SPATIALLY SIMILAR PRACTICE IMMEDIATELY FOLLOWING MOTOR SEQUENCE LEARNING ELIMINATES OFFLINE GAINS

A Thesis

by

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ABSTRACT

Robust *offline* performance gains, beyond those that would be anticipated by being exposed to additional physical practice, have been reported during procedural learning. However, practice of unrelated procedural task performance within 4-6 hour after initial practice has been revealed to eliminate offline improvement. The present experiment assessed the relative impact of experiencing supplemental practice of a spatially or a motorically-similar procedural task immediately following practice of a target motor sequence task. Based on a contemporary model of procedural skill acquisition forwarded by Hikosaka and colleagues, we assumed exposure to a spatial compatible motor sequence rather than interfering would support rapid improvement in the production of the spatial variant of the target task without compromising important memory processes, which are conducted offline to improve delayed performance of the target task.

Findings revealed the often demonstrated offline gain when the target task was performed in the absence of interfering task practice as well as the elimination of such gains when target task practice was followed with additional practice of either a novel or motorically-similar motor sequence task. While immediate performance of the spatially-similar task was facilitated by preceding target task training, offline gains for the target task no longer emerged. These data are consistent with a central premise of Hikosaka *et al.'s* model that a spatial reference system plays an important role early during motor sequence learning but highlight the sensitivity of offline gains to task practice order.

DEDICATION

In the memory of my grandfather, the late Shri. Madan Lal Nayyar

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TABLE OF CONTENTS

Page

LIST OF FIGURES

INTRODUCTION

Spatially Similar Practice Immediately Following Motor Sequence Learning Eliminates Offline Gains

Procedural motor learning involves both *fast* and *slow* stages (Karni, *et al*., 1998). Fast learning is manifest as rapid improvements in performance within a practice session while slow learning is reflected in delayed, incremental gains associated with continued practice across additional sessions that may occur over days or months. Improvements in skilled behavior are, at least in part, due to consolidation processes that are responsible for converting labile memories into more robust forms. Specifically consolidation is important for (a) the *stabilization* of memories following a bout of practice often manifest behaviorally as an increased resistance to interference, and (b) the *enhancement* of memories revealed by performance improvements that occur offline in the absence of additional practice (Diekelmann & Born, 2007). Procedural memory stabilization, via consolidation, is assumed by many to be a time-dependent process requiring approximately 4-6-hour between the initial bout of practice and the presentation of interfering activity [1]. Enhancement through consolidation, on the other hand, is significantly greater if the learner sleeps between training and test especially for procedural tasks that are learned explicitly (Press, Casement, Pascual-Leone, & Robertson, 2005).

[1] There has been some discussion recently regarding the specific contributions of time and sleep to the stabilization process. While this debate is outside the scope of the present work, brief overviews of this debate are offered elsewhere by (Diekelmann & Born, 2007; Song, 2009)

Relationship between Procedural Memory Stabilization and Enhancement

Walker, Brakefield, Hobson, & Stickgold (2003) provided early evidence of the sleep-dependent nature of procedural task enhancement. They revealed greater than 20% improvement in speed and accuracy of a short finger sequencing task when assessed after a 24-hour interval that included sleep that was not present when a similar test was administered across waking hours of similar lengths (Press, *et al*., 2005; Walker, Brakefield, Hobson, & Stickgold, 2003). However, some of the sleep-supported enhancement for the initially practiced motor sequence was eliminated when individuals experienced practice of a second finger sequencing task immediately after the first. This was manifest as a loss of overnight improvement in accuracy but not speed. However, if the interfering task practice occurred at least 6-h after the initial bout of practice, reliable overnight gains in both speed and accuracy returned. Walker *et al.* concluded that with the passage of sufficient time, in this case approximately 6-hour, memory stabilization was achieved affording further sleep-dependent consolidation eventually leading to performance enhancement during the delayed test.

More recent work by Korman *et al.*, (2007) further probed the association between procedural memory stabilization and enhancement while questioning the assumption that the stabilization component merely requires the passage of time after initial training but enhancement via consolidation, requires sleep. Korman *et al.* had participants perform a motor sequencing task, similar to that used by Walker *et al.* that involved fast and accurate strings of fingers and thumb movements of the non-dominant hand. Participants were trained with this sequence in the morning and performance was tested 24-hour later. The 24-hour retest followed normal overnight sleep (Walker *et al.,* 2003). Some individuals were administered additional practice with an alternative sequence either 2-hour or 8-hour after completion of the practice of the to-be-learned motor sequence. As anticipated, test performance after the 24-hour delay for the condition involving no supplemental practice exhibited approximately 26% improvement of the to-be-learned sequence beyond that observed at the conclusion of the training phase. Performance of the individuals exposed to the interfering task practice 2-hour and 8-hour after original practice verified Walker's earlier findings. That is, a loss of offline improvement due to practice with a motor sequence that created interference experienced shortly after practice with the target sequence (i.e., 2-hour) but a reliable latent performance benefit when the interference was presented after an 8-hour interval. The critical contribution from the work of Korman *et al.* however was the subsequent demonstration that a robust offline enhancement emerged for learners assigned to a 2-hour interference condition if they were afforded a 90-min nap immediately after training of the to-be-learned sequence. Moreover, for those individuals just trained on the primary motor sequence in the absence of interference, the same nap resulted in an earlier expression of performance enhancement, that is, within 8-hour of the previous training bout.

These results suggest that sleep has an important contribution for consolidation processes responsible for establishing both improved resistance to interference (i.e., stabilization) as well as offline learning (i.e., enhancement). Indeed, Korman *et al.'s* findings question the traditional model of motor memory consolidation which assumes stabilization is time sensitive but offline gains require a sleep period soon after training. These data are crucial to a recent proposal that motor sequence representation can be developed through time-dependent synaptic consolidation requiring a temporary buffer or through sleep-dependent system consolidation that involves a redistribution of sequence knowledge to different neuronal networks for long-term storage (Diekelmann & Born, 2007). While these data are important for elucidating the role of sleep for motor sequence stabilization and enhancement, for the present work, it is most critical to note that these data demonstrate that alternative task practice in close temporal proximity to the to-be-learned task practice does not mandate that the often demonstrated offline performance enhancement will be reduced or eliminated.

Procedural Learning Involves the Development of Spatial and Motor Representations across Practice

In the present work rather than use sleep, in the form of a nap, to probe the robustness of offline procedural learning, we evaluate the impact of the structure of the task that is used to interfere with consolidation leading to the deterioration of memory stabilization and the subsequent expression of offline learning. The notion that the structure of the motor sequence, used to create interference, might have some influence on the emergence of offline learning has as its theoretical backdrop a model of procedural learning proposed by Hikosaka *et al.* (1999, 2002). The central feature of this model is the existence of two representational formats of procedural knowledge that are developed in parallel but independently across extended practice. One representational scheme relies on the use of a spatial coding system whereas the other relies on representing procedural task knowledge in motor coordinates. Of critical importance to the present work is Hikosaka and colleague's claim that as procedural learning proceeds there is a gradual transition in use from the spatial to motor representational systems. That is, the spatial coding system is preferentially active in the early stages of learning whereas the motor coding system is more influential at later stages of learning. The use of these distinct systems for procedural learning seems ubiquitous having been demonstrated with animal and human models as well as being supported by unique neural circuits (Hikosaka, et al., 1999; Hikosaka, Nakamura, Sakai, & Nakahara, 2002).

An experimental approach that has been used to support the existence of the two-representational system model for procedural learning of Hikosaka and colleagues is illustrated in the work of Korman, Raz, Flash, and Karni (2003). In this study, a short motor sequence was practiced and subsequently followed by a series of delayed re-tests (Walker, *et al.,* 2003). First, after a 24-hour delay, performance enhancement for the trained sequence was revealed as expected based on previous findings of Walker and others. Other transfer tests included performance of the trained sequence executed with the non-trained hand as well as a novel sequence performed independently with the trained and untrained hands were administered after the initial bout of training. Only performance of the trained sequence with the untrained hand revealed reliable generalization. That is, transfer was evident when participants executed a response that had the same spatial layout as the originally learning task manifest as similar execution and error rates to that observed for the trained sequence. These data are congruent with Hikosaka *et al.'s* model (1999, 2002) which suggests that spatial coding was established for the trained sequence and was used to support the initial performance with the non-trained hand in the initial phase of practice with this transfer task. Importantly, Korman *et al.*, (2003) provided an additional five practice sessions of the target sequence. When the same aforementioned transfer tests were administered after this additional practice, the large performance gains achieved for the target sequence as a result of additional practice were less transferable. These data suggest that additional procedural knowledge gained from extensive practice becomes more sequence-specific. Within the context of Hikosaka's model, the additional practice resulted in the development of a motor code that had no overlap with non-trained hand or novel sequence performance. Hence no transfer was observed. These data have been replicated numerous times in recent years using a variety of procedural tasks (Cohen, Pascual-Leone, Press, & Robertson, 2005; Kovacs, Muhlbauer, & Shea, 2009; Panzer, *et al.,* 2009; Park & Shea, 2003; Verwey & Wright, 2004).

Nature of Interfering Procedural Task Might Influence Stabilization and Subsequent Offline Improvement

Recall that Walker *et al.* (2003) presented evidence for the detrimental role of interfering task practice experienced in close proximity to primary task learning for subsequent offline learning. The task used by Walker *et al.* to create interference was one that was quite dissimilar to the to-be-learned sequence. Specifically, the to-be-learned task involved a five-element sequence, executed by the left hand, described in terms of the spatial location of each sequence element and indicated by the number sequence 4-1-3-2-4 with “1” being the leftmost and “4” being the rightmost location on a keyboard. In terms of the “motor code” this sequence could also be referenced in terms of the index, middle, ring, and little fingers that are used for each sequence element with “1” being associated with the little and “4” the index fingers. The interfering task consisted of the sequence 2-3-1-4-2 had limited overlap in terms of spatial or motor coding with the target task[2]. That is, the serial order of spatial locations and/or effectors (i.e., fingers used) was not similar for the target and interference tasks. This was in essence true for the related study conducted by Korman *et al* (2007) in which the interfering tasks was merely a reversed form of the target sequence such that the only the first and last key presses were in the same spatial location and used the same effector.

In the proposed work we consider the case in which an interfering sequence maintained either a common spatial or motor structure with the to-be-learned sequence, subsequently referred to as the target sequence, and the resultant impact on offline learning. To directly assess this issue we adopted a similar approach to that used by Cohen *et al.* (2005) in which participants first practiced the target sequence with their non-dominant hand followed immediately by additional practice with one of three interfering sequences, (a) a *novel* sequence with no relationship to the motor and spatial

[2] In Walker *et al*. (2003) the use of these tasks were counterbalanced with respect to being used as the target and interference task.

target sequence executed with the dominant hand, (b) a *spatial* sequence that involved the same serial order of locations as the target sequence executed with the dominant hand (thus changing the order of fingers used), or (c) a *motor* sequence that involves the same serial order of finger presses as the target sequence executed with the dominant hand thus changing the spatial location order (Figure 1).

It was anticipated that delayed test performance for a no-interference condition should reveal the demonstrated offline learning while the novel interference condition should diminish or eliminate this benefit (Walker *et al.*, 2003). Importantly, since the spatial sequence shares a common coding format with the target sequence and given the present experiment exposes the learners to relatively limited practice for which spatial coding would be especially relevant (cf. Korman *et al.*, 2003; Wright *et al.,* 2010), it was expected that additional practice with this task would not inhibit the emergence of offline enhancement. In contrast, exposure to supplemental training with the motor sequence interference condition should eliminate the emergence of offline enhancement for the target sequence because, with minimal practice, it is unlikely that a motor code will be established thus removing the potential for this practice bout to establish a stable target task memory that is ready to undergo overnight consolidation.

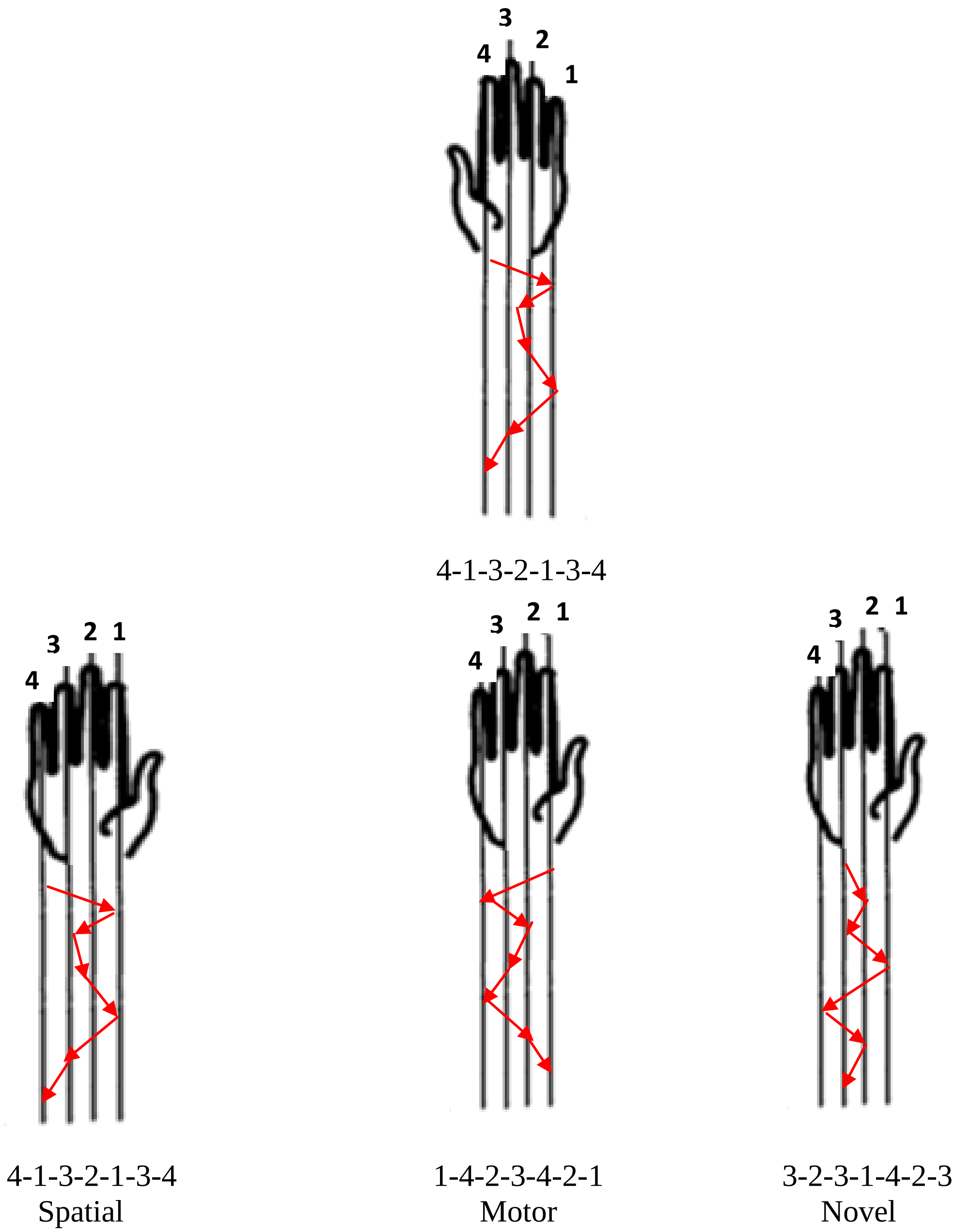

Figure 1. The target sequence (top panel) was used throughout the practice and test trials for all participants. This sequence was performed with the left hand. The spatial (left bottom panel), motor (center bottom panel), and novel (left bottom panel) were sequences used to interfere with the knowledge of the target sequence gained through practice immediately after practice with the target sequences.

METHODS

Participants

A total of Sixty-eight (68) individuals, enrolled as undergraduate students at Texas A & M University, served as participants in this experiment. Participation in this study fulfilled a research requirement for undergraduate class. Informed consent was obtained prior to any participation in the experiment.

Tasks

All participants performed a target sequence, 4-1-3-2-1-3-4, on a standard PC keyboard using the V, B, N, M keys where “1” was the leftmost key (V key) and “4” was the rightmost key (i.e., M key). All individuals performed the target sequence with their non-dominant throughout practice. In addition, all participants performed the target sequence during the delayed test. Some individuals were administered further practice with an alternative sequence to potentially induce interference. The nature of the sequence each individual was exposed to in order to attempt to create interference with the target sequence depended on the experimental condition to which they were assigned. Individuals assigned to the “spatial” condition performed a seven-key sequence, 4-1-3-2-1-3-4, with the dominant hand. For this case, the spatial organization of the task is the same as the target sequence but requires a new sequence of effector execution. Individuals assigned to the ‘motor’ condition performed a seven-key sequence, 1-4-2-3-4-2-1, with the dominant hand. For this task, the serial order of effectors for the task is the same as for the target sequence but involves a new spatial layout. Individuals assigned to the 'novel' condition performed a seven-key sequence, 3-2-3-1-4-2-3, with the right-hand. For this condition, both the serial order of effectors as well as the spatial layout differed from the target sequence.

Procedure

Prior to participation in the experiment all participants gave an informed consent. All participants subsequently engaged in practice of the target sequence. A practice trial consisted of repeating the required target sequence for 30-s followed by 30-s rest. Twelve (12) 30-s practice trials of the target sequence were completed by each participant. This will be followed by additional practice, using the same 30-s of practice followed by 30-s of rest protocol, in one of five experimental conditions. First, some participants were required to complete further practice in one of the aforementioned interference tasks, (a) *novel*, (b) *spatial*, or (c) *motor*. The remaining two experimental conditions were controls that entailed individuals experiencing either, (a) *no additional practice* prior to the delayed test, or (b) an *extended practice* group in which the participants were administered three additional trials of practice of the target task immediately after completion of the initial practice bout with this task. All participants, except the individuals that performed the three additional trials immediately after practice ended (i.e., extended condition), were subsequently administered a three 30-s trial test of the target sequence 24-hour after the completion of the initial practice of the target sequence.

For all trials, *speed*, defined as the correct number of sequences executed in 30-s and, *error rate*, defined as the percentage of erroneous key presses in 30-s, were recorded and subsequently used as the primary dependent variables of interest. For the present work, offline learning is defined as a positive performance improvement that is larger than that observed for the mean performance observed for those individuals that experienced trials 13-15 immediately following trials 1-12 (i.e., the extended condition)[3]. Based on the previous reports from Walker *et al.* (2003), the no interference condition is expected to reveal evidence of offline performance enhancement. Based on the model of sequence learning of Hikosaka and colleagues (Hikosaka, *et al.*, 1999), it was anticipated that exposure to supplemental practice of a sequence that reflects the same spatial structure as the target sequence, even in close temporal proximity, should not interfere with the necessary consolidation processes that would occur to support the emergence of offline enhancement. In contrast, practice of a motor sequence that has a similar effector requirement as the target task or the novel sequence that does not resemble features of the target task, should serve as interference thus influencing the extent of offline learning reflected in the delayed test.

[3] This expectation is based on using speed as the dependent variable which is expected to increase with practice. Obviously, the reverse effect is anticipated for accuracy which is expected to decrease with practice.

RESULTS

Performance during the Initial Practice Phase

To assess performance during the initial practice phase mean *speed* and *error rate* was calculated for each individual in each of the five experimental conditions (spatial, motor, novel, no, and extended conditions) for each trial of the target sequence. These data were subjected to a 5 (Interference: spatial, motor, novel, no, extended) x 12 (Trial: 1-12) analysis of variance (ANOVA) with repeated measures of the last factor. Figure 2 displays mean speed and mean error rate for the target sequence across the 12 trials of initial practice. Formal analyses[4] of these data using the 5 (Interference: spatial, motor, novel, no, extended) x 12 (Trial: 1-12) ANOVA with repeated measures of the last factor revealed a significant main effect of Trial for mean speed, $F(11,572) = 76.04$, $p < .01$, and for mean error rate, $F(11,572) = 4.92$, $p < .01$. Thus, as expected, general performance of the target sequence improved with the initial bout practice (~162% increase in speed or an additional 7.23 sequences per 30-s combined with a 63% reduction in error). As expected, given no exposure at this point to potentially interference sequence practice, this improvement was similar across all interference conditions as evidenced by the lack of significant interference main effect [mean speed, $F(4,52) = 0.22$, $p = .93$; mean error rate, $F(4,52) = 0.16$, $p = .96$] and interference x trial [mean speed, $F(44,572) = 0.53$, $p = .99$; mean error rate, $F(44,572) = 0.71$, $p = .92$].

[4] For the purpose of analyses 3 participants failed to complete both days of the experiment, and an additional 8 individuals had performance (speed and/or error) that was greater than 2 standard deviations beyond the mean performance for the experimental group to which they were assigned.

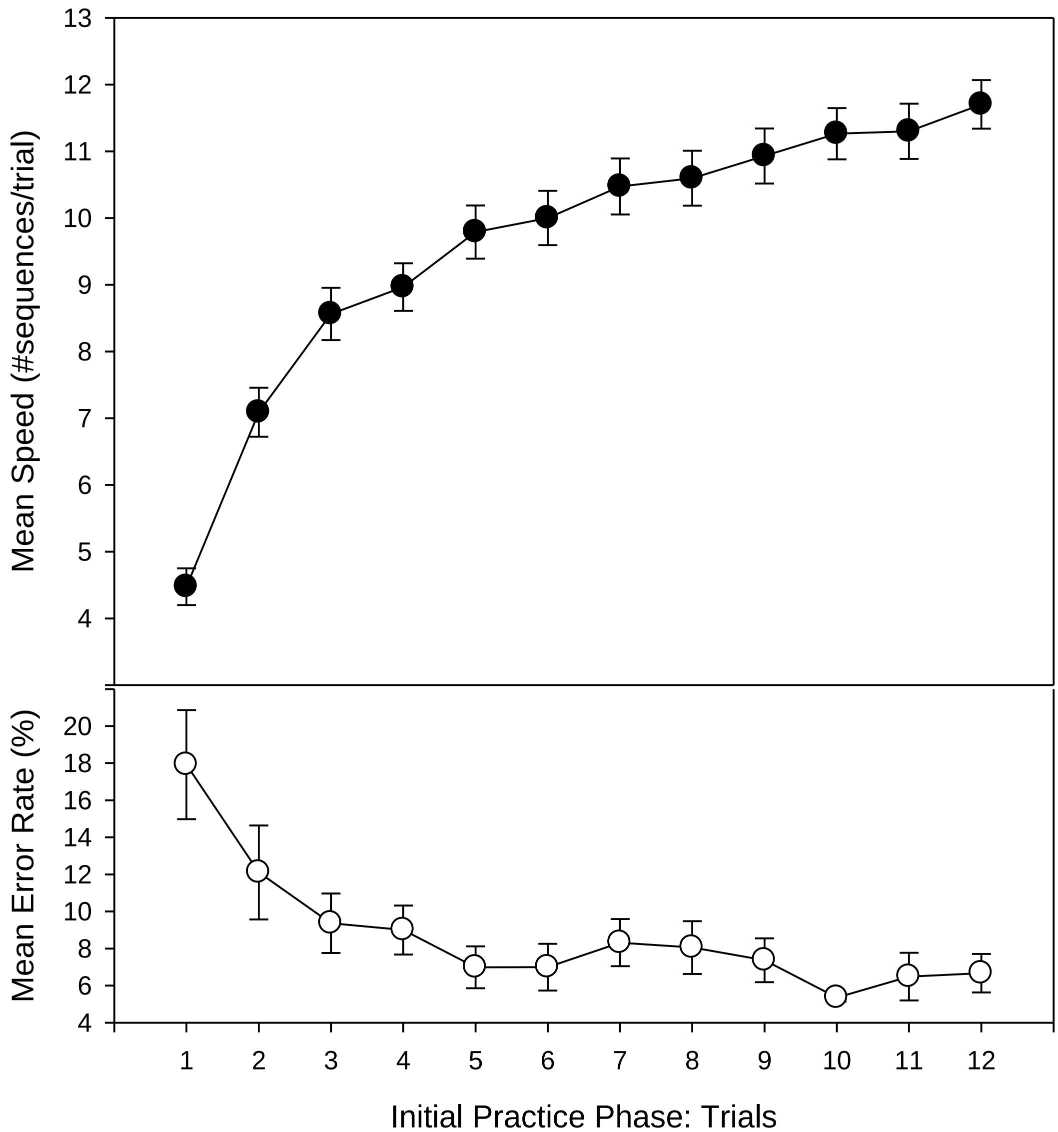

Figure 2. Mean Speed (top panel) and Error Rate (bottom panel) across the twelve 30-s trials of the initial practice phase. Since all participants were exposed to the same training during this period these data are collapsed across interference conditions (novel, spatial, motor, no, and extended). Error bars are standard errors.

Performance of Target Task and Interfering Task during the Initial Practice Phase

Mean speed and error rate was also calculated for each individual for each trial of the interfering sequence (spatial, motor, and novel conditions). For the purpose of analysis these data were combined with trials from the initial practice phase during which the target sequence was performed and was subjected to formal analysis using a 3 (Interference: spatial, motor, novel) x 2 (Sequence: target, interference) x 12 (Trial: 1-12) ANOVA with repeated measures on the last two factors.

Mean speed

Figure 3 displays Mean Speed (top panel) and mean Error Rate (bottom panel) for the target (black bars) and interference (red bars) sequences for each of the interference (novel, motor, and spatial) conditions. Formal analysis using a 3 (Interference: spatial, motor, novel) x 2 (Sequence: target, interference) x 12 (Trial: 1-12) ANOVA with repeated measures on the last two factors revealed a significant main effect of Sequence, $F(1,30) = 49.64$, $p < .01$, and Trial, $F(11,330) = 68.19$, $p < .01$, as well as a significant Interference x Sequence interaction, $F(2,30) = 5.94$, $p < .01$. The main effect of Trial indicated that practice generally resulted in an improvement in mean across trials.

Interpretation of the main effect of Sequence is superseded by the significant Interference x Sequence interaction (Figure 3). Simple main effect analysis indicated that the interaction was a function of the spatial interference condition demonstrating

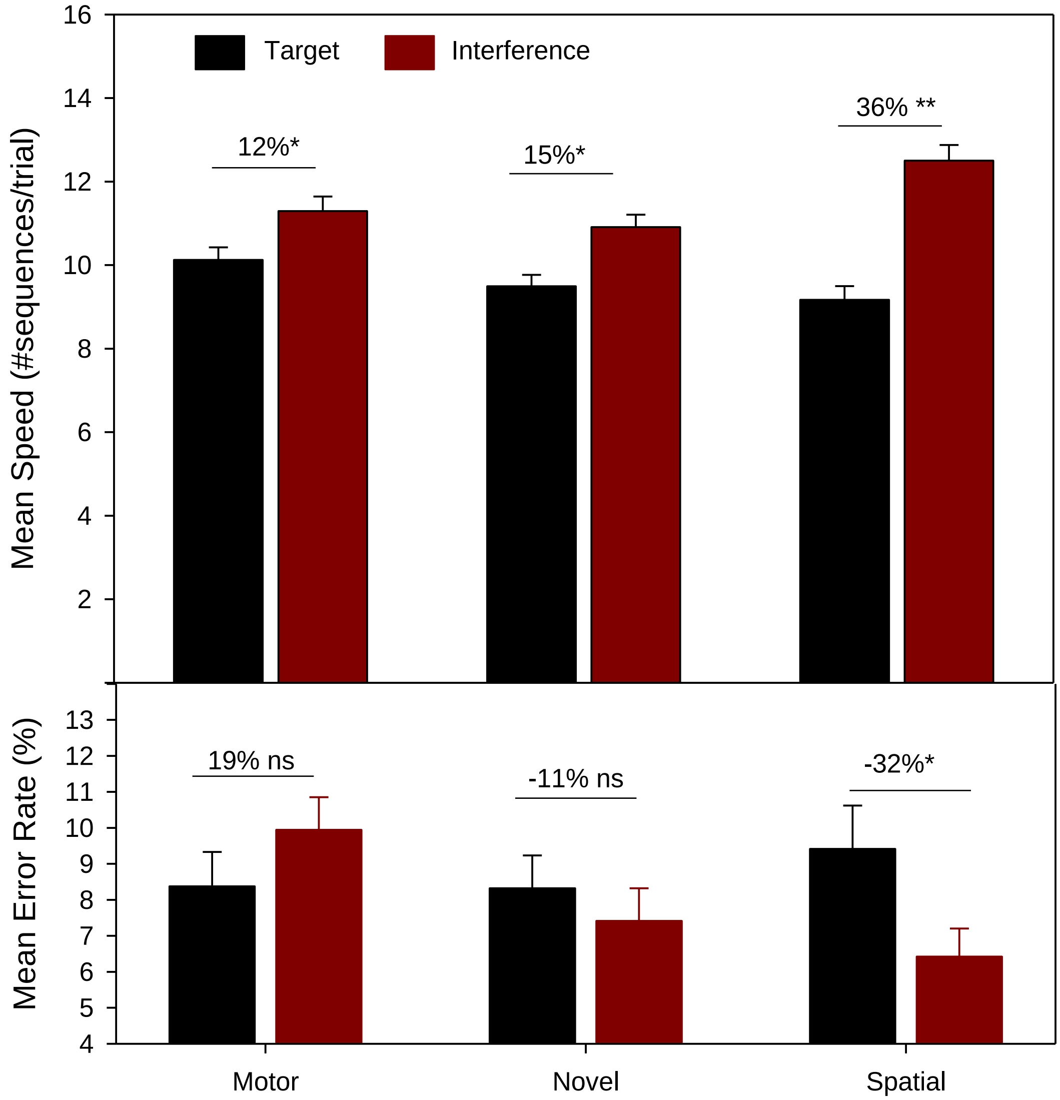

Figure 3. Mean Speed (top panel) and mean Error Rate (bottom panel) for the target (black bars) and interference (red bars) sequences for each of the interference (novel, motor, and spatial) conditions. Error bars are standard errors. * = p<. 05 and ** = p< .01.

reliably greater transfer of mean speed for performance of the 'spatial' interference sequence following practice of the target sequence, $F(1,30) = 47.15, p < .01$ compared to the novel, $F(1,30) = 8.53, p < .01$, and motor, $F(1,30) = 5.90, p < .05$, interference conditions. Transfer of mean speed was similar for the latter two conditions. The lack of a significant Interference x Sequence x Trial interaction, $F(22,330) = .84$, $p = .68$, suggests that this transfer benefit for mean speed from practice of the target sequence was present across all trials (i.e., early and late trials) when compared to the novel and motor interference conditions.

Mean error rate

Analysis of mean error rate using the 3 (Interference: spatial, motor, novel) x 2 (Sequence: target, interference) x 12 (Trial: 1-12) ANOVA with repeated measures on the last two factors revealed a significant main effect of Trial, $F(11,330) = 4.84$, $p < .01$, and a significant Interference x Sequence interaction, $F(2,30) = 3.52$, $p < .05$. As was the case with mean speed, the main effect of Trial indicated that practice resulted in a reduction in error rate across the 12 30-s trials (Figure 3, bottom panel). Simple main effect analysis of the Interference x Sequence interaction revealed findings similar to those reported for mean speed. Specifically, this interaction was a function of the spatial interference condition demonstrating greater transfer, in this in extent of erroneous performance, for execution of the interference sequence following practice of the target sequence, $F(2,30) = 6.03$, $p < .01$ compared to the novel, $F(1,30) = 8.53$, $p < .01$, and motor, $F(1,30) = 5.90$, $p < .05$, interference conditions. The latter interference conditions revealed no change in mean error rate from performance of the target to interference sequence. Again, the lack of a significant Interference x Sequence x Trial interaction, $F(22, 330) = 1.34$, $p = .14$, suggests that spatial interference sequence was performed with fewer error resulting from practice of the target sequence across all trials compared to the novel and motor interference conditions.

Assessment of Offline Learning: End of Practice versus Test Trial Comparison

The assessment of offline learning followed procedures previously adopted in studies addressing consolidation of procedural knowledge (Walker *et al.,* 2003, Wright *et al.,* 2010). This involved a comparison of performance (mean speed and error rate) at the conclusion of practice and test. Recall that for the present work, offline learning was defined as greater performance improvement (i.e., increased speed and/or reduction in error) from the conclusion of training to the delayed test trials compared to that observed for the individuals that experienced trials 13-15 immediately following trials 1-12. Mean speed and error rate were separately calculated for each individual for the last three 30-s trials of practice of the target task (e.g., Trials 10-12) and the three test trials. These data were submitted to a 5 (Interference: spatial, motor, novel, no, and extended) x 2 (Phase: practice, test) ANOVA with repeated measure of the last factor. Figure 4 depicts mean speed (top panel) and error rate (bottom panel) for the end of practice and test phases as a function of interference condition. Analysis of mean speed using a 5 (Interference: spatial, motor, novel, no, and extended) x 2 (Phase: practice, test) ANOVA with repeated measure of the last factor revealed a significant Phase main effect, $F(1, 52) = 43.41, p < .01$ and Interference x Phase interaction, $F(4, 52) = 2.50, p = .05$. Interpretation of the phase main effect was superseded by the significant Interference x Phase interaction. Simple main effects analysis indicated that this interaction was a result of the no, $F(1,52) = 31.21, p < .01$, spatial, $F(1.52) = 11.64, p < .01$, extended, $F(1,52) = 5.00, p < .05$, and novel, $F(1,52) = 4.26, p < .05$, interference conditions revealing greater mean speed during the test compared to the practice phase. This was not the case for the motor interference condition, $F(1,52) = 2.22$, $p > .05$, for which the improvement in mean speed was not significant.

For error rate (Figure 4, bottom panel), for all interference conditions, performance did not change from the completion of practice to test. This is supported by the lack of main effects of Interference, $F(4,52) = .87$, $p = .49$, Phase, $F(1,52) = 0.19$, $p = .67$, and the Interference x Phase interaction, $F(4,52) = .69$, $p = .60$.

Assessment of Performance from the Completion of Practice with Interfering Task and Test Trials

While the primary comparison regarding offline learning is made between the conclusion of practice and test performance it was also important to consider the relative performance from the conclusion of practice with the interfering task and the target task during the test trials. Mean speed and error rate were separately calculated for each individual assigned to the spatial, novel, and motor interference conditions for the last three 30-s trials of practice of the interference task (e.g., Trials 10-12 of Block 2) and the three test trials. These data were submitted to a 3 (Interference: spatial, motor, novel) x 2 (Phase: practice, test) ANOVA with repeated measure of the last factor. The formal analysis of mean speed and error failed to reveal main effects of interference [mean speed, $F(2,30) = 0.22$, $p = .81$; mean error, $F(2,30) = 1.17$, $p = .32$], phase [mean speed, $F(1,30) = 0.09$, $p = .77$; mean error, $F(1,30) = 0.21$, $p = .65$], or an interference

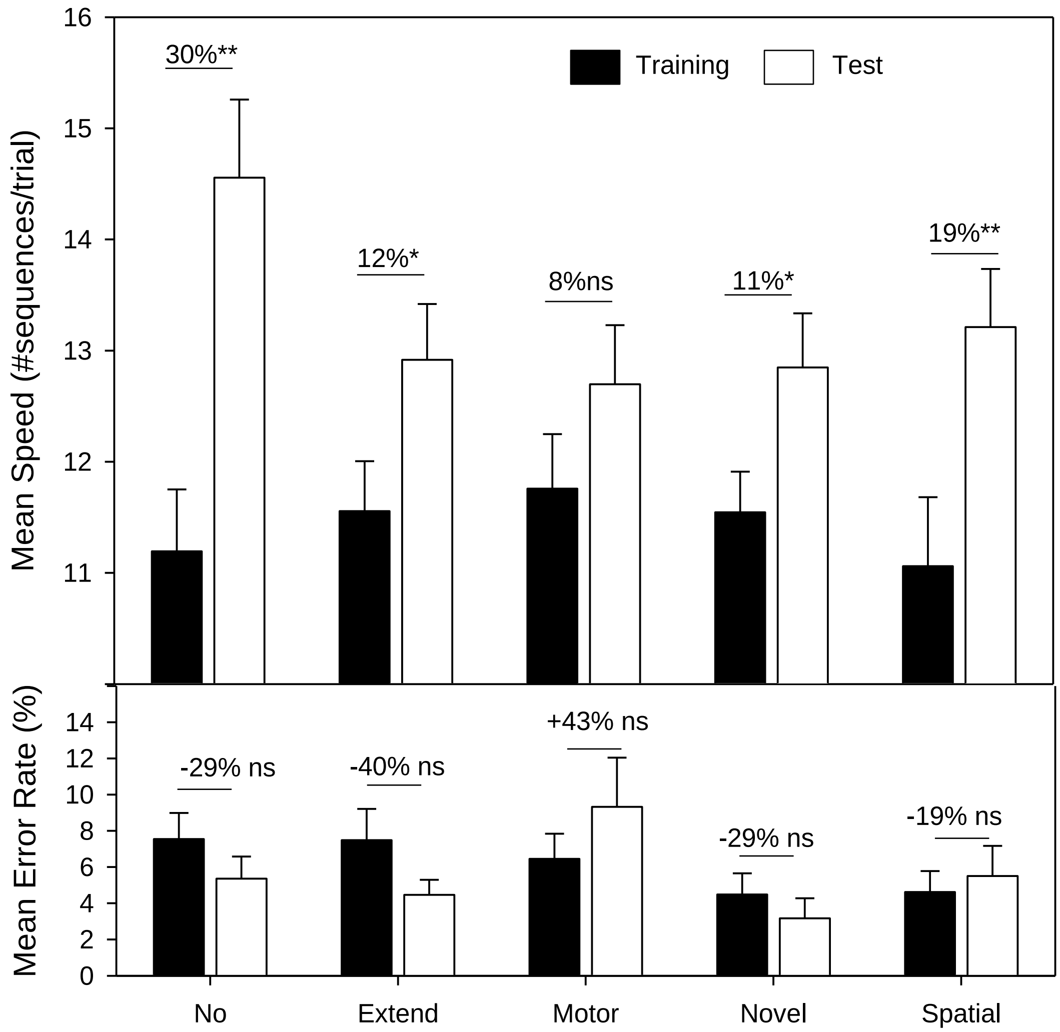

Figure 4. Mean Speed (top panel) and Error Rate (bottom panel) at the conclusion of training (black bars) and at test (white bars) for the participants exposed to the No, Extend, Motor, Novel, and Spatial interference conditions. Error bars are standard errors. * = p< .05 and ** = p< .01.

X phase interaction, [mean speed, $F(2,30) = .38$, $p = .69$; mean error, $F(2,30) = .34$, $p = .71$]. These data reveal that all interference groups had similar performance of their respective interfering sequence at the conclusion of the practice with this task [spatial, mean speed = 13.6 sequences/30-s, mean error = 6.5%; motor, mean speed = 13.2 sequences/30-s, mean error = 8.1%; novel, mean speed = 12.4 sequences/30-s, error = 6.3%]. Moreover, performance of the target at was test was similar across interference conditions and this performance was similar to that observed at the conclusion of practice with the respective interference sequences [spatial, mean speed = 13.2 sequences/30-s, mean error = 5.5%; motor, mean speed = 12.7 sequences/30-s, mean error = 9.3%; novel, mean speed = 12.8 sequences/30-s, error = 3.2%].

DISCUSSION

The purpose of the present work was to further examine offline procedural learning benefits that have been shown to surface after a post-practice delay that includes sleep (Walker *et al.*, 2003; Korman *et al.*, 2007). Specifically, we extended the notion, noted by Korman *et al.* (2007), that procedural task practice performed in close temporal proximity to target task acquisition doesn't always result in destabilizing current procedural knowledge such that anticipated offline benefits are lost. For example, Korman *et al.* (2007) demonstrated that administration of a 90 min nap prior to being exposed to 'interfering' procedural knowledge was sufficient to mitigate the impact of the interference and protect the original procedural task memory which was then available for offline improvement. The present work adopted a different approach to assessing the assumption that immediate practice of alternative procedural tasks creates interference thus rendering previously acquired procedural knowledge labile. In this work the nature of the interfering material was manipulated in terms of its similarity to the target sequence. Based on a model of sequence learning forwarded by Hikosaka *et al.* (2002) that proposes that procedural task practice results in the development of unique memory representations that support performance at different points during training, it was expected that motor as opposed to spatial similarity training would disrupt the establishment of memory for a target sequence to a greater extent. This in turn was anticipated to provide a greater barrier to supporting subsequent offline benefits similar to that which would emerge during delayed tests when no interfering activity was experienced. The following sections discuss the relevant findings with respect to alternative inference training and offline learning as Hikosaka *et al*.'s account of sequence learning.

Offline Benefits Apparent for Procedural Knowledge Implementation without Loss of Accuracy

Offline procedural knowledge enhancement appears quite robust having been demonstrated relatively frequently in the recent literature unless interference is experienced in a 4-6 hour window after training (Walker, *et al.,* 2003, although some recent concerns has been raised, Rickard, *et al.*, 2009). As expected, and consistent with the extant literature, the no interference condition revealed reliable offline improvement beyond that observed when merely administered additional practice trials without the overnight delay. The change in performance from the conclusion of practice to test for the no interference conditions was dramatically improved beyond that displayed by the extended condition. Specifically, a 30 % increase in mean speed (11.2 sequences/trial vs.14.6 sequence/trial) was accompanied by a 29% decrease in error (7.5% vs. 5.4%) for the no interference condition. This improvement seems particularly impressive given that there was already a 180% (4.2sequences/trial vs. 11.7sequence/trial) increase for mean speed and a greater than 50% reduction in error (16.2% vs. 7.4 %) across the initial physical practice phase. In comparison, the individuals in the extended group, those that performed three additional trials immediately after the 12 trial practice phase, while still continuing to improve with more practice, only revealed an 11% increase in movement speed (11.6 sequence/trial vs. 12.9 sequences/trial) and reduced error by 40% (7.5% vs. 4.5%).

These data confirm previous work addressing procedural memory consolidation for motor sequence tasks (Walker, *et al.*, 2003, Song, 2009; Wright *et al.*, 2010). The observed offline improvement was restricted to performance speed but there was no concomitant loss in accuracy. It should be noted however that error rate was extremely low in the present work. Using the no interference group for the purpose of illustration, error rate at the time of test was a little more than 5% which, translated, was approximately 5 erroneous keystrokes per 30-s trial. The data from the present work, as well as that from Kuriyama, Stickgold, & Walker (2004), demonstrate that offline benefits are not restricted to just simple, short motor sequences. Indeed, the changes in performance (mean speed and error) across practice, as well as the overnight enhancement, reported in the present work are in keeping with the levels reported for the more complex motor sequences, induced through increasing sequence length and moving from uni-manual to bi-manual production, used by Kuriyama *et al.* (2004).

Unrelated Task Practice Impedes Offline Learning

Given that offline learning was reported, the more critical question central to the present work is whether the manifestation of this improvement is mediated by exposure to alternative task training shortly after target task practice. For example, Walker *et al.*, (2003) reported that the immediate practice of an alternative motor sequence task impeded the expression of offline improvements as evidenced by the loss of enhancement for accuracy while still performing at a relatively faster speed. Thus, it appears that the additional practice of a different motor sequence hindered further improvement of the memory for the acquired sequence knowledge but did not exert a deleterious impact on the execution rate of keyboarding. Similar findings have been reported elsewhere (Korman *et al.*, 2007) and have used alternative means (e.g., transcranial magnetic stimulation) of interfering with consolidation of implicitly acquired sequence knowledge (Robertson *et al.*, 2005).

The present findings are generally in line with these aforementioned expectations. When faced with additional novel task practice, performance was essentially the same as that exhibited by the extended condition thus indicating that novel task exposure probably led to some improvement with practice that was non-task specific (Figure 4). The acquisition of procedural knowledge that is not sequence-specific is not uncommon and is illustrated in findings from the work of Shea *et al.* (2006). In this work, young and old individuals learned motor sequence tasks using a protocol that included infrequent performance of random sequences within an extended bout of practice with a repeating sequence. As expected, sizeable and significant gains were made in sequence-specific knowledge as evidenced by continued improvements in performance of the repeated sequence trials. However there was also a, albeit much smaller, reduction in the time to perform random sequences across training suggesting that acquisition of non-sequence specific information occurs. Similar improvements appeared to have occurred quite rapidly for the novel interference condition across the test trials. Importantly, the outcome for this condition with respect to offline learning was similar to those reported in previous work indicating that that exposure to an unrelated sequence task removes the expression of offline learning (Walker *et al.,* 2003; Korman, *et al.,* 2007).

Supplemental Practice of a Spatially Similar Task after Target Task Practice Supports Immediate Performance but Eliminates Offline Consolidation

In the present work the critical comparison focused on the performance of the individuals that were administered practice in the spatial interference condition. We operated from the position, based on work by Hikosaka, et al., (1999) that sequence knowledge, acquired early in practice, is represented in the spatial domain and as such experiencing alternative task practice that had congruent features with the target task would not de-stabilize the extant knowledge for the target task in the short-term while affording offline consolidation at a later time. Moreover, previous work by Wright *et al.,* (2010) has demonstrated that despite increasing the extent of practice beyond those typically used in studies examining procedural skill learning, offline improvements can still emerge. In the present work, we assumed that practice of the spatially similar task might have an advantage through the immediate availability of a spatial code developed through practice of the target task which, in turn, would minimize interference with the developed target task memory. If this occurred, it was hypothesized that target task knowledge would remain available for consolidation that could occur offline and bring about delayed performance improvement.

The key results associated with the spatial interference condition provided somewhat mixed support for the expectations delineated in the previous section. In short, two critical findings surfaced. First, it was clear that the participants in this condition were very capable of using the spatial information that was developed during practice of the target task. Generalization to the spatial interference task was significantly more successful than accomplished for the novel or motor task. As can be seen in Figure 3, the performance of the spatial task exhibited twice the improvement in speed compared to the novel and motor interference conditions while also revealing a concomitant reduction in error rate. These data are congruent with Hikosaka's model for procedural sequence skill acquisition (Hikosaka, et al., 1999; Hikosaka, Nakamura, Sakai, & Nakahara, 2002). Specifically, the claim that early in learning the spatial referencing system is very critical and preferred by the learner to establish a task representation that can be used to support subsequent performance. The lack of interaction with the trial factor indicates that the generalization to the spatial task from target task training was superior throughout performance of the interfering tasks. This is reflected in an immediate benefit observed for the spatial interference condition in terms of the savings (difference in performance from the first trial of the practice with the target task compared to the first trial of practice with the interference task) when transferring to the supplemental training. Specifically, for mean speed, the novel (32%) and motor (21%) interference conditions demonstrated reasonable savings but the novel (32% loss in accuracy) condition accomplished this while exhibited a greater error rate than the motor condition (30% reduction in error). In contrast, the savings observed for execution of the spatial task were dramatically greater than the other interference conditions for both mean speed (116% improvement) and error rate (reduced by 70%).

The second noteworthy finding from the present work addresses the impact of supplemental practice of the spatial task for subsequent offline learning. At first glance, evaluating the improvement from the end of target task practice to the eventual delayed test might be interpreted as indicative of an offline gain. As can be seen in Figure 4, there was a reliable improvement in performance (~19% in mean speed and error rate) across the delayed interval. Yet, it is important to note that this gain was less than that observed for the control condition (~30% in mean speed and error rate) during which no interfering task practice was administered. It appears then that facilitating the immediate performance of a sequence task by using of a spatial code developed during previous practice with the target task actually impeded the completion of important consolidation process that are responsible for enriching the procedural knowledge of the target task offline.

One might argue that the change in performance for the target task from training to test for the individuals assigned to the spatial interference condition merely reflects a more modest offline gain than observed for the control condition. If this is true, this would nonetheless still be in line with the position that offline learning was negatively influenced by practice of a spatially similar task occurs in close temporal proximity. However, we contend that the performance improvement that is displayed at the time of test for the spatial interference condition, rather than being a small offline gain, merely reflects an updated task representation for the target task that resulted from the same spatial code being utilized during supplemental practice.

To support this claim it is first worth considering a previous study by Wright *et al*., (2010) in which some individuals were afforded the opportunity to experience twice the amount of practice than the typical practice condition used in many of the previous studies addressing procedural learning and offline gain (Walker *et al*., 2003). While the additional practice in the study by Wright *et al*. was with the target task, it is reasonable to assume that the improvement observed during such practice was due, at least in part, to enriching the spatial representation of the target task much like we assume to be the case in the present study during the engagement of extra practice with the spatial interference task. This assumption is based on the central premise of Hikosaka's model that during the initial stage of practice the allocentric reference frame is critical to task acquisition. Importantly, for the interpretation of findings in the present work, is Wright *et al*. demonstration that mean speed for the target task exhibited a significant offline gain following supplemental practice of the target task. This was despite the fact that the absolute level of performance in Wright *et al*., was considerably greater at test (~27 sequences/30-s or ~220 ms/keystroke) compared to that reported in the present work (~13 sequences/30-s or ~330 ms/keystroke) because the target task in Wright *et al*. involved a five key sequence compared to the seven key sequence in the present study. Thus, Wright *et al*., was able to demonstrate continued gains across physical practice of a target task that presumably involved some updating of the spatial code governing implementation of the task, without diminishing the materialization of further offline gains manifest during the delayed test.

Why Then is There No Further Offline Gain Observed for the Target Task at the Time of the Delayed Test?

Rather than reveal additional performance gains at the time of test, the spatial interference group displayed performance that was similar to that achieved at the end of practice with the spatial interference task. It appears then that access to an established allocentric or spatial code, through practice with the target task, while sufficiently malleable to use to facilitate transfer to the spatial variation of the interference sequences is not involved in subsequent updating of the task knowledge associated with the target task.

Spatial Codes and Knowledge Contained in Procedural Task Representations are not the same

To answer this one has to view the spatial code used at the time of execution and the task representation for the target task as separate entities. In essence, the spatial code is a temporary or transient form of information that helps implementation of tasks during performance and fosters the accumulation of knowledge that represents the demands of the procedural task. Congruent with Hikosaka's model, during initial practice a spatial code and motor code are activated but it is the spatial code that is easier to use to support the performer's initial efforts to successfully execute the target task. Through continued execution, knowledge about the qualities (associations between stimuli and responses, directions of the movements of the stimulus and fingers, forces required, etc.) of the sequence are accumulated and stored as procedural knowledge that represents this particular sequential behavior. At the conclusion of practice with the target task, a task representation has been developed as a result of using an allocentric referencing system, the spatial code, which can be retrieved at a later date to support further efforts to execute the target task. On immediate transfer to the spatial interference task, the spatial code that is still available from the performance of the target task can be immediately utilized to support the production of a new task that has the same spatial layout. A by-product of using the same spatial code is that knowledge contained within the representation for the target task experiences additional updating in concert with development of the knowledge representation of the new spatial variant. Thus, at the time of test for the target task, performance improves beyond that observed at the completion of physical practice with this task. This results from the additional updating of the target task representation that occurred while performing the spatial interference task that adopted the same spatial referencing system or spatial code.

The Importance of Serial Order as a Determinant of Consolidation that Supports Offline Gains

The question as to why there is no further offline updating of the target task still needs to be resolved. One possibility is that consolidation that is necessary for offline gains, that which has been the subject of much recent experimental work (Walker, *et al*., 2003), is implemented on the basis of the serial order prior to the advent of the period of consolidation. So in the case of the present experiment, any consolidation that is undertaken to enrich the knowledge of the practiced tasks would only occur for the activity engaged at the conclusion of the practice bout. In the present experiment it was the interfering task, not the target task, that was the final task practiced. Thus, if serial order governs the specific knowledge or task representation that is susceptible to further consolidation offline gains for the target task would not be expected. Indeed, it would be the spatial variant, or for that matter, the motor or novel variants, in the alternative interference conditions, that would be expected to reveal delayed enhancement. In the present experiment delayed performance of the interfering tasks was not assessed but clearly a future experiment needs to evaluate this account for the unfolding of offline performance gains.

This proposal does have some support in the extent literature. In the original work of Walker *et al*., (2003) one group (Group 2, see p. 618) involved a task sequence similar to that used in the present work. The practice of a target sequence of five responses was immediately followed by a similar amount of practice of a novel sequence. When a test was conducted 24-hour later, following a night of sleep, the anticipated offline gain for the target task was only observed for speed but not accuracy. Yet, for the interfering task, offline enhancement was reported for both speed and accuracy. Thus, it was the final task practiced on the previous day that appeared to garner the greatest advantage from consolidation that occurs in the delay between practice and test. These data are in line with the explanation offered for the present findings that serial order is critical when predicting optimal offline gain.

Hikosaka's Model of Procedural Learning: Further Supporting Evidence

A number of observations from the present work are consistent with the central elements of a recent model of procedural task learning forwarded by Hikosaka and colleagues (Hikosaka, et al., 1999; Hikosaka, Nakamura, Sakai, & Nakahara, 2002). Specifically, initial practice of a motor sequence task leads to the establishment of a memory representation that is developed through the use of a spatial or allocentric reference scheme for determining the demands of the sequential behavior. This allocentric reference system, referred to as the spatial code, can be used early in practice to facilitate the production of a procedural task. Primary evidence from the present work in support of this facet of Hikosaka's model was the rapid acquisition of the spatial interference task following practice of the target task. In this condition, the initial performance gain (difference in performance of the first trial of the target task and the spatial interference task) was greater than 100%.

In contrast, performance both during practice of the respective interfering task as well as the subsequent delayed test with the target task was similar for the motor and novel interference conditions. First, unlike the spatial task, the gain from target task practice to the initial trial of the interference task for the motor and novel conditions was only 30%

and 22% respectively. Moreover, both of these conditions revealed only a small performance gain, one significantly less than observed for the spatial interference condition, at the delayed test. Given the similarity in performance of the motor and spatial tasks, it was proposed that the small improvements in training and at test were most likely a result of non-task specific cognitive and motor processes (Shea *et al*., 2006). These data are in line with the claim that an effector-specific frame of reference has yet to be used to direct the updating of the task representation and that the use of a motor code to aid task production doesn't occur until later in practice (Cohen, Pascual-Leone, Press, & Robertson, 2005; Kovacs, Muhlbauer, & Shea, 2009; Panzer, *et al.*, 2009; Park & Shea, 2003; Verwey & Wright, 2004). These data are congruent with the central theme of Hikosaka's model that details a differential role of allocentric and egocentric reference systems during the time course of procedural skill acquisition.

CONCLUSIONS

Robust *offline* performance gains, beyond those that would be anticipated by merely experiencing physical practice, have been noted during the unfolding of procedural skill learning. Such latent improvements can be mitigated via practice of unrelated procedural task within a short time frame following the initial practice of the to-be-learned procedural skill. In the present experiment it was revealed that while a motorically similar or a novel procedural task did indeed diminish the emergence of offline performance gains, the practice of a spatially similar task led to improved performance of the target task during a delayed test. However, this improvement was argued to be a result of an updated task representation for the target task through practice of the spatial interference task not due to offline consolidation that occurred between the conclusion of practice and test episodes (Wright *et al*., 2010). These data revealed the importance of serial order in determining knowledge that undergoes consolidation outside the boundaries of physical practice of the procedural tasks. This proposal led to the novel proposal that the last task during any practice bout involving multiple procedural tasks will be the task whose knowledge representation will be most susceptible to further enhancement consolidation. With respect to the present work, this assertion would be true for each of the tasks utilized to interfere (i.e., motor, spatial, and novel). Finally, evidence from practice performance of the interference task and the resultant improvement in the target task performance following such practice was congruent with a contemporary model of procedural task acquisition forwarded by Hikosaka and colleagues. This model argues that a spatial not motor reference system plays an important role early during motor sequence learning.

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