). Effector-dependent and response location learning of probabilistic sequences in serial reaction time tasks. *Experimental Brain Research, 171,* 469–480.

Destrebecqz, A., & Cleeremans, A. (2001). Can sequence learning be implicit? New evidence with the process dissociation procedure. *Psychonomic Bulletin & Review, 8,* 343–350.

Doyon, J., Korman, M., Morin, A., Dostie, V., Hadj Tahar, A., Benali, H., et al. (2009). Contribution of night and day sleep vs. simple passage of time to the consolidation of motor sequence

and visuomotor adaptation learning. *Experimental Brain Research, 195,* 15–26.

Fischer, S., Hallschmid, M., Elsner, A. L., & Born, J. (2002). Sleep forms memory for finger skills. *Proceedings of the National Academy of Sciences of the United States of America, 99,* 11987–11991.

Genzel, L., Quack, A., Jager, E., Konrad, B., Steiger, A., & Dresler, M. (2012). Complex motor sequence skills profit from sleep. *Neuropsychobiology, 66*(4), 237–243. http://dx.doi.org/10.1159/000341878.

Gerloff, C., & Andres, F. G. (2002). Bimanual coordination and interhemispheric interaction. *Acta Psychologica, 110,* 161–186.

Ghilardi, M. F., Moisello, C., Silvestri, G., Ghez, C., & Krakauer, J. W. (2009). Learning of a sequential motor skill comprises explicit and implicit components that consolidate differently. *Journal of Neurophysiology, 101*(5), 2218–2229. http://dx.doi.org/10.1152/jn.01138.2007.

Goedert, K. M., & Willingham, D. B. (2002). Patterns of interference in sequence learning and prism adaptation inconsistent with the consolidation hypothesis. *Learning & Memory, 9,* 279–292.

Goschke, T., & Bolte, A. (2012). On the modularity of implicit sequence learning: independent acquisition of spatial, symbolic, and manual sequences. *Cognitive Psychology, 65*(2), 284–320.

Hallgato, E., Gyori-Dani, D., Pekar, J., Janacsek, K., & Nemeth, D. (2013). The differential consolidation of perceptual and motor learning in skill acquisition. *Cortex, 49*(4), 1073–1081.

Hoerger, M. (2013). Z_H: an updated version of Steiger's Z and web-based calculator for testing the statistical significance of the difference between dependent correlations. Retrieved from http://www.psychmike.com/dependent_correlations.php.

Hotermans, C., Peigneux, P., Maertens de Noordhout, A., Moonen, G., & Maquet, P. (2006). Early boost and slow consolidation in motor skill learning. *Learning & Memory, 13,* 580–583.

Howard, J. H., Jr., & Howard, D. V. (1997). Age differences in implicit learning of higher order dependencies in serial patterns. *Psychology & Aging, 12,* 634–656.

Keisler, A., Ashe, J., & Willingham, D. T. (2007). Time of day accounts for overnight improvement in sequence learning. *Learning & Memory, 14,* 669–672.

Keisler, A., & Willingham, D. T. (2007). Non-declarative sequence learning does not show savings in relearning. *Human Movement Science, 26,* 247–256.

Korman, M., Raz, N., Flash, T., & Karni, A. (2003). Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proceedings of the National Academy of Sciences of the United States of America, 100,* 12492–12497.

Krakauer, J. W., & Shadmehr, R. (2006). Consolidation of motor memory. *Trends in Neuroscience, 29,* 58–64.

Kuriyama, K., Stickgold, R., & Walker, M. P. (2004). Sleep-dependent learning and motor-skill complexity. *Learning & Memory, 11,* 705–713.

Manoach, D. S., Cain, M. S., Vangel, M. G., Khurana, A., Goff, D. C., & Stickgold, R. (2004). A failure of sleep-dependent procedural learning in chronic, medicated schizophrenia. *Biological Psychiatry, 56,* 951–956.

Maquet, P., Schwartz, S., Passingham, R., & Frith, C. (2003). Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. *Journal of Neuroscience, 23,* 1432–1440.

Meier, B., & Cock, J. (2010). Are correlated streams of information necessary for implicit sequence learning? *Acta Psychologica (Amst), 133*(1), 17–27. http://dx.doi.org/10.1016/j.actpsy.2009.08.001.

Meier, B., Weiermann, B., & Cock, J. (2012). Only correlated sequences that are actively processed contribute to implicit

sequence learning. *Acta Psychologica (Amst), 141*(1), 86–95. http://dx.doi.org/10.1016/j.actpsy.2012.06.009.

Meier, B., Weiermann, B., Gutbrod, K., Stephan, M. A., Cock, J., Müri, R. M., et al. (2013). Implicit task sequence learning in patients with Parkinson's disease, frontal lesions and amnesia: the critical role of fronto–striatal loops. *Neuropsychologia, 51*(14), 3014–3024. http://dx.doi.org/10.1016/j.neuropsychologia.2013.10.009.

Morris, R. G. (2006). Elements of a neurobiological theory of hippocampal function: the role of synaptic plasticity, synaptic tagging and schemas. *European Journal Neuroscience, 23,* 2829–2846.

Németh, D., & Janacsek, K. (2011). The dynamics of implicit skill consolidation in young and elderly adults. *Journal of Gerontology. Series B, Psychological Sciences and Social Sciences, 66B,* 15–22.

Németh, D., Janacsek, K., Londe, Z., Ullman, M. T., Howard, D. V., & Howard, J. H., Jr. (2010). Sleep has no critical role in implicit motor sequence learning in young and old adults. *Experimental Brain Research, 201,* 351–358.

Peigneux, P., Laureys, S., Fuchs, S., Destrebecqz, A., Collette, F., Delbeuck, X., et al. (2003). Learned material content and acquisition level modulate cerebral reactivation during posttraining rapid-eye-movements sleep. *Neuroimage, 20,* 125–134.

Perruchet, P., Bigand, E., & Benoit-Gonin, F. (1997). The emergence of explicit knowledge during the early phase of learning in sequential reaction time tasks. *Psychological Research, 60,* 4–13.

Press, D. Z., Casement, M. D., Pascual-Leone, A., & Robertson, E. M. (2005). The time course of off-line motor sequence learning. *Cognitive Brain Research, 25,* 375–378.

Remillard, G. (2003). Pure perceptual-based sequence learning. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 29,* 581–597.

Remillard, G. (2008). Implicit learning of second-, third-, and fourth-order adjacent and nonadjacent sequential dependencies. *Quarterly Journal of Experimental Psychology, 61,* 400–424.

Remillard, G., & Clark, J. M. (2001). Implicit learning of first-, second-, and third-order transition probabilities. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 27,* 483–498.

Robertson, E. M., Pascual-Leone, A., & Press, D. Z. (2004). Awareness modifies the skill-learning benefits of sleep. *Current Biology, 14,* 208–212.

Robertson, E. M. (2009). From creation to consolidation: A novel framework for memory processing. *PLoS Biol, 7*(1), e1000019.

Romano, J. C., Howard, J. H., Jr., & Howard, D. V. (2010). One-year retention of general and sequence-specific skills in a probabilistic, serial reaction time task. *Memory, 18,* 427–441.

Shanks, D. R., & Cameron, A. (2000). The effect of mental practice on performance in a sequential reaction time task. *Journal of Motor Behavior, 32,* 305–313.

Siengsukon, C. F., & Boyd, L. A. (2009). Sleep to learn after stroke: implicit and explicit off-line motor learning. *Neuroscience Letters, 451,* 1–5.

Song, S. (2009). Consciousness and the consolidation of motor learning. *Behavioral Brain Research, 196,* 180–186.

Song, S., Howard, J. H., Jr., & Howard, D. V. (2007). Implicit probabilistic sequence learning is independent of explicit awareness. *Learning & Memory, 14,* 167–176.

Spencer, R. M., Gouw, A. M., & Ivry, R. B. (2007). Age-related decline of sleep-dependent consolidation. *Learning & Memory, 14,* 480–484.

Spencer, R. M., Sunm, M., & Ivry, R. B. (2006). Sleep-dependent consolidation of contextual learning. *Current Biology, 16,* 1001–1005.

Steele, C. J., & Penhune, V. B. (2010). Specific increases within global decreases: a functional magnetic resonance imaging investigation of five days of motor sequence learning. *Journal of Neuroscience, 30,* 8332–8341.

Stephan, M. A., Meier, B., Orosz, A., Cattapan-Ludewig, K., & Kaelin-Lang, A. (2009). Interference during the implicit learning of two different motor sequences. *Experimental Brain Research, 196*(2), 253–261. http://dx.doi.org/10.1007/s00221-009-1845-y.

Sun, F. T., Miller, L. M., Rao, A. A., & D'Esposito, M. (2007). Functional connectivity of cortical networks involved in bimanual motor sequence learning. *Cerebral Cortex, 17*(5), 1227–1234.

Walker, M. P., Brakefield, T., Hobson, J. A., & Stickgold, R. (2003). Dissociative stages of human memory consolidation and reconsolidation. *Nature, 425,* 616–620.

Walker, M. P., Brakefield, T., Morgan, A., Hobson, J. A., & Stickgold, R. (2002). Practice with sleep makes perfect: sleep-dependent motor skill learning. *Neuron, 35,* 205–211.

Walker, M. P., Brakefield, T., Seidman, J., Morgan, A., Hobson, J. A., & Stickgold, R. (2003). Sleep and the time course of motor skill learning. *Learning & Memory, 10,* 275–284.

Weiermann, B., Cock, J., & Meier, B. (2010). What matters in implicit task sequence learning: perceptual stimulus features, task sets, or correlated streams of information? *Journal of Experimental Psychology. Learning, Memory, and Cognition, 36*(6), 1492–1509. http://dx.doi.org/10.1037/a0021038.

Wilkinson, L., & Jahanshahi, M. (2007). The striatum and probabilistic implicit sequence learning. *Brain Research, 1137,* 117–130.

Witt, K., Margraf, N., Bieber, C., Born, J., & Deuschl, G. (2010). Sleep consolidates the effector-independent representation of a motor skill. *Neuroscience, 171,* 227–234.