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Abstract

Recent research has demonstrated that memory consolidation processes can be accelerated if newly learned information is consistent with pre-existing knowledge. Until now, investigations of this fast integration of new information into memory have focused on the declarative and perceptual systems. We employed a unique manipulation of a motor sequence learning paradigm to examine the effect of experimentally-acquired memory on the learning of new motor information. Results demonstrate that new information is rapidly integrated into memory when practice occurs in a framework that is compatible with the previously-acquired memory. This framework consists of the ordinal representation of the motor sequence. This enhanced integration cannot be explained by differences in the explicit awareness of the sequence and is only observed if the previously-acquired motor memory was consolidated overnight. Results are consistent with the schema model of memory consolidation and offer insights into how previous motor experience can accelerate learning and consolidation processes.

Keywords: Schema, Motor Sequence Learning, Memory Consolidation, Integration

Introduction

The learning of new information is rarely done from a blank slate; rather, it occurs in the context of relevant, pre-existing memories. Critically, novel information is learned faster if it is compatible with existing knowledge, a result that is achieved via the integration of new information into the previously acquired memory (Lewis & Durrant, 2011; van Kesteren, Ruiter, Fernández, & Henson, 2012). A seminal example of this integration into memory was provided by a series of studies in which rats acquired flavor/location associations (Tse et al., 2011; Tse et al., 2007). After consolidation of this associative “map”, new flavor/location pairs were rapidly acquired and stored in the cortex if presented in a framework compatible with the consolidated map. This research served as the initial experimental support for the schema model of memory consolidation that posited the consolidation of hippocampal-mediated memory traces is *accelerated* if the newly encoded memory is consistent with previously acquired knowledge, or “cognitive schemata”. Such schemata are conceptualized as cognitive frameworks stored in the neocortex that encompass knowledge abstracted from previous experiences (Lewis & Durrant, 2011).

These initial animal studies triggered considerable interest in human research which provided additional experimental support for the schema model of memory consolidation in the declarative and perceptual domains (Hennies, Lambon Ralph, Kempkes, Cousins, & Lewis, 2016; Sommer, 2017; van Buuren et al., 2014; Wagner et al., 2015). However, similar research in the motor domain is scarce. This is particularly striking, as the fast integration of new motor information into pre-existing memory is necessary for many daily activities (e.g., changing from an AZERTY to QWERTY keyboard or adding a step into a dance number). Moreover, there is increasing evidence that the motor memory system - at least with respect to sequence learning - shares neural networks and processes with other memory systems. It is therefore tempting to speculate that integration processes observed in other memory systems would also apply to the motor domain. Specifically, it has been shown that, in parallel

to cortico-striatal and -cerebellar networks (Doyon et al., 2009), the hippocampus - the involvement of which was historically limited to the declarative system - plays a crucial role in motor sequence memory processes (Albouy, Sterpenich, et al., 2013; Albouy, King, Maquet, & Doyon, 2013; Albouy et al., 2008; Schendan, Searl, Melrose, & Stern, 2003). Hippocampo-frontal networks support an abstract/cognitive representation of the motor sequence (Albouy et al., 2015; Albouy, Fogel, et al., 2013) that is thought to encompass the spatial aspect of the task or the ordinal information (i.e., serial order) of the sequence (King, Hoedlmoser, Hirschauer, Dolfen, & Albouy, 2017). We suggest that these abstract/cognitive sequence representations supported by hippocampo-cortical networks can be abstracted and subsequently used to accelerate the integration of new motor elements into memory.

The present series of experiments tested whether integration of new motor information into memory can be accelerated through the availability of a pre-existing abstract task representation. Based on evidence that: (i) the hippocampus supports abstract representations of motor sequence learning (Albouy, King, et al., 2013) and binds elements to their ordinal positions (Hsieh, Gruber, Jenkins, & Ranganath, 2014); (ii) sleep participates in hippocampal-mediated memory consolidation through the building of abstract representations (Lewis & Durrant, 2011); and, (iii) sleep consolidates ordinal/abstract rather than transition-based/motor information (Albouy et al., 2015; Albouy, Fogel, et al., 2013; Song & Cohen, 2014), we hypothesized that the abstract representation acquired during motor sequence learning (and consolidated overnight) encompasses the ordinal information of the learned sequence and that new motor information would be rapidly integrated into memory if compatible with such a representation.

Materials and Methods

Ethics statement

This study was approved by the local medical ethical committee. All participants gave their written informed consent before the start of the study and received compensation for their participation. Procedures were executed in conformity with the approved guidelines.

Participants

One hundred thirty-four young (age range = 18 to 31 years; mean age = 22.4 years, 88 females), right-handed (Oldfield, 1971), healthy participants were recruited for this research (across the three experiments). They were all non-smokers and did not take psychoactive medications (e.g., anti-anxiety or -depression). No participants had a history of neurological or psychiatric disorders, including anxiety (Beck, Epstein, Brown, & Steer, 1988) and depression (Beck, Steer, Ball, & Ranieri, 1996). None of the participants were professional typists or classified as musicians (i.e., not currently playing and less than 5 years of experience on an instrument requiring dexterous finger movements). Of those 134 individuals who met the inclusion criteria listed above, six were excluded from data analyses. Two participants did not complete the second experimental session, one had missing data in Session 1 due to a computer malfunction, one took a sleep aid between the 2 testing days and 2 failed to perform the correct sequence. Participant characteristics for each experimental group are summarized in Table 1. Sample size was determined with G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) and based on detecting significant differences between experimental groups in our primary experiment. As the integration of novel motor information into memory has not been previously investigated, a literature-based *a priori* estimation of the hypothesized effect size was not possible. A hypothesized effect of $f=0.35$ ($\eta_p^2=0.11$) was chosen as this represents a medium effect size. Corresponding power analysis

(Effect size $f=0.35$, $\alpha=0.05$, Power=0.80) resulted in an estimated 18 subjects per group. Group sample sizes can be found in Table 1.

Table 1. Participant characteristics and sleep/vigilance data.

	Experimental Groups						
	Experiment 1a			Experiment 1b		Experiment 2	
	Same	New	Compatible	Incompatible	Compatible Control	Immediate Compatible	Immediate Incompatible
n	17	19	20	18	17	19	18
Females	11	13	13	12	11	13	13
Mean Age (yrs)	22.6 ± 2.9	21.8 ± 2.6	22.7 ± 2.3	21.4 ± 2.6	21.9 ± 2.6	22.7 ± 2.9	23.3 ± 2.9
BAI	3.9 ± 4.1	4.1 ± 3.9	5.5 ± 4.7	7.4 ± 4.3	3.5 ± 3.8	4.5 ± 3.8	5.7 ± 3.8
BDI	3.7 ± 2.8	3.3 ± 2.9	3.5 ± 3.6	4.7 ± 2.8	2.7 ± 4.4	4.2 ± 3.3	4.2 ± 3.3
Handedness	86.5 ± 14.4	89.2 ± 14.4	87.8 ± 10.8	87.2 ± 11.7	91.9 ± 13.5	95.0 ± 8.6	92.7 ± 10.5
PSQI	2.9 ± 1.4	3.1 ± 1.3	3.2 ± 1.4	2.8 ± 1.5	3.1 ± 1.5	3.0 ± 2.7	3.7 ± 1.6
S1: SMS duration (h)	7.8 ± 1.2	8.5 ± 0.9	8.2 ± 0.9	8.0 ± 1.4	8.2 ± 1.0	8.2 ± 0.8	8.6 ± 1.1
S2: SMS duration (h)	8.1 ± 1.0	8.5 ± 0.8	7.9 ± 0.70	7.8 ± 2.1	8.2 ± 1.5	N/A	N/A
S1: SMS quality	4.9 ± 0.8	4.6 ± 0.6	5.3 ± 0.7	4.6 ± 1.1	5.0 ± 0.7	5.0 ± 1.0	5.1 ± 1.1
S2: SMS quality	4.8 ± 1.1	4.5 ± 1.0	4.7 ± 1.0	4.8 ± 0.9	5.0 ± 0.7	N/A	N/A
S1: SSS	2.0 ± 0.5	2.0 ± 0.6	2.1 ± 0.7	2.3 ± 0.8	2.2 ± 0.6	2.3 ± 1.0	2.1 ± 0.6
S2: SSS	1.8 ± 0.8	2.3 ± 0.8	2.1 ± 0.8	2.3 ± 1.0	2.0 ± 0.5	N/A	N/A
S1: PVT (ms)	355 ± 29	345 ± 27	334 ± 24	335 ± 26	355 ± 38	350 ± 25	330 ± 24
S2: PVT (ms)	355 ± 30	341 ± 23	332 ± 23	336 ± 31	355 ± 39	N/A	N/A

Group means ± SD for participant characteristics as well as sleep and vigilance scores from the two experimental sessions. S1 = Session 1; S2 = Session 2; BAI = Beck's anxiety inventory (Beck et al., 1988); BDI = Beck's Depression Inventory (Beck et al., 1996); PSQI = Pittsburgh Sleep Quality Index (Buysse, Reynolds, Monk, Berman, & Kupfer, 1989); SSS = Stanford Sleepiness Scale (MacLean, Fekken, Saskin, & Knowles, 1992); SMS = St. Mary's sleep questionnaire (Ellis et al., 1981); PVT = psychomotor vigilance task (Dinges & Powell, 1985). Handedness scores are from (Oldfield, 1971). Note that two participants (1 in the New and Compatible Control groups) had missing data for the PVT due to computer malfunction and thus these individuals were not included in the group means.

Motor task

Participants performed an explicit serial reaction time task (SRTT; (Nissen & Bullemer, 1987)) that was coded and implemented with PsychToolbox in MATLAB (Mathworks Inc., Sherborn, MA). Participants were comfortably seated in front of a laptop screen and a specialized keyboard was placed on the participant's lap below a desk, effectively preventing participants from viewing their own fingers during task performance. During the task, eight squares were presented on the screen, each corresponding spatially to one of the eight keys on the keyboard and to one of 8 fingers (no thumbs). The color of the outline of the squares alternated between red and green, indicating rest and practice blocks, respectively. After each rest block (15s), the outlines of all squares changed from red to green, indicating that participants should get ready to perform the task. Subsequently, one of the eight squares was colored (i.e., filled) green and participants were instructed to press the corresponding key with the corresponding finger as fast as possible. As soon as a key was pressed, independent of whether the response was correct or not, the next square in a sequence changed to green. Each block of practice included 64 key presses. Depending on the specific experimental run (pseudo-random vs. sequence; see below for details), the order in which the squares were filled green (and thus the order of finger movements) followed either a pseudo-random or a fixed, repeating sequential pattern. During the sequence runs, the participants performed a repeating 8-element sequence (whereby each of the 8 fingers was pressed once in a sequence) that was repeated 8 times per block. Participants were explicitly informed when the stimuli would follow a repeating sequential pattern, but were not given any additional information such as what the pattern was or how many elements the sequence was composed of. During the pseudo-random run, there was no repeating sequence, but each key was pressed once every 8 elements (i.e., no repeating elements) and thus each finger was also pressed 8 times per block.

Experimental Design

Experiment 1a consisted of two visits to the laboratory on consecutive days. The two sessions occurred at approximately the same time of day, thus minimizing any influence of circadian phase variation on behavior (Smarr, Jennings, Driscoll, & Kriegsfeld, 2014). Participants were instructed to have a good night of sleep before each session and to avoid alcohol and caffeine the day before and the day of the two sessions. Sleep quality and quantity for the nights before each session were assessed with the St. Mary's sleep questionnaire (Ellis et al., 1981). Additionally, participants wore an actiwatch (Cambridge Neuroscience, Cambridge, UK) during the 24 hours separating the 2 experimental sessions. Sleep duration prior to the second session self-reported by the participants was visually verified with actigraph data. Vigilance at the time of testing was assessed subjectively and objectively at the beginning of each session using the Stanford sleepiness scale [SSS; (MacLean et al., 1992)] and the psychomotor vigilance task [PVT; (Dinges & Powell, 1985)], respectively. Group means for the sleep and vigilance data are provided in Table 1. During the first session (Day 1), each participant completed 4 blocks of the pseudo-random SRTT to become familiar with the task. Participants then completed 20 blocks of the sequential SRTT (Training), which was immediately followed (< 2-minute break) by a short post-training test of 4 blocks on the sequential SRTT. Participants in all 4 groups performed the same 8-element sequence during the training and test runs on Day 1 (see Figure 1). A generation task was performed at the end of the session in order to assess awareness of the sequential knowledge. During this task, participants were asked to self-generate (i.e., not visually cued), and at their own pace, the sequence of finger movements completed in that particular session. Unbeknownst to the participants, the generation task consisted of 24 key presses (ideally corresponding to 3 repetitions of the 8-element sequence). Note that one participant in the New experimental group did not complete the generation task in Session 2 due to experimenter error and thus was excluded from corresponding analyses. Before leaving the lab, the participants were reminded of the instructions to

avoid alcohol consumption, to not practice the task at home and to have a good night of sleep (monitored by the actiwatch).

The second testing session (Day 2) was nearly identical to the first, with the following exceptions. First, the pseudo-random (task familiarization) run was not completed. Second, and most importantly, participants in the 4 experimental groups completed different movement sequences (Figure 1). While participants in the Same group executed the same sequence as on Day 1, participants in the New group performed a sequence consisting of the same elements (i.e., finger presses), but all new movement transitions (i.e., no two consecutive finger presses were the same as in Session 1). To investigate the integration of new motor information into pre-existing motor sequence knowledge, the last two experimental groups (labeled Compatible and Incompatible) performed a relatively similar sequence as on Day 1, but 2 elements were interchanged (blue arrows in Figure 1). This manipulation resulted in a sequence in which 50% of the transitions were novel (these *novel transitions* were also performed by the New group on Day 2; red lines in Figure 1) and 50% of the transitions were performed on Day 1 (these *learned transitions* were also performed by the Same group on Day 2; black lines in Figure 1). Critically, the sequences performed in the Compatible and Incompatible groups consisted of the same movement transitions, but differed based on their ordinal structure (i.e., the serial position of the elements in the sequence). Thus, these two groups performed the same movement transitions, but the sequences started at different points such that the ordinal structure on Day 2 was either highly **compatible** compared to initial training (75% ordinal compatibility across the two days) or was predominantly **incompatible** as compared to Day 1 (12.5% ordinal compatibility across the two days). This design allowed us to investigate the influence of the ordinal information on (i) integration processes with the analysis of performance on the shared novel (i.e., to-be-integrated) transitions (and also common with the New group) and (ii) retention processes with the analysis of the shared learned transitions (and also common with the Same group).

Group	Day 1									Day 2									# of Day 2 Learned Transitions	# of Day 2 Novel Transitions	Day 1 / Day2 Ordinal Compatibility
	Ordinal Position									Ordinal Position											
	I	II	III	IV	V	VI	VII	VIII	I	I	II	III	IV	V	VI	VII	VIII	I			
Same										4	7	3	8	6	2	5	1	4	8	0	High (8/8)
New										1	6	3	5	7	2	8	4	1	0	8	Low (2/8)
Compatible	4	7	3	8	6	2	5	1	4	4	7	2	8	6	3	5	1	4	4	4	High (6/8)
Incompatible										8	6	3	5	1	4	7	2	8	4	4	Low (1/8)
Compatible Control	3	8	6	2	5	1	4	7	3	2	8	6	3	5	1	4	7	2	4	4	High (6/8)

Figure 1. Experimental groups. Roman numerals label the serial (i.e., ordinal) positions of the keys and fingers to be pressed in the sequence. Arabic numerals indicate the fingers to be pressed (1 = left little finger, 2 = left ring, 3 = left middle, 4 = left index, 5 = right index, 6 = right middle, 7 = right ring, and 8 = right little finger). Note that this numbering of the fingers is used here to facilitate understanding of the task; participants were not given this information. The four groups of participants in Experiment 1a (Same, New, Compatible and Incompatible) were trained on the same sequence on Day 1 but different sequences on Day 2 (see the text for details). The Day 2 sequence elements in red font denote those that are in a different ordinal position relative to Day 1. Blue arrows indicate the elements that switched ordinal positions across the two testing days. Day 2 novel transitions that were shared across the New, Compatible and Incompatible groups are underlined in red, whereas learned transitions that were common across the Same, Compatible, and Incompatible groups are underlined in black. The columns on the far right indicate the number of Day 2 transitions that were learned on Day 1, the number of Day 2 transitions that were novel and the compatibility of the ordinal structure across the two testing days (parenthetic clause indicates number of sequence elements out of 8 that are in the same ordinal positions). The Compatible Control group was included as part of Experiment 1b for comparison with the Incompatible group from Experiment 1a. Compatible Control performed the same movement transitions on Day 2 as both the Compatible and Incompatible groups, but at a different starting point (see the text for details).

The Compatible and Incompatible groups were specifically designed to differ with respect to ordinal compatibility between sequences performed in the two testing sessions (i.e., 75% vs. 12.5%, respectively). A consequence of our design was that these two groups also differed on whether the

starting / initial elements of the Day 2 sequence matched those of the initially learned sequence of Day 1. More specifically, for the Compatible group, the initial elements of the sequences performed across the two days were identical (i.e., 4-7), whereas the beginning elements of the two sequences across testing days differed in the Incompatible group. One could argue that this group difference in the Day 2 starting elements, and not necessarily the ordinal structure of the *full* 8-element sequence, could be the primary contributor to any performance differences. To test for this possibility, an additional group (Compatible Control; see Figure 1) was included as part of Experiment 1b and compared to the Incompatible group from Experiment 1a. Critically, Compatible Control completed the same movement transitions on Day 2 as the Compatible and Incompatible groups, with the same high ordinal compatibility as the Compatible group, but the initial elements of the Day 2 sequence in Compatible Control differed from the initial elements of the sequence learned on Day 1. This allowed us to address the specific influence of whether similar starting elements across the two sequences influenced performance. The experimental protocol for the Compatible Control group was identical to that outlined for Experiment 1a, with the exceptions of the different sequences completed and that actigraphs were not used to verify the participants' self-reported sleep durations between the two testing days.

Experiment 2 investigated whether the effects observed in Experiment 1 were dependent on the acquired motor memory trace (i.e., schema) having the opportunity to consolidate overnight. To test this possibility, we assessed integration/retention processes for the Incompatible and Compatible groups **immediately** (i.e., 15 minutes) after the initial training session rather than after a 24-hour consolidation interval. The experimental protocol for this experiment was nearly identical to Experiment 1a, with the following exceptions. First, and as highlighted above, the two testing sessions were completed in short succession in the same testing day. After Session 1, participants in Experiment 2 watched a nature movie without sound for 15 minutes before beginning the second testing session.

The second testing session was then completed well before the memory acquired during the initial testing session had the opportunity to consolidate. Second, as the primary research question of interest was based on how the ordinal information available during practice influences the integration of new motor information into pre-existing knowledge, Experiment 2 consisted of only the Compatible and Incompatible conditions. Note that one participant in the Immediate Incompatible group had missing data from the Session 2 test phase (4 post-training blocks) due to a computer malfunction and thus was excluded from the analyses of this phase.

Data Analyses

For the SRTT, mean response time (RT – reflecting performance speed) and percentage of correct movement transitions (% Correct – reflecting movement accuracy) were computed for each block of the task for (1) all sequence elements (and thus all movement transitions) in sessions 1 and 2, (2) the elements that form the shared novel transitions in Session 2 (i.e., elements 3, 5, 2 and 8 as part of the transitions 7-2, 2-5, 6-3 and 3-8, respectively – see Figure 1) and (3) the elements that form the shared learned transitions in Session 2 (i.e., elements 7, 6, 1 and 4 as part of the transitions 4-7, 8-5, 5-1 and 1-4, respectively). Data were analyzed using repeated measures ANOVAs ($\alpha = 0.05$) separately for the training and test runs from the different sessions with block and group as factors of interest. In case of violation of the sphericity assumption, Greenhouse-Geisser corrections were applied. For the generation task, the percentage of correct transitions and the percentage of correct ordinal positions generated were extracted and analyzed using one-way ANOVAs ($\alpha = 0.05$).

Open Practices

Ethical approval granted by the local ethics committee does not permit the publication of data online. If readers would like to access these data, additional ethical approval (on an individual user and purpose basis) will be required. Such requests can be made directly to the local medical ethical

committee. The authors are also happy to support such ethical approval applications. Requests for custom Matlab code can be made to the authors. The experiments reported in this article were not formally preregistered.

Results

Experiment 1a

Initial motor sequence learning

Data from Day 1 (Figure 2A, left panel) showed that motor performance computed across all transitions significantly improved across blocks of practice, as indicated by both faster RTs and more correct transitions (RT: $F_{(7.27,509.09)}=123.17$, $\eta_p^2=0.637$, $p<0.001$; % Correct: $F_{(19,1330)}=2.59$, $\eta_p^2=0.036$, $p<0.001$). However, and as expected, performance did not differ among the 4 groups during initial training (RT group main effect: $F_{(3,70)}=0.89$, $\eta_p^2=0.037$, $p=0.45$; RT block by group interaction: $F_{(21.81,509.09)}=0.79$, $\eta_p^2=0.032$, $p=0.74$; % Correct group main effect: $F_{(3,70)}=2.07$, $\eta_p^2=0.081$, $p=0.11$; % Correct block by group: $F_{(57,1330)}=0.70$, $\eta_p^2=0.029$, $p=0.96$). Similarly, there were no group differences during the short post-training test provided immediately after training on Day 1 (RT group effect: $F_{(3,70)}=0.65$, $\eta_p^2=0.027$, $p=0.59$; RT block by group interaction: $F_{(7.84,183.05)}=1.46$, $\eta_p^2=0.058$, $p=0.18$; % Correct group main effect: $F_{(3,70)}=0.51$, $\eta_p^2=0.022$, $p=0.67$; % Correct block by group: $F_{(9,210)}=0.32$, $\eta_p^2=0.014$, $p=0.97$). Collectively, these data indicate that the four groups performed similarly prior to the experimental manipulation.

Figure 2. Performance on all transitions in Experiment 1a. Mean response time (top row) and percentage of correct transitions (bottom row) is shown in (a) for all transitions on Days 1 and 2 as a function of the 20 practice blocks during training and the 4 post-training test blocks, separately for the four groups. Shaded regions represent standard errors of the mean. The main effect of group (collapsed across blocks) during training and test sessions on Day 2 is depicted in (b). Brackets indicate significant pairwise differences between groups ($p < .05$). Error bars represent standard errors of the mean. Tr = training.

Enhanced performance when new motor information is presented within a compatible ordinal-based framework

According to models of memory integration (Tse et al., 2007; van Kesteren et al., 2012), if previously acquired knowledge of the motor sequence is developed during initial training on Day 1, subsequently consolidated and then activated during practice on Day 2, encoding of the new motor elements will be facilitated through rapid integration into the pre-existing memory. Analyses indeed

revealed that the 4 groups differed with respect to both movement speed and accuracy computed across all transitions (RT: $F_{(3,70)}=6.39$, $\eta_p^2=0.215$, $p<0.001$; % Correct: $F_{(3,70)}=6.01$, $\eta_p^2=0.205$, $p=0.001$) as well as the changes in RT across blocks ($F_{(12.20,284.69)}=3.81$, $\eta_p^2=0.140$, $p<0.001$) (Figure 2A, right panel). Follow-up comparisons to the main effects of group (see Figure 2B) revealed that even though half of the transitions were novel in the Compatible group, performance did not significantly differ as compared to the Same group (RT: $F_{(1,35)}=0.92$, $\eta_p^2=0.026$, $p=0.34$; % Correct: $F_{(1,35)}=0.05$, $\eta_p^2=0.001$, $p=0.82$), but was better as compared to the New (RT: $F_{(1,37)}=8.78$, $\eta_p^2=0.191$, $p=0.005$; % Correct: $F_{(1,37)}=10.51$, $\eta_p^2=0.221$, $p=0.003$) and Incompatible groups (RT: $F_{(1,36)}=4.24$, $\eta_p^2=0.105$, $p=0.047$; % Correct: $F_{(1,36)}=4.66$, $\eta_p^2=0.114$, $p=0.038$). The difference between the Compatible and Incompatible groups was especially striking considering that participants performed the same movement transitions but within different ordinal contexts. Moreover, even though the sequence to perform in the Incompatible group included 50% of transitions that were already learned on Day 1, overall performance was comparable to the New group (RT: $F_{(1,35)}=1.04$, $\eta_p^2=0.029$, $p=0.31$; % Correct: $F_{(1,35)}=2.56$, $\eta_p^2=0.068$, $p=0.12$) and, unsurprisingly, significantly worse than the Same group (RT: $F_{(1,33)}=8.76$, $\eta_p^2=0.209$, $p=0.006$; % Correct: $F_{(1,33)}=4.58$, $\eta_p^2=0.121$, $p=0.040$). These results indicate that the performance of a sequence of movements that includes new transitions to be integrated is critically influenced by the ordinal context provided during practice and whether this context is consistent with the one acquired during initial training and subsequently consolidated overnight.

To further investigate the significant block x group interaction revealed on Day 2 response times, follow-up pairwise comparisons were performed. Significant interactions were observed between the Compatible group and the 3 other groups (Compatible vs. Same, $F_{(5.01,175.34)}=2.56$, $\eta_p^2=0.068$, $p=0.029$; Compatible vs. New, $F_{(3.63,134.47)}=4.01$, $\eta_p^2=0.098$, $p=0.006$; Compatible vs. Incompatible, $F_{(4.78,172.13)}=3.82$, $\eta_p^2=0.096$, $p=0.003$). Data inspection revealed substantial decreases in RT in the Compatible group early during the training session, suggesting that the new motor elements

were rapidly assimilated into the motor sequence. Interestingly, performance changes across blocks in the Incompatible group were indistinguishable from those observed when the sequence to perform was entirely new ($F_{(3.27,114.53)}=0.59$, $\eta_p^2=0.017$, $p=0.64$) and significantly different from both the Same ($F_{(3.89,128.29)}=6.21$, $\eta_p^2=0.158$, $p<0.001$) and Compatible groups. These results suggest that previously acquired knowledge on the sequence task not only influences overall motor performance during the learning of new motor elements, but also the rate of learning.

Integration of novel information is enhanced when compatible with previously acquired task knowledge

To determine the contribution of integration of novel information versus the retention of previously learned information to the overall pattern of performance observed on Day 2, we extracted performance on the 4 novel transitions that were common across Compatible, Incompatible and New groups (red lines in Figure 1) and performance on the 4 learned transitions that were common across the Same, Compatible and Incompatible groups (black lines in Figure 1), respectively.

Results show that performance on novel, to-be-integrated transitions significantly differed among the three groups (RT: $F_{(2,54)}=3.54$, $\eta_p^2=0.116$, $p=0.036$; % Correct: $F_{(2,54)}=4.41$, $\eta_p^2=0.140$, $p=0.017$; see Figures 3A and B). While performance was similar between Incompatible and New groups (RT: $F_{(1,35)}=0.050$, $\eta_p^2=0.001$, $p=0.82$; % Correct: RT: $F_{(1,35)}=0.59$, $\eta_p^2=0.016$, $p=0.45$), it was significantly better in Compatible as compared to the two other groups (RT Compatible vs. Incompatible, $F_{(1,36)}=5.29$, $\eta_p^2=0.128$, $p=0.027$; RT Compatible vs. New, $F_{(1,37)}=4.60$, $\eta_p^2=0.110$, $p=0.039$; % Correct Compatible vs. Incompatible, $F_{(1,36)}=6.41$, $\eta_p^2=0.15$, $p=0.016$; % Correct Compatible vs. New, $F_{(1,37)}=7.07$, $\eta_p^2=0.161$, $p=0.011$). These data indicate that integration of new motor information into memory was specifically facilitated if this new information was compatible with the previously acquired, ordinal-based sequence representation.

Figure 3. Shared novel and learned transitions in Experiment 1a. Mean response time (RT; top row) and percentage of correct transitions (bottom row) on Day 2 are shown in (a) as a function the 20 practice blocks during training and the 4 post-training test blocks. Results are shown separately for the novel transitions shared among the New, Compatible, and Incompatible groups (left panel) and learned transitions shared among the Same, Compatible, and Incompatible groups (right panel). Shaded regions represent standard errors of the mean. Main effect of group (collapsed across blocks) during training (Tr) and test (Te) sessions on the Day 2 novel transitions are depicted in (b) for RT (left) and percentage of correct transitions (right). Brackets indicate significant pairwise differences between groups ($p < .05$). Error bars represent standard errors of the mean. Transition type (Novel vs. Learned) $\times$ group (Compatible vs. Incompatible) interactions are depicted in (c) for the Day 2 test phase. The asterisk indicates a significant interaction ($p < 0.05$). For completeness, performance on the shared learned and novel transitions is also depicted for the Same and New groups, respectively. Error bars represent standard errors of the mean.

It could be argued that the enhanced integration of novel motor information demonstrated in the Compatible group was over-estimated due to the inclusion of all 4 novel transitions. Specifically, this

analysis included the transitions 7-2, 2-8, 6-3 and 3-5 (Figure 1); however, elements 8 and 5 (i.e., the motor response as part of the transitions 2-8 and 3-5) were in the same ordinal positions as in Session 1 for the Compatible group (positions 4 and 7, respectively) but not the Incompatible group (positions 1 and 4, respectively). As the ordinal information of a motor sequence has been shown to be specifically consolidated over offline intervals including sleep (Song & Cohen, 2014), perhaps the ordinal similarity of these specific elements across the two testing sessions inflated the performance on these novel transitions. In other words, one could wonder whether the better performance on the novel transitions in the Compatible group can be attributed to enhanced consolidation of the ordinal positions of these specific elements and not necessarily to enhanced integration of novel motor information into a previously acquired memory. To assess this possibility, we compared the integration of only the transitions 7-2 and 6-3 (i.e., excluding transitions including elements 8 and 5 that were in the same ordinal position in the two testing days) between the Compatible and Incompatible groups. As elements 2 and 3 in the Compatible experimental group were in distinct ordinal positions relative to Session 1, the analysis of these elements avoids the potential confound described above. Results of a 2 (group: Compatible / Incompatible) x 20 (block) ANOVA on only these 2 novel transitions from the Day 2 training phase revealed a highly significant group difference in accuracy (% Correct: $F_{(1,36)}=8.44$, $\eta_p^2=0.190$, $p=0.006$) and a trend for a difference in RT ($F_{(1,36)}=3.46$, $\eta_p^2=0.088$, $p=0.071$). Thus, the enhanced performance demonstrated by the Compatible group cannot be solely explained by better consolidation of the ordinal positions of these specific elements, but rather suggest that the novel transitions were better integrated into the previously acquired memory.

Regarding performance of the learned transitions in Session 2, the changes in RT across blocks ($F_{(10.02,260.49)}=3.83$, $\eta_p^2=0.128$, $p<0.001$) differed among the groups. Further investigation indicated that practice-related changes in RT differed between Incompatible and the other two groups [Same vs. Incompatible: $F_{(4.24,139.77)}=4.95$, $\eta_p^2=0.131$, $p=0.001$; Compatible vs. Incompatible: $F_{(4.64,167.18)}=3.86$,

$\eta_p^2=0.097$, $p=0.003$]. Visual inspection suggested that the differences among the three groups were largest during the early blocks of the Day 2 training phase and were smallest during the later training blocks.

Although the group main effect on RT for the learned transitions indicated only a trend for a significant difference ($F_{(2,52)}=2.72$, $\eta_p^2=0.095$, $p=0.075$), there was a significant difference in accuracy ($F_{(2,52)}=3.20$, $\eta_p^2=0.109$, $p=0.049$). Follow-up comparisons revealed that the Incompatible group had significantly worse accuracy than Same ($F_{(1,33)}=6.13$, $\eta_p^2=0.157$, $p=0.019$) but was not statistically different from Compatible ($F_{(1,36)}=1.80$, $\eta_p^2=0.048$, $p=0.19$).

Failure to fully integrate new motor information even after extensive practice within an incompatible task representation

To investigate the level of performance on all, the 4 novel as well as the 4 learned transitions after extensive practice on Day 2, performance during the post-training test was analyzed (Figures 2 and 3, test session). Interestingly, there was a trend for a significant group difference with respect to movement accuracy (i.e., % Correct) during the test phase for all transitions ($F_{(3,70)}=2.73$, $\eta_p^2=0.104$, $p=0.051$) and shared novel transitions ($F_{(2,54)}=2.78$, $\eta_p^2=0.093$, $p=0.071$) and a significant group effect for the shared learned transitions ($F_{(2,52)}=3.82$, $\eta_p^2=0.128$, $p=0.028$). This group difference was attributed to the higher accuracy in the Same group relative to both Incompatible ($F_{(1,33)}=7.19$, $\eta_p^2=0.179$, $p=0.011$) and Compatible ($F_{(1,35)}=5.95$, $\eta_p^2=0.145$, $p=0.020$).

With respect to RT, the group differences observed during training on Day 2 tended to decrease after practice, as there were no group effects during the post-training test on all transitions ($F_{(3,70)}=1.34$, $\eta_p^2=0.054$, $p=0.27$; Figure 2B), shared novel transitions ($F_{(2,54)}=0.94$, $\eta_p^2=0.033$, $p=0.40$; Figure 3B) or shared learned transitions ($F_{(2,52)}=0.58$, $\eta_p^2=0.022$, $p=0.56$; Figure 3B). However, and critically, a comparison between the shared novel and learned transitions between the Compatible and Incompatible groups during the test session revealed a significant transition-type by group interaction (RT:

$F_{(1,36)}=5.11$, $\eta_p^2=0.124$, $p=0.030$; Figure 3C). Follow-up comparisons indicated that performance was similar during the test session for the learned and novel transitions in the Compatible group ($F_{(1,19)}=0.03$, $\eta_p^2=0.002$, $p=0.86$), suggesting optimal integration of the novel elements to the level of previously learned information. In contrast, performance on novel transitions in the Incompatible group remained significantly worse than on the learned transitions ($F_{(1,17)}=12.66$, $\eta_p^2=0.423$, $p=0.002$), indicating that the capacity to integrate novel motor information into an incompatible, ordinal-based memory representation remains severely hindered even after extensive practice.

Explicit Awareness

At the end of each session, the explicit awareness of the sequence was assessed with a generation task. The percentage of correct transitions as well as the percentage of correct ordinal positions generated did not differ among the 4 groups (Day 1 transitions: $F_{(3,70)}=0.28$, $\eta_p^2=0.012$, $p=0.84$; Day 1 ordinal: $F_{(3,70)}=0.11$, $\eta_p^2=0.005$, $p=0.95$; Day 2 transitions: $F_{(3,69)}=0.39$, $\eta_p^2=0.017$, $p=0.76$; Day 2 ordinal: $F_{(3,69)}=0.65$, $\eta_p^2=0.028$, $p=0.58$). It is worth noting that the awareness scores were higher on Day 2 as compared to Day 1 (across all experimental groups). This observation can likely be attributed to the participants' being more familiar with the experimental protocol and thus perhaps expecting an assessment of sequence awareness at the end of the session, which could have boosted Day 2 awareness scores. Regardless, these results collectively indicate similar level of sequence awareness among the groups, suggesting that the pattern of results observed above cannot be explained by differences in explicit knowledge of the sequential material. This statement is of course limited to the time point in which sequence awareness was assessed; perhaps awareness probes administered in the middle of the training sessions (when performance differences were larger) would have revealed different results.

Table 2. Experiment 1 generation task.

		Experimental groups				
		Same	New	Compatible	Incompatible	Compatible Control
% correct transitions	Day 1	55.75 ± 38.34	54.23 ± 35.72	63.91 ± 36.52	59.90 ± 31.34	58.82 ± 34.10
	Day 2	83.63 ± 29.11	81.52 ± 26.26	71.36 ± 35.76	73.40 ± 30.85	77.49 ± 28.81
% correct ordinal positions	Day 1	48.04 ± 40.45	49.56 ± 35.52	53.33 ± 43.21	46.06 ± 39.62	40.93 ± 38.39
	Day 2	79.17 ± 35.81	73.96 ± 37.50	60.05 ± 40.88	65.69 ± 35.65	59.07 ± 40.78

Group means ± SD for the generation task performed at the end of Day 1 and Day 2 sessions for Experiments 1a and 1b. [Data from Compatible Control in Experiment 1b are included here as this group was compared to Incompatible from Experiment 1a]. As expected on Day 1, the percentage of correct transitions as well as the percentage of correct ordinal positions generated did not differ among the 4 groups from Experiment 1a. Similarly, on Day 2, no group difference was observed on these 2 measures. Altogether, the generation results suggest similar level of sequence awareness among the groups.

Experiment 1b

It could be argued that the enhanced integration observed in the Compatible group in Experiment 1a may not necessarily be the result of the compatibility of the ordinal structure of the full 8-element sequence, but rather to the identical starting elements of the sequences across the two testing days (i.e., 4-7). An additional experimental group (Compatible Control; see Figure 1) was then included and compared to the Incompatible group from Experiment 1a to test for this possibility. Critically, Compatible Control still completed the same movement transitions on Day 2 as Incompatible and with the same high ordinal compatibility as Compatible; but, the initial elements of the Day 2 sequence in the Compatible Control group differed from the initial elements of the sequence learned on Day 1. If the enhanced integration in the Compatible group observed in Experiment 1a was attributed to the ordinal structure of the *entire* 8-element sequence (and not to the same starting elements across the two testing days), then one would expect to replicate this enhanced integration in the Compatible Control group. It should be noted that our statistical analyses compared Incompatible

from Experiment 1a to Compatible Control; however, for comparison purposes, the corresponding figures depict Incompatible, Compatible Control and Compatible.

Results from Session 1 (Figure S1) indicated that the Incompatible and Compatible Control groups did not differ in performance (RT: $F_{(1,33)}=1.19$, $\eta_p^2=0.035$, $p=0.28$; % Correct: $F_{(1,33)}=0.77$, $\eta_p^2=0.023$, $p=0.39$) or change in performance across blocks during the training run (RT: $F_{(4.33,142.79)}=1.25$, $\eta_p^2=0.036$, $p=0.29$; % Correct: $F_{(19,627)}=1.31$, $\eta_p^2=0.038$, $p=0.17$). The groups also performed comparably in the Session 1 post-training test (RT group main effect: $F_{(1,33)}=0.39$, $\eta_p^2=0.012$, $p=0.54$; RT group x block interaction: $F_{(3,99)}=1.59$, $\eta_p^2=0.047$, $p=0.20$; % Correct group main effect: $F_{(1,33)}=1.98$, $\eta_p^2=0.057$, $p=0.17$; % Correct group x block interaction: $F_{(3,99)}=1.27$, $\eta_p^2=0.037$, $p=0.29$). These results indicate equivalent performance during the initial training session (i.e., prior to the experimental manipulation), a critical result given that the Compatible Control group was exposed to a different ordinal framework in Session 1 relative to Incompatible.

Analyses of overall (i.e., all transitions) performance during the Day 2 training session revealed that Compatible Control was significantly faster compared to Incompatible (Figure S1; RT: $F_{(1,33)}=8.97$, $\eta_p^2=0.214$, $p=0.005$; % Correct: $F_{(1,33)}=0.11$, $\eta_p^2=0.003$, $p=0.74$). The rate of change in RT across blocks also differed between these two groups (RT: $F_{(4.76,157.05)}=3.78$, $\eta_p^2=0.103$, $p=0.003$; % Correct: $F_{(19,627)}=1.54$, $\eta_p^2=0.045$, $p=0.065$), as group differences in RT were largest during the early training blocks.

Critically, Compatible Control was significantly faster than Incompatible on both novel and learned transitions during Session 2 training (Figure 4; RT Novel: $F_{(1,33)}=4.18$, $\eta_p^2=0.112$, $p=0.049$; RT Learned: $F_{(1,33)}=14.81$, $\eta_p^2=0.310$, $p<0.001$; % Correct Novel: $F_{(1,33)}=0.09$, $\eta_p^2=0.003$, $p=0.77$; % Correct Learned: $F_{(1,33)}=0.00$, $\eta_p^2<0.001$, $p=0.95$). The rate of change of RT across blocks also significantly differed between Compatible Control and Incompatible for both novel and learned transitions, as the group differences were largest during the early training blocks and decreased as a

function of practice (RT Novel: $F_{(6.31,208.39)}=3.26$, $\eta_p^2=0.090$, $p=0.004$; RT Learned: $F_{(4.65,153.55)}=3.31$, $\eta_p^2=0.091$, $p=0.009$; % Correct Novel: $F_{(19,627)}=1.31$, $\eta_p^2=0.038$, $p=0.17$; % Correct Learned: $F_{(19,627)}=1.70$, $\eta_p^2=0.049$, $p=0.032$). The latter result is consistent with the lack of group differences during the Session 2 test phase (RT Novel: $F_{(1,33)}=0.40$, $\eta_p^2=0.012$, $p=0.53$; RT Learned: $F_{(1,33)}=2.59$, $\eta_p^2=0.073$, $p=0.12$; % Correct Novel: $F_{(1,33)}=0.39$, $\eta_p^2=0.012$, $p=0.54$; % Correct Learned: $F_{(1,33)}=0.60$, $\eta_p^2=0.018$, $p=0.45$).

The results of this control experiment replicate the primary findings from Experiment 1a and collectively demonstrate that the enhanced integration of novel motor elements into memory was not attributed specifically to the consolidation of the starting elements of the sequence. Instead, results show that enhanced integration is attributed to the compatibility of the ordinal structure of the entire 8-element sequence. It is worth noting that the Compatible and Incompatible groups in Experiment 1a differed with respect to both movement speed and accuracy for the novel transitions during the Day 2 training phase (Figure 3B), whereas Compatible Control as part of Experiment 1b was different from Incompatible with respect to speed only (Figure 4B).

Figure 4: Shared novel and learned transitions in Experiments 1a and 1b. Mean response time (top row) and percentage of correct transitions (bottom row) on Day 2 are shown in (a) as a function of the 20 practice blocks during training and 4 post-training test blocks. Results are shown separately for novel (left) and learned (right) transitions shared between the Compatible Control group in Experiment 1b and the Compatible and Incompatible groups in Experiment 1a. Shaded regions represent standard errors of the mean. Group averages (collapsed across blocks) during training (Tr) and test (Te) sessions in Day 2 are depicted in (b). Error bars represent standard errors of the mean and brackets denote significant group differences ($p < .05$).

Explicit Awareness

The percentage of correct transitions as well as the percentage of correct ordinal positions generated

did not differ between the Compatible Control and Incompatible groups (see Table 3; Session 1

transitions: $F_{(1,33)}=0.01$, $\eta_p^2<0.001$, $p=0.92$; Session 1 ordinal: $F_{(1,33)}=0.15$, $\eta_p^2=0.005$, $p=0.70$; Session

2 transitions: $F_{(1,33)}=0.08$, $\eta_p^2=0.002$, $p=0.78$; Session 2 ordinal: $F_{(1,33)}=0.42$, $\eta_p^2=0.012$, $p=0.52$). These

results indicate that the enhanced integration in the Compatible Control group (relative to Incompatible) cannot be explained by differences in explicit knowledge of the sequential material assessed at the end of the practice sessions.

Experiment 2

Experiment 2 tested whether the effects observed in Experiment 1a were dependent on the acquired motor memory trace (i.e., schema) having the opportunity to consolidate overnight. To address this question, integration/retention processes were assessed for the Incompatible and Compatible groups **immediately** (*Imm*; i.e., 15 minutes) after the initial training session rather than after a 24-hour consolidation interval.

Results from Session 1 (Figure S2) indicated that the two *Immediate* groups improved performance as a function of task practice (RT: $F_{(6.38,223.26)}=57.29$, $\eta_p^2=0.620$, $p<0.001$; % Correct: $F_{(19,665)}=3.77$, $\eta_p^2=0.097$, $p<0.001$), but did not differ in overall performance (RT: $F_{(1,35)}=0.06$, $\eta_p^2=0.002$, $p=0.81$; % Correct: $F_{(1,35)}=0.84$, $\eta_p^2=0.023$, $p=0.37$) or change in performance across blocks (RT: $F_{(6.38,223.26)}=1.16$, $\eta_p^2=0.032$, $p=0.33$; % Correct: $F_{(19,665)}=0.61$, $\eta_p^2=0.017$, $p=0.90$). The Immediate Compatible and Immediate Incompatible groups also performed comparably in the Session 1 post-training test (RT group main effect: $F_{(1,35)}=0.57$, $\eta_p^2=0.016$, $p=0.45$; RT group x block interaction: $F_{(3,105)}=0.19$, $\eta_p^2=0.005$, $p=0.90$; % Correct group main effect: $F_{(1,35)}=0.80$, $\eta_p^2=0.022$, $p=0.38$; % Correct group x block interaction: $F_{(2.46,86.02)}=0.06$, $\eta_p^2=0.002$, $p=0.97$). These results collectively indicate equivalent performance in the two Immediate groups during the initial training session (i.e., prior to the experimental manipulation).

In contrast to Experiment 1a, the two groups of Experiment 2 did not differ on overall (i.e., all transitions) performance tested during Session 2 which took place immediately after initial training (Figure S2; RT: $F_{(1,35)}=0.64$, $\eta_p^2=0.018$, $p=0.43$; % Correct: $F_{(1,35)}=0.13$, $\eta_p^2=0.004$, $p=0.72$).

Importantly, integration processes also did not differ between the 2 Immediate groups, as no group effect was observed on performance of the 4 shared novel transitions (RT: $F_{(1,35)}=0.23$, $\eta_p^2=0.007$, $p=0.64$; % Correct: $F_{(1,35)}=0.13$, $\eta_p^2=0.004$, $p=0.72$; Figure 5A-B). These results indicate that the ordinal context did not influence the integration of new motor information if the ordinal-based framework acquired during the initial training session did not have the opportunity to consolidate overnight.

It is important to note that the findings of Experiment 2 also rule out, albeit indirectly, that the integration results of Experiment 1a can be attributed to the degree of similarity between sequences on the two testing days. Specifically, the Compatible group presents higher similarity between sequences, as only 2 elements were interchanged from Day 1 to Day 2. Conversely, similarity was lower between sequences in the Incompatible group, as 2 elements were exchanged *and* the sequences started at a different starting point). If these differences in similarity were the driving force behind the results from Experiment 1a, a similar pattern would have been expected for Experiment 2, which was not the case.

Figure 5: Shared novel and learned transitions in Experiment 2. Mean response time (top row) and percentage of correct transitions (bottom row) during Day 2 are shown in (a) as a function of the 20 practice blocks during training and the 4 post-training test blocks. Results are shown separately for novel (left) and learned (right) transitions shared between the Immediate Compatible and Immediate Incompatible groups. Shaded regions represent standard errors of the mean. Group averages (collapsed across blocks) during training (Tr) and test (Te) sessions in Day 2 are shown in (b). Error bars represent standard errors of the mean.

Analyses of the 4 shared learned transitions in Experiment 2 also demonstrated no significant group effect (RT: $F_{(1,35)}=1.23$, $\eta_p^2=0.034$, $p=0.28$; % Correct: $F_{(1,35)}=0.007$, $\eta_p^2<0.01$, $p=0.93$; Figure 5A-B), but a significant block by group interaction, as group differences in RT were largest at the beginning of the Session 2 training session and decreased thereafter ($F_{(7.26,253.99)}=6.01$, $\eta_p^2=0.146$, $p<0.001$). Interestingly, the pattern of results observed on the learned transitions in Experiment 2 was

similar to Experiment 1a. These findings indicate that, unlike the effects reported on the integration of novel motor information, the effect observed on the retention of previously acquired elements in Experiment 1a can be explained by the dissimilarity between sequences across the two testing sessions, irrespective of whether or not the acquired memory trace was consolidated.

Last, we assessed performance on the 4 shared novel and learned transitions in the two Experiment 2 groups after extensive practice, (i.e. during the Session 2 post-training test). Consistent with the data from the training phase, results revealed no differences between groups (RT Novel: $F_{(1,34)}=0.35$, $\eta_p^2=0.010$, $p=0.56$; % Correct Novel: $F_{(1,34)}=0.11$, $\eta_p^2=0.003$, $p=0.74$; RT Learned: $F_{(1,34)}=0.30$, $\eta_p^2=0.009$, $p=0.59$; % Correct Learned: $F_{(1,34)}=2.63$, $\eta_p^2=0.072$, $p=0.11$).

Results from Experiment 2 collectively indicate that optimal integration of new motor information only takes place when this information is consistent with a *consolidated* representation of the motor sequence.

Explicit Awareness

The percentage of correct transitions as well as the percentage of correct ordinal positions generated did not differ between the 2 control groups (see Table 3; Session 1 transitions: $t_{(1,35)}=0.62$, $\eta_p^2=0.017$, $p=0.43$; Session 1 ordinal: $t_{(1,35)}=0.04$, $\eta_p^2=0.001$, $p=0.83$; Session 2 transitions: $t_{(1,35)}=0.02$, $\eta_p^2=0.001$, $p=0.86$; Session 2 ordinal: $t_{(1,35)}=1.18$, $\eta_p^2=0.03$, $p=0.28$).

Table 3. Experiment 2 generation task.

		Experimental Groups	
		Immediate Compatible	Immediate Incompatible
% correct transitions	S1	73.68 ± 28.49	80.19 ± 21.58
	S2	90.62 ± 20.76	89.61 ± 14.35
% correct ordinal positions	S1	59.43 ± 40.89	62.27 ± 42.90
	S2	80.04 ± 33.83	66.67 ± 41.11

Group means $\pm$ SD for the generation task performed at the end of sessions 1 and 2 2 (S1 and S2) for the two control groups. There were no differences in sequences awareness in sessions 1 or 2.

Discussion

Our results indicate that performance on new motor sequence elements was better when this novel motor information was presented in a framework consistent with previous task experience. Practice within an incompatible framework resulted in poorer integration, a deficit that was not alleviated by extended practice. The framework in which new motor elements were integrated consisted of the associative map that binds motor events to their ordinal positions in the acquired movement sequence. Importantly, the integration advantage was (i) not related to explicit awareness of the sequence assessed at the end of training; (ii) only observed when the ordinal-based sequence representation was consolidated overnight and (iii) due to the abstraction of the ordinal structure of the entire sequence.

These results are remarkably consistent with the schema model of memory consolidation. If an associative schema (e.g., flavor/location map in Tse et al., 2011; Tse et al., 2007) is acquired, consolidated and activated during a subsequent learning episode, encoding of new information is facilitated if compatible with the pre-existing schema. Our results suggest that the associative map between motor events and their ordinal positions acquired during training and consolidated overnight serves as a cognitive-motor schema within which new motor elements are rapidly integrated. The learning of the ordinal representation of motor sequences is described as a goal-oriented process during which a motor event is linked to a spatio-temporal context (Song & Cohen, 2014). This binding between elements and their spatial (Tse et al., 2011; Tse et al., 2007) or temporal contexts (Hsieh et al., 2014) has been described, in the declarative memory domain, to be supported by the hippocampus. We suggest that the *development* of an ordinal-based cognitive-motor schema is supported by hippocampo-

cortical networks. Based on animal (Tse et al., 2011; Tse et al., 2007) and more recent human neuroimaging studies (Hennies et al., 2016; Sommer, 2017) demonstrating that schema-mediated *integration* is supported by a rapid neocortical process that is less dependent on the hippocampus, it can be speculated that the fast integration of new motor elements into a pre-existing schema (i.e., in the Compatible group) bypasses the hippocampus and recruits predominantly cortical (frontal and/or parietal) areas. This explanation, however, remains to be tested.

Previous research has shown that the ordinal representation of motor sequences is specifically consolidated over intervals including sleep (Song & Cohen, 2014). Sleep is also known to contribute to the building of cognitive schemata and memory integration processes (e.g., Lewis & Durrant, 2011). While our design cannot address the specific effect of sleep on this process, our data show enhanced integration after 24 hours including sleep but not after 15 minutes of wakefulness. Moreover, previous research has demonstrated a preferential role of sleep in the consolidation of goal-oriented (abstract) – and not motor-oriented (movement) - representations of motor sequences (Albouy et al., 2015; Albouy, Fogel, et al., 2013). Such abstract motor sequence representations are supported by hippocampo-cortical networks (Albouy et al., 2015), again providing a link among abstract/ordinal representations, hippocampal activity and sleep-related processes.

Although previous research has demonstrated that post-learning sleep specifically favors the consolidation of an ordinal representation of motor sequences (Song & Cohen, 2014), this earlier work did not investigate the integration of novel motor information into a previously-acquired memory, which is the defining feature of the schema model of memory consolidation. Moreover, while our results are generally consistent with Song and Cohen (2014), integration processes observed in the current study cannot be explained solely by an overnight, ordinal-based performance enhancement. First, our results show that the ordinal context specifically influenced integration of new - but not retention of learned - information, effectively ruling out a general, ordinal-based performance

enhancement. Second, analyses excluding the sequence elements presented in the same ordinal positions across sessions (i.e., elements 5 and 8 in the Compatible group) showed an identical pattern of integration. This indicates that enhanced performance on the novel transitions within a compatible schema can be attributed to better integration of new motor information rather than to enhanced consolidation of the ordinal positions learned in the first session.

Our design also provided the opportunity to investigate whether the availability of a cognitive-motor schema influenced performance on previously learned information. Results demonstrated no deficit in retention of previously learned movements when practice took place within a compatible schema (i.e., similar performance on learned transitions in the Compatible and Same groups), indicating that new motor information can be incorporated into pre-existing memory without any cost to the consolidated memory trace of the learned material. This is consistent with recent results showing that newly acquired and older motor memories can coexist (Szegedi-Hallgató et al., 2017). Conversely, our results showed that practicing the task in an *incompatible* schema transiently disrupted performance on previously learned transitions. This interference, however, was also observed in Experiment 2 when the retest session occurred 15 minutes following initial training. Thus, this transient interference appears to be related to the dissimilarity between the different movement sequences across testing days as opposed to a failure to activate a consolidated cognitive-motor schema.

Our results can be conceptualized as a particular form of transfer or generalization. Previous research has extensively investigated transfer in the motor sequence domain (e.g., between sequences, limbs, tasks and keyboard set-ups; Albouy et al., 2015; Brown & Robertson, 2007; Genzel et al., 2012; Korman et al., 2003). As our research specifically probed the integration of new motor information into previously acquired memory, we argue that our data better reflect memory updating or modification processes as opposed to simple transfer. Moreover, the results from Experiment 2 showed that better performance in the Compatible group was not attributed to simple transfer based on sequence similarity

across the two testing sessions, but was only observed if the acquired cognitive-motor schema was consolidated overnight. Our results can nonetheless be discussed within a recently proposed framework on the generalizability of acquired memories (Robertson, 2018). It was suggested that two criteria must be met for an acquired memory to generalize to a novel context/task: the tasks must share an abstract structure and the previously acquired memory must be in an unstable state. Our results suggest that in the motor sequence domain, the abstract structure formed as a result of previous experience/knowledge that facilitates generalization consists of the associative map binding motor events to their ordinal positions. Based on memory reactivation theories (e.g., Lee, Nader, & Schiller, 2017), it could be speculated that reactivation of the ordinal representation in the Compatible group returned the acquired memory trace to a labile form and this favored generalization. This explanation, however, remains to be tested.

It should be emphasized that this is not the first research to incorporate the concept of schema in the motor domain. Notably, Schmidt's schema theory (1975) focused on how discrete motor skills are learned via task practice. However, and as previously highlighted (Müller et al., 2016), it does not address how these skills are consolidated into memory, and more specifically, how new movements can be rapidly integrated into pre-existing schema, therefore bypassing the standard memory consolidation process. Moreover, the majority of experimental evidence in support of Schmidt's theory is based on studies demonstrating that variable – as opposed to constant – task practice facilitates retention and transfer. This evidence has been questioned (e.g., van Rossum, 1990) and many, but certainly not all, of these previous studies were confounded by other relevant variables (e.g., practice order; (Sherwood & Lee, 2003)).

Conclusions

Our results demonstrate that new motor sequence information can be rapidly integrated (i.e., learned) within a compatible and previously-acquired memory trace. Novel information that is

incompatible with consolidated memories results in worse integration. These findings suggest that motor learning and consolidation processes can be accelerated through the availability of a pre-existing memory within which new information can be rapidly integrated. These results are consistent with the schema model of memory consolidation and provide experimental evidence of this model in the motor sequence domain. This adds to the growing body of literature demonstrating that models of memory consolidation are consistent across memory systems, and thus continues to challenge the historical dichotomist view of memory organization according to which declarative and motor memories are supported by distinct brain networks and physiological processes.

Author Contributions:

BRK and GA designed the research. BRK, ND, MAG, ZR and GA performed the research. BRK and GA contributed analytic tools. BRK, ZR and GA analyzed the data. BRK, ND, MAG, ZR, SS and GA wrote the paper.

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Conflicts of Interest

The authors report no conflicts of interest.

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Figure S1.

Figure S1: Response time (top) and percentage of correct transitions (bottom) computed across all transitions are plotted for the Compatible Control group (magenta) as part of Experiment 1b as well as the Compatible (blue) and Incompatible (green) groups from Experiment 1a. Shaded regions represent standard error of the mean. There were no group differences in Session 1 Training or Test phases (see main text for statistics), indicating comparable performance prior to the experimental manipulation. The Compatible Control group was significantly faster than the Incompatible group during Session 2 Training (RT: $F_{(1,33)}=8.97$, $\eta_p^2=0.214$, $p=0.005$; % Correct: $F_{(1,33)}=0.11$, $\eta_p^2=0.003$, $p=0.74$), replicating the results from Experiment 1a and demonstrating that the ordinal compatibility of the complete (8-element) sequences across the two testing days – and not the similarity of the beginning elements of the sequences only – influences motor performance. Figure 4 in the main text depicts RT and percentage correct separately for the shared novel and learned transitions in Session 2.

Figure S2.

Figure S2: Response time (top) and percentage of correct transitions (bottom) computed across all transitions are plotted for Immediate Incompatible (green) and Immediate Compatible (blue) groups from Experiment 2. Shaded regions represent standard error of the mean. There were no group differences in Session 1 Training or Test phases (see main text for statistics), indicating comparable performance prior to the experimental manipulation. In contrast to Experiment 1a, there were no group differences in Session 2 training phase (RT: $F_{(1,35)}=0.64$, $\eta_p^2=0.018$, $p=0.43$; % Correct: $F_{(1,35)}=0.13$, $\eta_p^2=0.004$, $p=0.72$), demonstrating the ordinal compatibility of the sequences across the two testing days fails to influence motor performance if the memory trace acquired on Day 1 does not have the opportunity to consolidate overnight. See Figure 5 in the main text for depiction of the shared novel and learned transitions in Session 2.