

217 Recent studies have shown that frontoparietal cortices and interconnecting regions in the basal ganglia and the cerebellum are related to motor skill learning. We propose that motor skill learning occurs independently and in different coordinates in two sets of loop circuits: cortex–basal ganglia and cortex–cerebellum. This architecture accounts for the seemingly diverse features of motor learning. Addresses *Laboratory of Sensorimotor Research, National Eye Institute, National Institute of Health, Building 49, Room 2A50, Bethesda, Maryland 20892, USA; e-mail: oh@lsl.nei.nih.gov †Center for the Neural Basis of Cognition, 115 Mellon Institute, 4400 Fifth Avenue, Pittsburgh, Pennsylvania 15213-2683, USA; e-mail: kae@cnbc.cmu.edu ‡Wellcome Department of Cognitive Neurology, Institute of Neurology, 12 Queens Square, London WC1N 3BG, UK; e-mail: ksakai@fil.ion.ucl.ac.uk §Laboratory for Mathematical Neuroscience, RIKEN Brain Science Institute, 2-1 Hirosawa, Wako, Saitama, 351-0198, Japan; e-mail: hiro@brain.riken.go.jp

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Abbreviations BG basal ganglia CB cerebellum DA dopamine M1 primary motor cortex preSMA presupplementary motor area SEF supplementary eye field SMA supplementary motor area

Introduction Neuroscience has evolved from the study of simple behaviors to examinations of complex behaviors. In particular, we are beginning to learn more about complex motor behaviors. We are usually unaware of how intricately our tongue moves during conversation and how elaborate our finger movements are during typing. Such awesome but implicit complexities had discouraged scientific approaches to skilled behaviors until recently. A major breakthrough occurred when human imaging studies were developed. Recent imaging studies have addressed complex motor learning in human subjects. Their remarkable results have promoted neural theories of motor learning and have also renewed interest in studies of motor control on animal subjects. In this review, we integrate diverse data obtained recently on the motor control of complex behaviors and provide a common ground for researchers working on motor skill learning. Due to space limitations, we leave out several important topics in motor learning, including visuomotor associations, sensorimotor adaptations, cellular mechanisms of neural plasticity, and motor learning in birds. Multiple neural mechanisms for motor skill learning A complex motor skill is often composed of a fixed sequence of movements [1,2]. It has been suggested that the supplementary motor area (SMA) plays an important role in sequential movements [3]. By training monkeys to perform different movements in specific orders, Shima and Tanji [4•] found that many neurons in the SMA become active specifically at particular transitions, not in response to particular movements. Neurons in the presupplementary motor area (preSMA), a cortical area anterior to the SMA, may be active specifically at certain rank orders in a sequence. On the basis of these results, Tanji proposed that the SMA and the preSMA work together to produce sequential movements correctly [5••]. How are such motor sequences acquired in the brain? To address this question, Hikosaka et al. [6] devised a sequential button press task, called the 2×5 task, in which the subject (either monkey or human) learned to press buttons in the correct order, by trial and error. This task enables the testing of an infinite number of different sequences and the effect of well-learned motor skills simultaneously on the same subject. Using this task, Nakamura et al. showed that the preSMA, rather than the SMA, is crucial for learning new sequences. Many neurons in the preSMA were activated during learning of new sequences, but not during the performance of learned sequences [7]. Furthermore, functional blockade of the preSMA led to selective deficits in learning new sequences [8]. The anterior cingulate cortex, ventral to the preSMA, may also contribute new sequence learning [9•]. As well as higher premotor areas, the primary motor cortex (M1) has been implicated in motor learning. Functional [10•,11•] and structural [12] changes occur in M1 during simple motor learning. Consistent with these observations, functional neuroimaging studies on human subjects

revealed that motor skill learning is associated with activation of many brain areas in the frontoparietal cortices. Researchers have begun asking how these areas contribute to motor learning. By applying the 2×5 task to human subjects (in a 2×10 version), Sakai et al. [13] demonstrated learning-related transition of activation from frontal to parietal areas. By using functional magnetic resonance imaging, they showed that the dorsolateral prefrontal cortex and the preSMA were activated during early stages of learning, whereas more parietal areas — the intraparietal sulcus and the precuneus — were activated at later stages. Toni et al. [14] and Petersen et al. [15] also reported dynamic changes in human cortical activation during motor learning. Furthermore, a change in motor Central mechanisms of motor skill learning

Okihide Hikosaka*, Kae Nakamura†, Katsuyuki Sakai‡, Hiroyuki Nakahara§ effector (finger versus arm) affects activation of sensorimotor cortex, but not parietal cortex [16]. Awareness of performance — explicit learning — is correlated with activation of the prefrontal cortex and preSMA, but not sensorimotor cortex [17]. Related behavioral studies also suggest that different brain areas control different aspects of motor learning. With practice, accuracy of performance was acquired earlier than speed of performance [6]. Accuracy was effector-unspecific, in the early learning stage, whereas the speed was 218 Cognitive neuroscience

Figure 1 Motor cortex BG Motor CB Associative CB Motor Motor output Sensory input
 Reward error [34] Novelty [35] Sensorimotor error [36] Timing [38•] SMA preSMA
 Premotor cortex Spatial sequence Motor sequence Coordinates: spatial (kinematic) motor (dynamic) [21, 52, 54••] Transfer: effector-unspecific effector-specific [16, 18, 19•, 20•, 52, 54••] Awareness: explicit (conscious) implicit (unconscious) [2, 17] Attention: high low [2] Learning: fast slow [52, 54••] Performance: accuracy speed [65] Current Opinion in Neurobiology Memory: short long [6, 59] Prefrontal parietal cortex BG Associative Scheme of motor skill learning. We propose that motor skill learning operates as the interaction of two orthogonal connections: intracortical serial connections (horizontal arrows) and cortico–BG/cortico–CB loop circuits (vertical arrows). A sequence of movements is represented in two ways — spatial sequence and motor sequence. The left side of the figure is characteristic of the spatial sequence, the right side is characteristic of the motor sequence. The frontoparietal cortices form loop circuits with the associative region of the BG and CB, whereas the motor cortices form loop circuits with the motor region of the BG and CB. At the beginning of learning, movements are executed individually through the spatiomotor conversion process (horizontal connections). After learning, the movement sequence is represented by at least two networks in different coordinates: a spatial sequence supported by the parietal–prefrontal cortical loops and a motor sequence supported by the motor cortical loops (vertical connections). Spatial sequences are effector-unspecific (unless coding of space is effector-centered), are usually processed explicitly and therefore quickly acquired (as they may be accompanied by spatial attention or working memory), but require maximum attention. Motor sequences are effector-specific (as different effectors may perform different sequences), are usually processed implicitly and therefore slowly acquired, but require minimum attention. Performance on the basis of the spatial sequence mechanism is accurate in space but slow (as its output must be converted to motor coordinates). Performance on the basis of the motor sequence mechanism is quick. Long-term retention of a motor skill is supported mainly by the motor sequence mechanism so that its speed is maintained even without awareness. Signals from the frontoparietal cortices and the motor cortices are sent to different functional divisions of the BG and CB (vertical arrows). In the BG, the signals are evaluated for their reward or likelihood values; in the CB, they are evaluated for their sensorimotor or timing errors (gray lines). Hence, the performance of the spatial and motor sequence mechanisms can be optimized independently. Note that the scheme may fail to account for the following kinds or aspects of motor learning. First, non-sequential motor skills: sequencing may not be important for some motor skills such as adaptation in a force

field [59] and arbitrary visuomotor associations [60]. Second, non-spatial sequences: learning can occur for a sequence of objects or colors, for which the preSMA [61], but not the dorsolateral prefrontal cortex [62], is recruited. Third, abstract rules: learning can transfer to another sequence that shares the same global structure, not elements [63,64]. Fourth, temporal sequences: timing errors may be encoded in the cerebellar posterior lobe [38•], an important area for future research. effector-specific [18,19•,20•]. Learning occurred independently for the kinematics — the spatial reference — of movements and for the dynamics — the load bearing — of movements [21]. The motor skill, once established, was maintained for a long time, mainly in the form of speed [6]. For a more extensive review on behavioral studies of motor skill learning, the reader is referred to Willingham [2], in which important concepts are described. These results suggest that motor skill learning may be the integrative product of multiple neural mechanisms, each contributing to a different aspect of learning. How, then, do different neural mechanisms interact with each other to acquire and store motor skills efficiently? The basal ganglia and the cerebellum may play crucial roles. Learning is optimized by the basal ganglia and the cerebellum In addition to human functional imaging studies [22,23], several lines of evidence suggest that both the basal ganglia (BG) and the cerebellum (CB) are involved in motor sequence learning. Several studies implicate the BG. Activity of monkey caudate neurons is related to spatial sequence [24]. Dopamine depletion disrupts skilful performance of sequential movements [25]. Population activity of striatal neurons changes with long-term motor learning [26]. Reversible blockade of the anterior striatum (associative region) leads to deficits in learning new sequences, and blockade of the posterior striatum (motor region) leads to disruptions in the execution of learned sequences [27]. The CB also seems necessary for motor skill learning. Cerebellar blockade disrupts learning of complex goaldirected behaviors [28]. Cerebellar lesions impair motor sequence learning, but not conditional visuomotor learning or spatial working memory [29]. In contrast, blockade of the dorsal part of the dentate nucleus (which is connected with M1) does not affect learning new sequences, but disrupts the performance of learned sequences [30]. Long-term memories for motor skills may be stored in the CB [31•]. The conclusions of these studies seem inconsistent but may reflect anatomical and functional differentiation in the CB between motor and associative regions [32•]. What then is unique about the BG or the CB, compared with the cerebral cortex? Doya [33••] proposed that learning in the BG and the CB is guided by error signals, unlike in the cerebral cortex. This error signal may be mediated by midbrain dopamine (DA) neurons in the BG and by climbing fibers in the CB. DA neurons encode reward expectation error [34] and/or novelty [35], whereas climbing fibers encode sensorimotor error signals [36], which possibly include a timing error [37•,38•] (Figure 1). In the BG, cortical signals are integrated with reward error signals carried by DA neurons in striatal projection neurons: visual and memory responses of caudate neurons were strongly modulated by reward expectation [39]. In the CB, cortical signals and sensorimotor error signals carried by the climbing fibers are integrated in Purkinje cells [40]. These signals would, at least partly, be relayed back to the cerebral cortex. Thus, signals originating from the cerebral cortex are optimized in terms of their reward value and sensorimotor accuracy, by going through the BG and cerebellar loop circuits, respectively. This feedback is likely to be a critical process for motor skill learning.

Rules, concepts, and models for motor learning Having reviewed the literature on motor skill learning, we are struck by the diversity of brain structures and mechanisms that are supposedly responsible for motor skill learning. To understand the nature and mechanisms of motor skill learning, it is necessary to integrate such diversity of information into schemes or models [2,33••,41–45]. To make such attempts realistic, the concepts of coordinate transformation and loop circuits must be incorporated. For simple reaching to a visual target, for example, the target position is first coded in spatial coordinates — for example, centered

around the eye, head or object — and then converted to motor coordinates — for example, joint angles or muscle forces. This coordinate transformation process may roughly correspond to the intracortical connections from the association cortices to the motor cortices [46•,47,48•] (horizontal connections in Figure 1). The frontoparietal cortices and the motor cortices form loop circuits with different regions in the BG and the CB (vertical connections in Figure 1) [49,50•,51]. The scheme shown in Figure 1 was derived from the above considerations [52,53]. According to this model, a motor sequence is learned by two sets of cortex–BG and cortex–CB loop circuits independently, but in different coordinates — spatial and motor. The scheme successfully accounts for various lines of experimental observations, including coordinate transformation, hand transfer, awareness, and attentional cost. Nakahara et al. [54•] elaborated this scheme by formulating a neural network model and successfully replicated various experimental results of the 2'5 task in a unified manner. One problem foreseen with this neural network was that the spatial and motor mechanisms might produce different results because they work independently. Such ‘between network error’, which is inherent to any parallel network model, was solved in this model by a kind of conflict monitor, corresponding to the preSMA. The proposed architecture turned out to be robust. Even if one of the spatial or motor mechanisms was destroyed, the other mechanism could still learn the sequence, though not perfectly [54•]. Once a sequence is implemented as a motor sequence, the spatial sequence mechanism can work on other sequences so that eventually many sequences can be learned.

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Conclusions and future directions Motor skills emerge from our experience, not from knowledge, as they easily escape our consciousness. Naturally, we acquire many motor skills and execute them without awareness. Such ever-changing and hidden properties of motor skills have impeded analytical approaches. The discovery of synaptic plasticity in single neurons was revolutionary, but was far from sufficient to explain motor skills. Recent integrative and multidisciplinary approaches have begun to suggest that essential features of motor skills reside in dynamic interactions between multiple neural networks. Such networks are composed of loop circuits formed by the frontoparietal cortices, the BG, and the CB. These circuits acquire the same motor sequence in different coordinates, at diverse speeds, with varying robustness, and with different levels of attention and awareness. Their operation is likely optimized by learning mechanisms, each unique to the BG and CB. Such dynamic interactions of neural networks would thus create the emergent and ever-changing properties of motor skills. However, such integrative approaches have just started and modeling attempts of motor learning mechanisms have created more questions. Let us raise one important issue: timing. At the most advanced stage of a motor skill, movements of different body parts are accurately coordinated in time [55•]. A key structure for such a timing function might be the CB [37•,38•,56]. Related to timing is a phenomenon called ‘chunking’ [57] or ‘rhythm’ [58]. After practice, a long sequence of movements is often grouped into a series of chunks [1]. From these chunks may emerge the hierarchical organization of learned behavior. Update Lu et al. [66•] have recently found that many neurons in the supplementary eye field (SEF) were active in specific learned sequences of saccadic eye movements. These data, together with the preceding data on the SMA and preSMA, suggest that the medial frontal cortex represents learned sequences of eye–hand movements. They further suggest that the relationship between the eye and hand mechanisms is flexible, being either independent or well-coordinated, depending on the context or the level of practice.

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Psychological Science Schema and motor memory

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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

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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, Ruiters, 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 3

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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.

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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

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(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.

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Table 1. Participant characteristics and sleep/vigilance data.

Experiment 1a

Same New Compatible

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n 17 19 20 18 17 19 18 Females 11 13 13 12 11 13 13

Mean Age (yrs) BAI

BDI Handedness PSQI

S1: SMS duration (h) S2: SMS duration (h) S1: SMS quality

S2: SMS quality

S1: SSS

S2: SSS

S1: PVT (ms) S2: PVT (ms)

22.6 ± 2.9 3.9 ± 4.1 3.7 ± 2.8 86.5 ± 14.4 2.9 ± 1.4 7.8 ± 1.2 8.1 ± 1.0 4.9 ± 0.8 4.8
± 1.1 2.0 ± 0.5 1.8 ± 0.8 355±29 355±30

21.8 ± 2.6 4.1 ± 3.9 3.3 ± 2.9 89.2 ± 14.4 3.1 ± 1.3 8.5 ± 0.9 8.5 ± 0.8 4.6 ± 0.6 4.5
± 1.0 2.0 ± 0.6 2.3 ± 0.8 345±27 341±23

22.7 ± 2.3 5.5 ± 4.7 3.5 ± 3.6 87.8 ± 10.8 3.2 ± 1.4 8.2 ± 0.9 7.9 ± 0.7 5.3 ± 0.7 4.7
± 1.0 2.1 ± 0.7 2.1 ± 0.8 334±24 332±23

21.4 ± 2.6 7.4 ± 4.3 4.7 ± 2.8 87.2 ± 11.7 2.8 ± 1.5 8.0 ± 1.4 7.8 ± 2.1 4.6 ± 1.1 4.8
± 0.9 2.3 ± 0.8 2.3 ± 1.0 335±26 336±31

21.9 ± 2.6 3.5 ± 3.8 2.7 ± 4.4 91.9 ± 13.5 3.1 ± 1.5 8.2 ± 1.0 8.2 ± 1.5 5.0 ± 0.7

5.0 ± 0.7 2.2 ± 0.6 2.0 ± 0.5 355 ± 38

355 ± 39

22.7 ± 2.9 4.5 ± 3.8 4.2 ± 3.3 95.0 ± 8.6 3.0 ± 2.7 8.2 ± 0.8 N/A

5.0 ± 1.0 N/A 2.3 ± 1.0 N/A 350±25 N/A

23.3 ± 2.9 5.7 ± 3.8 4.2 ± 3.3 92.7 ± 10.5 3.7 ± 1.6 8.6 ± 1.1 N/A

5.1 ± 1.1 N/A 2.1 ± 0.6 N/A 330±24 N/A

Experimental Groups Experiment 1b

Incompatible Compatible Control

Experiment 2

Immediate Immediate Compatible Incompatible

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.

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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.

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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

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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).

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Group	Day 1									Day 2													
	Ordinal Position									Ordinal Position									# of Day 2 Learned Transitions	# of Day 2 Novel Transitions	Day 1 / Day2 Ordinal Compatibility		
	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		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

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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.

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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

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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.

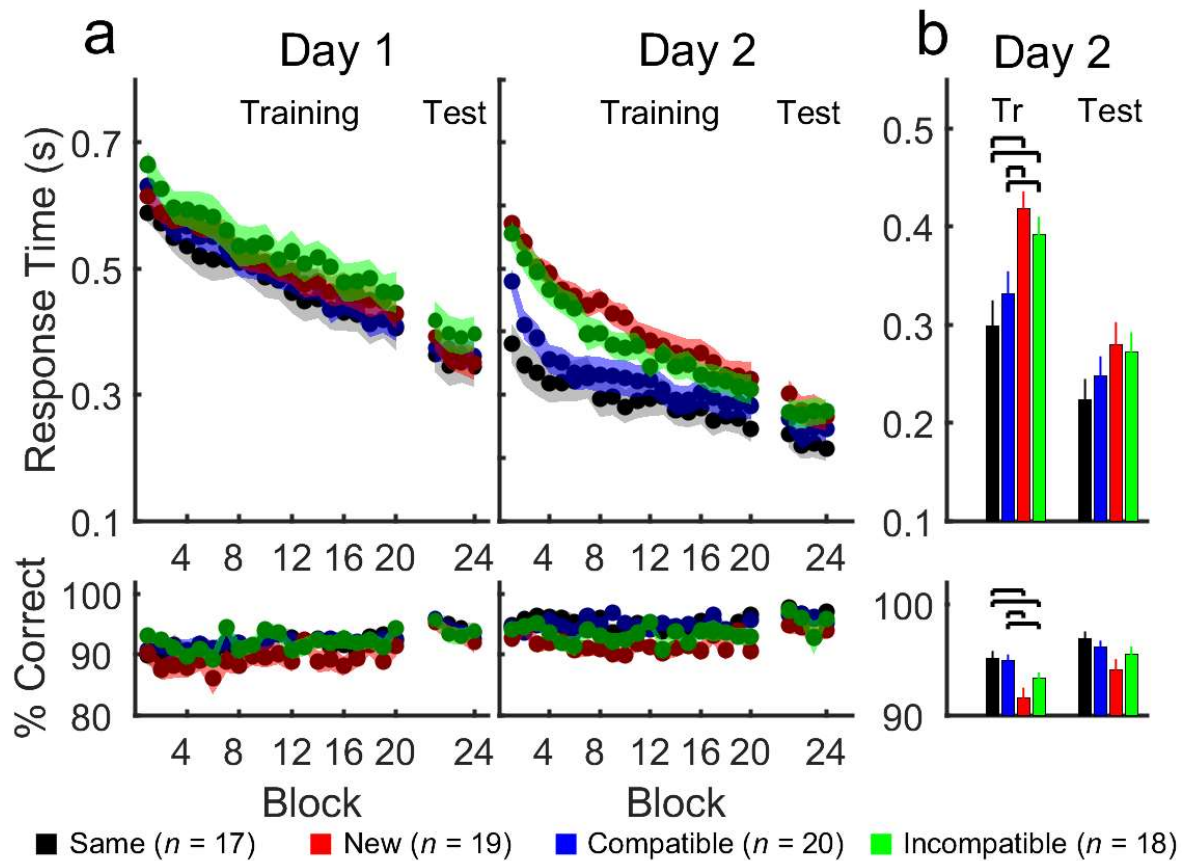


Figure 2. Performance on all transitions in Experiment 1a. Mean response time (top row) and percentage of correct transitions (bottom row) is shown in (a) for all transitions on Days 1 and 2 as a function of the 20 practice blocks during training and the 4 post-training test blocks, separately for the 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

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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

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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.

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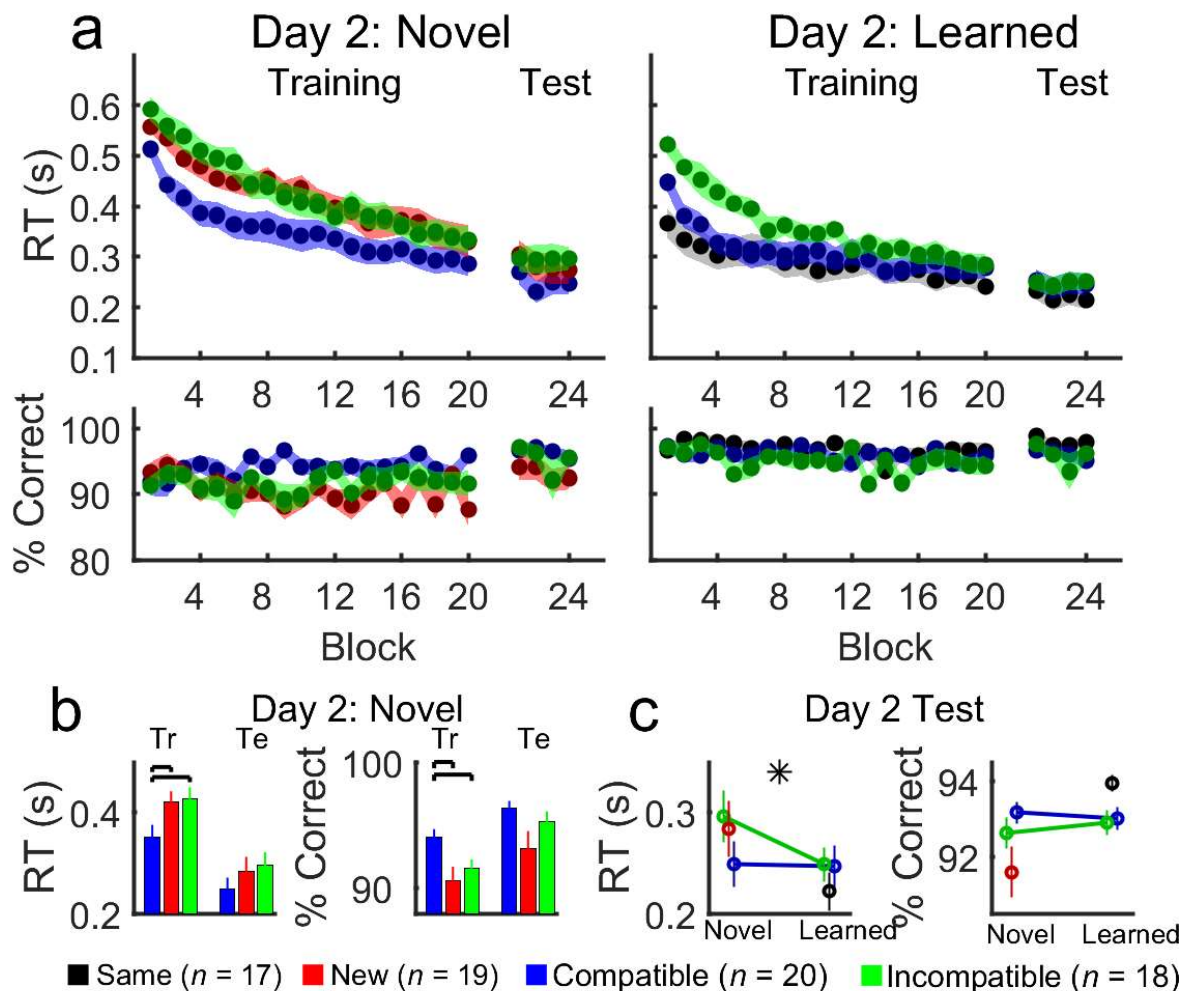


Figure 3. Shared novel and learned transitions in Experiment 1a. Mean response time (RT; top row) and percentage of correct transitions (bottom row) on Day 2 are shown in (a) as a function the 20 practice blocks during training and the 4 post-training test blocks. Results are shown separately for the 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) x 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 18

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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: $F_{(4.64,167.18)}=3.86$,

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$\eta_p^2=0.097$, $p=0.003$]. 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:

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$F_{(1,36)}=5.11$, $\eta_p^2=0.124$, $p=0.030$; 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.

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Table 2. Experiment 1 generation task. Same

Experimental groups Compatible

Compatible Control 58.82 ± 34.10 77.49 ± 28.81

40.93 ± 38.39 59.07 ± 40.78

% correct transitions

% correct ordinal positions

Day 1 Day 2

Day 1 Day 2

55.75 ± 38.34 83.63 ± 29.11

48.04 ± 40.45 79.17 ± 35.81

New

54.23 ± 35.72 81.52 ± 26.26

49.56 ± 35.52 73.96 ± 37.50

63.91 ± 36.52 71.36 ± 35.76

53.33 ± 43.21 60.05 ± 40.88

Incompatible

59.90 ± 31.34 73.40 ± 30.85

46.06 ± 39.62 65.69 ± 35.65

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

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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

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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).

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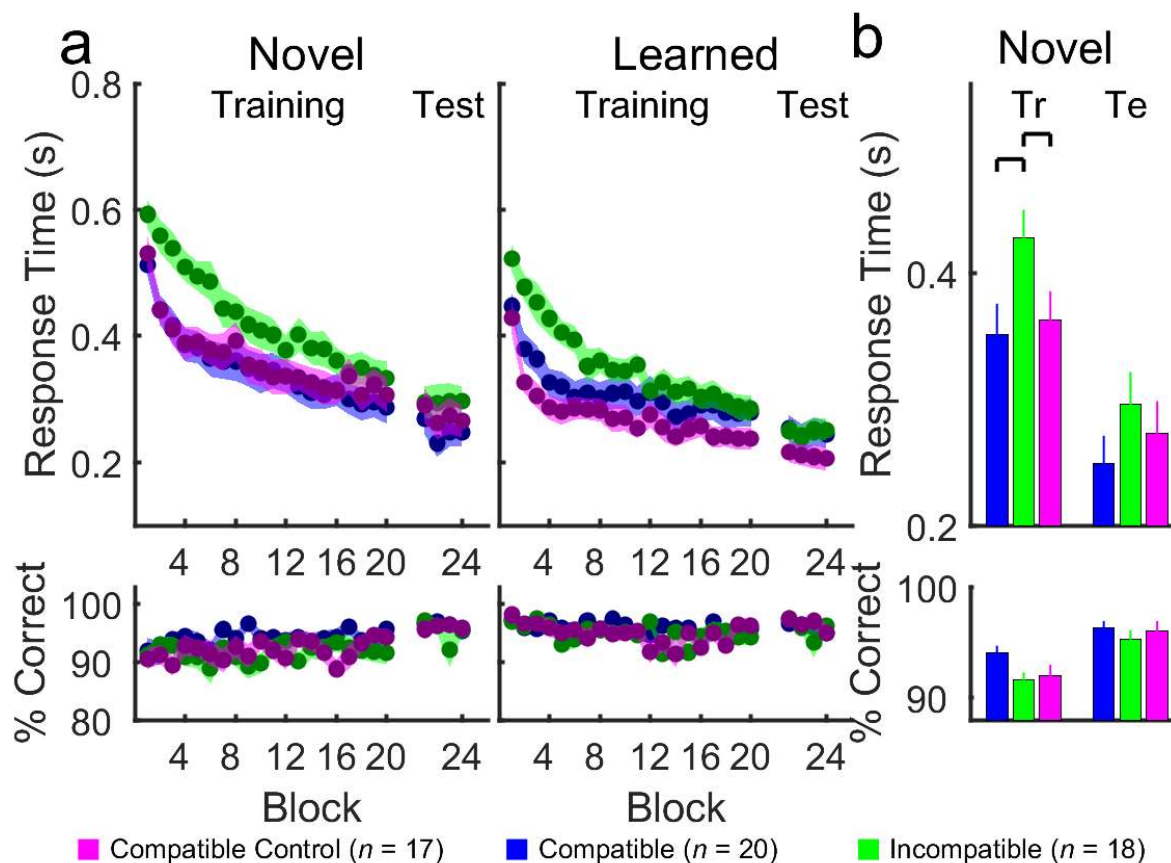


Figure 4: Shared novel and learned transitions in Experiments 1a and 1b. Mean response time (top row) and percentage of correct transitions (bottom row) on Day 2 are shown in (a) as a function of the 20 practice blocks during training and 4 post-training test blocks. Results are shown separately for 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

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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: $F_{(1,35)}=0.13$, $\eta_p^2=0.004$, $p=0.72$).

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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.

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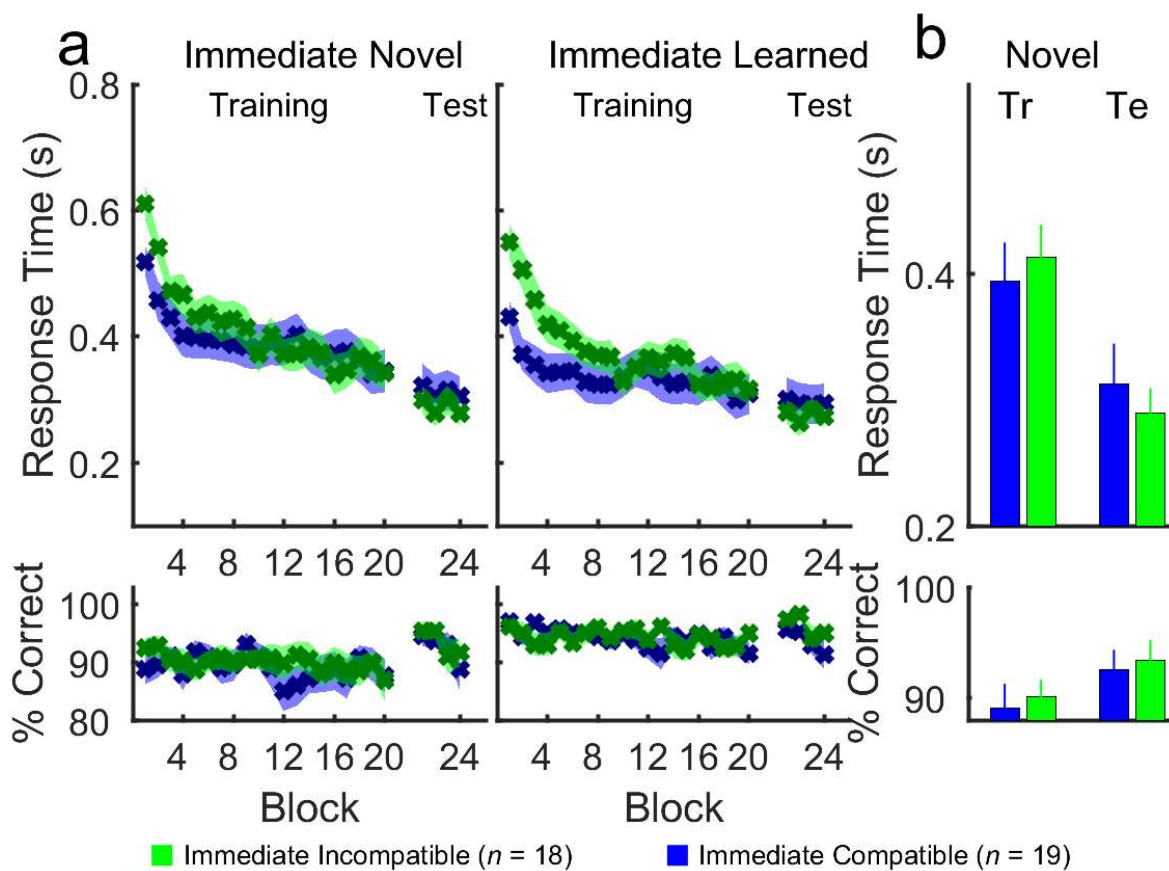


Figure 5: Shared novel and learned transitions in Experiment 2. Mean response time (top row) and percentage of correct transitions (bottom row) during Day 2 are shown in (a) as a function of the 20 practice blocks during training and the 4 post-training test blocks. Results are shown separately for novel (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

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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.

% correct transitions

% correct ordinal positions

Experimental Groups Immediate

Compatible S1 73.68 ± 28.49 S2 90.62 ± 20.76

S1 59.43 ± 40.89 S2 80.04 ± 33.83

Immediate Incompatible 80.19 ± 21.58

89.61 ± 14.35

62.27 ± 42.90 66.67 ± 41.11

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Group means ± 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- 30

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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

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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 (Szege-di-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

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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

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.

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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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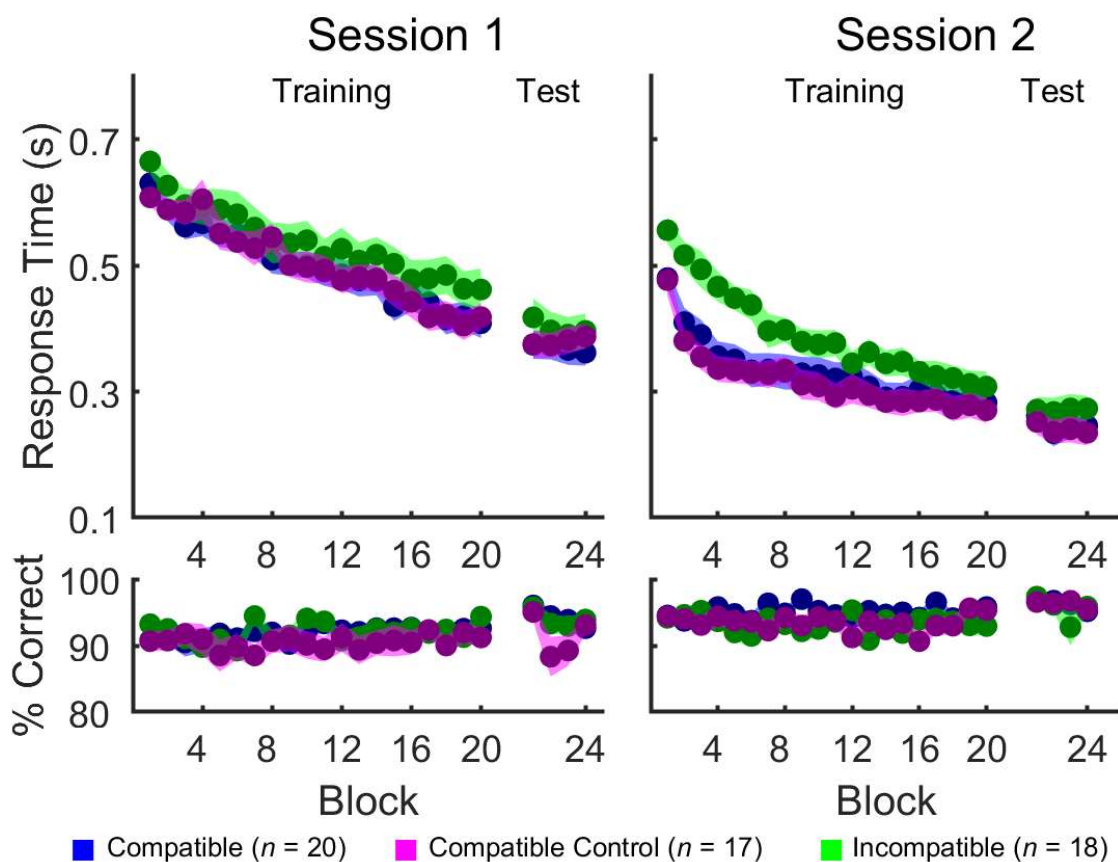
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Figure S1.

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.

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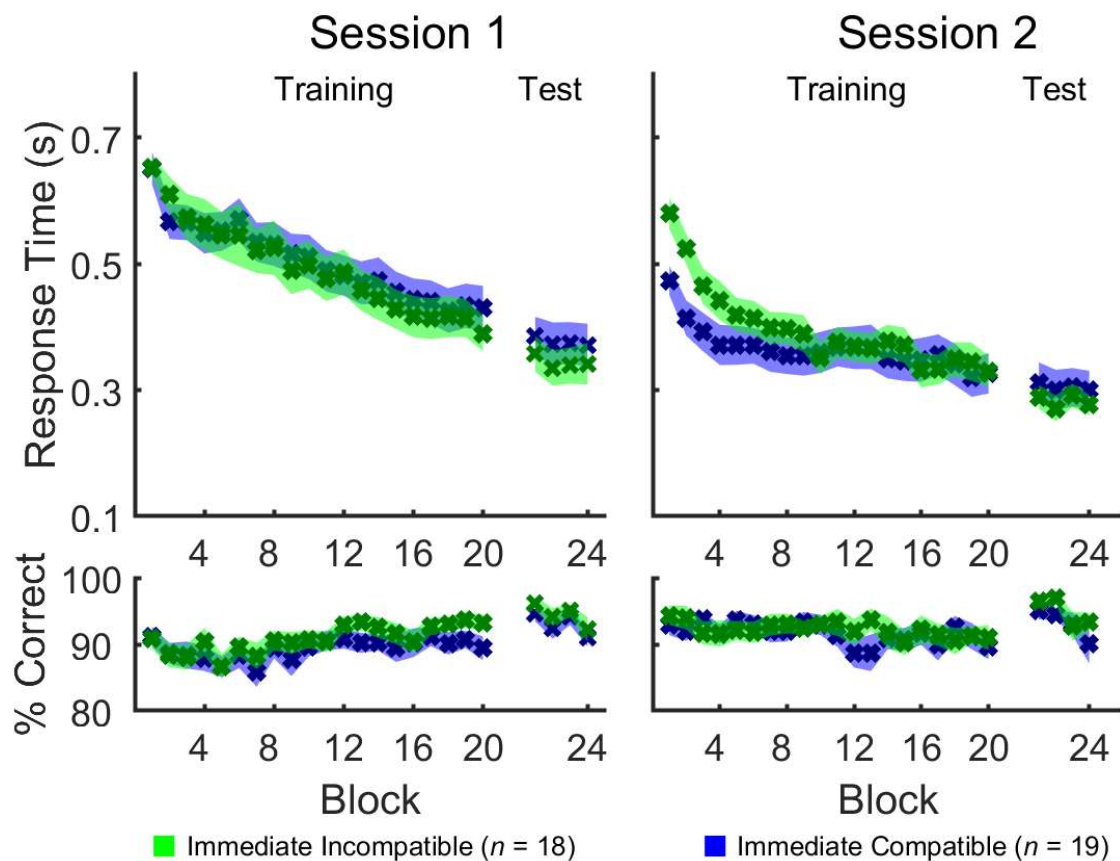
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Figure S2.

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.

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Cerebellum and M1 interaction during early learning of timed motor sequences

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Abstract

We used positron emission tomography (PET) to examine within-day learning of timed motor sequences. The results of this experiment are novel in showing an interaction between cerebellum and primary motor cortex (M1) during learning that appears to be mediated by the dentate nucleus (DN) and in demonstrating that activity in these regions is directly related to performance. Subjects were scanned during learning (LRN) across three blocks of practice and during isochronous (ISO) and perceptual (PER) baseline conditions. CBF was compared across blocks of learning and between the LRN and baseline conditions. Results demonstrated an interaction between the cerebellum and M1 such that earlier, poorer performance was associated with greater activity in the cerebellar hemispheres and later, better performance was associated with greater activity in M1. Inter-regional correlation analyses confirmed that as CBF in the cerebellum decreases, blood flow in M1 increases. Importantly, these analyses also revealed that activity in cerebellar cortex was positively correlated with activity in right DN and that DN activity was negatively correlated with blood flow in M1. Activity in the cerebellar hemispheres early in learning is likely related to error correction mechanisms which optimize movement kinematics resulting in improved performance. Concurrent DN activity may be related to encoding of this information and DN output to M1 may play a role in consolidation processes that lay down motor memories. Increased activity in M1 later in learning may reflect strengthening of synaptic connections associated with changes in motor maps that are characteristic of learning in both animals and humans.

Introduction

A growing body of evidence in both animals and humans has demonstrated plastic neuronal changes in the brain with learning of a motor skill (Doyon and Ungerleider, 2002, Doyon et al., 1996, Doyon et al., 1999, Doyon et al., 2002, Doyon et al., 2003, Gandolfo et al., 2000, Graybiel, 1995, Hikosaka et al., 2002b, Kleim et al., 2002a, Nudo et al., 1996, Thach, 1996). These experiments can be roughly divided into two categories: those that have focused on early rapid changes occurring over minutes (Classen et al., 1998, Doyon et al., 1996, Doyon et al., 1999, Doyon et al., 2002, Imamizu et al., 2000, Karni et al., 1995, Nezafat et al., 2001, Pascual-Leone et al., 1994, Shadmehr and Holcomb, 1997, Toni et al., 1998, Van Mier et al., 1998); and those that have examined relatively slowly developing changes occurring over days or weeks (Karni et al., 1995, Kleim et al., 2004, Lu et al., 1998, Nezafat et al., 2001, Nudo et al., 1996, Pascual-Leone et al., 1995, Penhune and Doyon, 2002). The results of these experiments have demonstrated the involvement of specific regions of motor cortex, the cerebellum and basal ganglia (BG) depending of the stage of motor learning. Drawing on work in experimental animals, Kleim et al., 2002a, Kleim et al., 2004 has hypothesized that early rapid plasticity of motor maps in M1 may be mediated by unmasking of latent connections, while longer-term changes are mediated by synaptogenesis and strengthening of cortical connections (Rioullet-Pedotti et al., 1998). In the cerebellum, early learning is probably mediated by error-correction mechanisms instantiated in the climbing fiber system of the cerebellar cortex (Ito, 2000), while later learning may involve plastic changes in regions of the cerebellar hemispheres and/or the cerebellar nuclei specific to the effector and internal model for the task (Imamizu et al., 2000, Lu et al., 1998, Nezafat et al., 2001). In the BG, it has been proposed that anterior putamen is more involved in early learning, while the posterior region is more important for later learning (Jueptner and Weiller, 1998, Miyachi et al., 2002).

More recently, it has been proposed that distinct cortico-cerebellar and cortico-striatal systems may be important for different stages of learning (Doyon and Ungerleider, 2002, Doyon et al., 2003), different modalities of learning (Doya, 2000, Doyon et al., 2003) or for learning different aspects of the same task (Hikosaka et al., 2002a, Middleton and Strick, 2000). Strikingly, however, there is little data allowing comparison of the neural mechanisms underlying the early and late periods of learning on the same task (Karni et al., 1995, Kleim et al., 2004, Nezafat et al., 2001). In a previous study of across-day learning (Penhune and Doyon, 2002), we showed that a dynamic network including the cerebellum, basal ganglia and motor cortical regions were differentially active on Day 1 of practice, after 5 days of training and at delayed recall. Based on these results, we proposed that the cerebellum is critically involved in optimizing

movement kinematics during early learning, but that later learning and delayed recall are mediated by the BG and motor cortical regions. Therefore, the present experiment was designed to examine within-day changes in the cortico-cerebellar and cortical–striatal networks. Most importantly, the experiment was designed to allow the direct assessment of the relationship between behavioral measures of learning and changes in the pattern of active brain regions and to allow the examination of the interaction between different brain regions across the course of learning.

Motor sequence learning in this experiment was conceptualized as the optimization with practice of specific parameters of motor response that result in improved precision and accuracy of performance. This is similar to the type of motor learning examined in studies of serial finger tapping (Karni et al., 1995) and force field learning (Nezafat et al., 2001). This contrasts with other paradigms, such as the serial reaction time task (SRT) that emphasize implicit or explicit learning of the order of a sequence of movements. The task used was the timed motor sequence task (TMST) developed in our previous study of across-day learning (Penhune and Doyon, 2002). The TMST requires subjects to reproduce a temporally complex sequence of finger taps in synchrony with a visual stimulus (Fig. 1, panel A). Subjects were scanned across three blocks of learning on the same task along with two baseline conditions. In order to identify changes in the pattern of active regions during learning, subtraction analyses contrasted blood flow across blocks of learning and between the learning and baseline conditions. To confirm the results of the subtraction analyses, normalized blood flow was extracted from regions identified in the subtraction analysis. Most importantly, regression analyses were performed to examine the relationship between behavioral measures of performance and blood flow across blocks of learning. Finally, inter-regional regression analyses were conducted to examine the interaction of the cerebellar and motor cortical regions seen to be active across blocks of learning. The results of this experiment are novel in showing a direct relationship between blood flow and performance, and in showing an interaction between the cerebellum and M1 during learning.

Section snippets

Subjects

Subjects were 12 healthy, right-handed volunteers selected to have no more than 1 year of musical training or experience (6 female, 6 male, average age = 24.8). Subjects were paid for their participation, and gave informed consent. The experimental protocol was approved by the Research Ethics Committee of the Montreal Neurological Institute.

Stimuli and task conditions

The TMST requires subjects to reproduce a temporally complex sequence of finger taps in synchrony with a visual stimulus (Fig. 1, panel A). Visual stimuli

Behavioral data

Subjects were able to learn the TMST sequences relatively quickly (Average 16 ± 8 trials to criterion). No subject failed to learn the sequence within the criterion training limit of 48 trials. For the LRN sequences, there was a significant improvement in performance across the three blocks of learning for all variables [see Fig. 1, panel C (percent correct: $F(2,22) = 5.0$; $P = 0.02$; response variance: $F(2,22) = 20.8$; $P < 0.001$; and response asynchrony: $F(2,22) = 17.9$; $P < 0.001$]. All measures

Discussion

The results of this experiment demonstrate an interaction between the cerebellum and motor cortex during within-day learning of a motor sequence task. Contrasts across blocks of practice show that the cerebellum was most active during early learning, while M1, IPL and the putamen were more active during later learning. These results were corroborated by analyses showing that nCBF in the cerebellum

decreased significantly across blocks of practice, while blood flow in M1, IPL and the putamen

Acknowledgments

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Recent computational and behavioral studies suggest that motor adaptation results from the update of multiple memories with different timescales. Here, we designed a model-based functional magnetic resonance imaging (fMRI) experiment in which subjects adapted to two opposing visuomotor rotations. A computational model of motor adaptation with multiple memories was fitted to the behavioral data to generate time-varying regressors of brain activity. We identified regional specificity to timescales: in particular, the activity in the inferior parietal region and in the anterior-medial cerebellum was associated with memories for intermediate and long timescales, respectively. A sparse singular value decomposition analysis of variability in specificities to timescales over the brain identified four components, two fast, one middle, and one slow, each associated with different brain networks. Finally, a multivariate decoding analysis showed that activity patterns in the anterior-medial cerebellum progressively represented the two rotations. Our results support the existence of brain regions associated with multiple timescales in adaptation and a role of the cerebellum in storing multiple internal models.

Expansion and Renormalization of Human Brain Structure During Skill Acquisition

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Research on human brain changes during skill acquisition has revealed brain volume expansion in task-relevant areas. However, the large number of skills that humans acquire during ontogeny militates against plasticity as a perpetual process of volume growth. Building on animal models and available theories, we promote the expansion–renormalization model for plastic changes in humans. The model predicts an initial increase of gray matter structure, potentially reflecting growth of neural resources like neurons, synapses, and glial cells, which is followed by a selection process operating on this new tissue leading to a complete or partial return to baseline of the overall volume after selection has ended. The model sheds new light on available evidence and current debates and fosters the search for mechanistic explanations.

Section snippets

Human Brain Plasticity: Expansion and Renormalization?

In 1894, Nobel Prize winner Santiago Ramón y Cajal, considered by many to be the father of modern neuroscience, proposed that mental activity might induce morphological changes in brain structure. Nearly 100 years later, studies using **magnetic resonance imaging (MRI)**, see Glossary and Box 1) have reported experience-dependent increases in regional estimates of human brain volume and cortical thickness in adulthood. For example, it has been found that London taxi drivers' gray matter in the

Expansion and Renormalization of Human Gray Matter Structure

Research has documented changes in human gray matter structure after a few months of training (e.g., 2, 5 as noted above) and has also indicated that such changes can emerge early during the learning process 7, 22, 23, 24. However, the fate and durability of these changes has not been tracked in the course of continuous learning in humans. Recently, we acquired up to 18 T1-weighted structural MR images over a 7-week period during which 15 right-handed adult participants practiced left-hand

Cellular Processes Potentially Underlying Gray Matter Changes

Increases and decreases of estimates of localized volume during learning as observed with MRI are most likely the result of a conglomerate of different cellular processes 14, 28. Figure 1 schematically illustrates these cellular processes. Several candidate mechanisms on the cellular and molecular level have been proposed that could account for MRI observations [14], including neurogenesis, synaptic changes, dendritic branching, and axon sprouting as well as changes in glial number and

Cortical Map Dynamics and Functional Changes

Similar to macroscopic changes in estimates of regional gray matter volume, cortical map plasticity follows a comparable pattern of expansion followed by renormalization during learning 16, 17, 18, 44, 45, 46, 47, 48, 49, 50. For example, it has been found that rats training to perform a skilled reaching task exhibit expanded cortical maps after 3 days of training [16]. After 8 days of training, however, these expansions had subsided, while behavioral performance remained stable. A similar

Formation and Elimination of Synapses

Research regarding learning-related changes in dendritic spines is consistent with the hypothesis that the memory trace serving skilled performance is often localized in rewired specific circuitry rather than in any large-scale expansion of tissue in the whole region 11, 36, 53. During motor skill acquisition or new sensory experiences, novel dendritic spines rapidly grow to form synapses in the sensory and motor cortices of rodents 19, 20, 21. In this process the dendrites are not merely

Plastic Changes: A Darwinian Learning Process

The pruning model of early development 56, 57, 58 posits the same general pattern of increase followed by decrease as described above, only on an ontogenetic timescale. The rapid increase of synapses after birth is followed by experience-dependent selective stabilization of behaviorally relevant connections and the elimination of those connections that prove to be non-functional [59], resulting in an overall trajectory of decrease from childhood to adolescence 60, 61 (but see also [62] for

Concluding Remarks and Future Perspectives

We have argued that the concepts of expansion, selection, and renormalization are consistent with animal models and theoretical accounts of skill acquisition and development and together contribute to a mechanistic understanding of human plasticity. Importantly, the expansion–renormalization model opens up several new research directions, informs predictions for work on experience-dependent and developmental changes in human brain structure (see Outstanding Questions), and calls for a critical

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Memory for Music Performance 1 Nature of memory for music performance skills Caroline Palmer McGill University In press, *Music, Motor Control and the Brain* E Altenmueller & M Wiesendanger, Editors Oxford University Press Running head: Memory for Music Performance Address correspondence to: Dr. Caroline Palmer Dept of Psychology McGill University 1205 Dr. Penfield Ave Montreal H3A 1B1 CANADA (514) 398-6128 caroline.palmer@mcgill.ca Memory for Music Performance 2 Abstract Although most studies of memory for music performance focus on dimensions of musical structure, recent studies suggest motoric factors of performance are also represented. Brain imaging measures collected during mental practice or listening tasks suggest that both motor and auditory cortical areas are active during musical thought processes. Four lines of behavioral studies with performers reveal motor-based representations: performers' musical interpretations, transfer of learning from one musical task to another, mental practice effects, and anticipatory movements. These sources of evidence implicate distinct motoric and nonmotoric (melodic) information in performers' memory for music. Implications from these behavioral tasks suggest that an accurate auditory and motor representation underlies successful performance from memory. Memory for Music Performance 3 Introduction Theories of memory often cite music performance as an example of expert memory, and many studies have examined the factors that influence performers' memory (see Gabrielsson, 1999; Palmer, 1997 for reviews). Music performance can be depicted as a cognitive skill with large memory demands, or as a motor skill with large physical execution demands. Cognitive dimensions of performers' memory for music are often described in terms of musical structure such as harmony, tonality, phrasing, and meter (Palmer, 1997; Gabrielsson, 1999; Palmer & Pfordresher, 2003). Motor aspects of performance are measured in physical dimensions such as fluency, speed, rhythmic precision, and hand coordination (Krampe & Ericsson, 1996; Drake & Palmer, 2000). Musicians' memory that allows them to perform a specific musical piece, referred to as "memory for performance", is distinguished here from other memories for performance (by oneself or someone else). Music performance is of much interest to psychologists precisely because it is demanding both cognitively and motorically. Memory for music entails sequences on the order of thousands of pitch events, that are produced at rates as high as 8-12 events per second, with less than 3% error (Palmer & van de Sande, 1993; Repp, 1996; Finney & Palmer, 2003). In addition to categorical pitch events, listeners (infants as well as adults) remember fine expressive nuances of performances, including timing, intensity, and articulation information that distinguish different performances of the same music (Palmer, Jungers, & Jusczyk, 2001). A more accurate conceptualization of the problem of describing memory for performance may be: what are the underlying features of music performance that are represented in memory? Which features are described in motor Memory for Music Performance 4 coordinates? How do factors such as maturation, musical

acculturation, and training influence the representation of those features? This chapter addresses these questions in the domain of piano performance. Piano is one of the most-often chosen instruments of study by children in North American schools (Johnson, 1994). Piano has consistently been among the most-often performed instrument by amateur musicians in American households (Gallup poll, 1994; 2000) and piano performance is one of the most easily measured instruments with the advent of MIDI. Thus, research in performance is based largely on measures of pianists' behaviors. Despite the rapid growth of research in piano performance during the past 20 years, less attention has been paid to the motor aspects of memory for performance (such as finger, hand movements) than to auditory (intensity, duration, etc) or structural aspects (phrase structure, rhythm, etc) .

A. Motor representations of piano performance Motor demands of piano performance are quite large, in particular, in terms of finger movements. One of the few models to attempt to capture aspects of motor difficulty is an ergonomic model of fingering in piano performance (Parncutt, Sloboda, Clarke, Raekallio, & Desain, 1997). This model, based on a series of rules, reflects specific ergonomic difficulties such as weak versus strong fingers and spans between finger pairs. Measures of pianists' fingering consistency and performance accuracy for musical exercises correlated negatively with the model's predictions of fingering difficulty (Sloboda, Clarke, Parncutt & Raekallio, 1998). The model compared favorably with performances that used the least difficult fingers; however, the model sometimes made predictions for simpler fingerings that were not preferred by the pianists. Memory for Music Performance 5

Imagery techniques applied to brain organization also support motoric and nonmotoric features of performers' memory for music. Pantev, Engelien, Candia and Elbert (2001) found enlarged representations of auditory and somatosensory cortex with musical practice. The somatosensory cortex showed neuronal changes specific to fingers used during practice. Pascual-Leone and colleagues (reviewed in PascualLeone, 1995) found changes in cortical motor areas as non-pianists practiced finger exercises; physical practice as well as a combination of mental and physical practice established those changes. With MEG techniques, Haueisen and Knösche (2001) reported that pianists displayed motor activity in the contralateral primary motor cortex while listening to familiar music (music they had performed). In addition, skilled violinists' fMRI measures demonstrated activity in primary auditory regions while they silently tapped the opening section of a violin concerto; amateur violinists' fMRI results did not indicate auditory stimulation (Lotze et al, 2003). To address whether co-activation in auditory and motor cortical areas arises from years of joint auditory-motor practice or over shorter time spans, Bangert and Altenmüller (2003) used DC-EEG with nonmusicians who were trained to associate a purely auditory (passive listening) task with a purely motoric (silent finger movement) task. One group had consistent mappings of auditory events to motor events, while another group learned with altered mappings. Only the consistent mapping group exhibited EEG additional activity of right anterior regions, which the authors took to indicate an audio-motor interface that developed in the Memory for Music Performance 6

first weeks of practice. Of interest is how far the behavioral changes following pairings of motor and auditory activity extend, both in time and across tasks.

B. Interpretive influences on performance memory The occasional errors that performers make (hitting the wrong key or chord) often display active memories for other to-be-performed events. For example, pitch errors tend to reflect tones intended for elsewhere in the same piece (Palmer & van de Sande, 1993). Such performance errors also indicate motoric features. Palmer and van de Sande (1993) documented pianists' errors in two-handed piano music; left-handed errors were more common than right-handed errors (regardless of pianists' handedness), consistent with Peter's (1985) findings of greater right-hand coordination skills among pianists. Harmonically related errors (a substituted pitch that arises from the same chord as the intended pitch) were more common than harmonically unrelated errors, even when they

required different hand or finger movements to produce (Palmer & van de Sande, 1993). Likewise, hand differences in errors occurred for both harmonically related and unrelated errors. Do motor factors interact with non-motor features of memory for performance? Palmer and van de Sande (1993) asked pianists to perform the same music with different melodic interpretations. The melody or primary (most important) voice is not directly marked in music notation, and performers often interpret the voice intended as melody as more important (Palmer, 1989). The voice interpreted as melody was less Memory for Music Performance 7 likely to contain errors, even when pianists changed their melodic interpretation for the same musical piece. Performers also made more errors in parts controlled by the left hand, regardless of hand dominance. Motor factors (hands and fingers used) did not interact with interpretive factors (melody being emphasized) in the likelihood of errors in the pianists' performance, suggesting that interpretive and motor factors are represented independently in memory for performance (Palmer & van de Sande, 1993).

C. Transfer of Performance Skills Another source of evidence for motoric dimensions of memory for performance is the conditions under which performers generalize what they know from one performance situation to another. In typical transfer of learning tasks, participants learn one task and then perform a second task. The ease with which they perform the second task is thought to reflect what was learned in the first task. The mirror symmetry of hand and finger movements in piano performance provides a convenient venue in which to test transfer of motor learning. Consider the sequence of finger movements 5-4-3-2-1 in the right hand (where thumb = 1), used to press adjacent keys on a piano; this sequence becomes 1-2-3-4-5 when the same keys are pressed by the left hand. Thus, the same melody can be played with different hand and finger movements in piano performance. In addition, different melodies (different pitch sequences) can be performed with the same hand and finger movements. Although the transfer of musical skills to math, spatial reasoning, and other tests of intelligence has been studied (Rauscher, Shaw & Ky, 1995; Memory for Music Performance 8 Schellenberg, 2004), fewer studies have examined the transfer of learning from one musical task to another musical task. Are well-learned motor movements transferred from one melody to another? Palmer and Meyer (2000) measured transfer of pianists' hand and finger movements from one practiced melody to a novel melody. When the second (novel) melody required the same finger movements as the initial melody performed, pianists were able to play it more quickly. Comparisons across age and skill levels indicated that the more advanced performers showed greatest transfer across motor movements, suggesting that they were able to generalize from one hand and finger set to another. The least skilled pianists showed no ability to generalize beyond the particular finger sequence learned. Does knowledge of a set of motor movements transfer across temporally distinct patterns in music performance? For example, can a pianist performing one rhythmic pattern with a set of finger movements such as 1-2-3-4-5 generalize those same finger movements to produce a different rhythmic pattern as fluently as the first pattern? Using a similar transfer of learning task, Meyer and Palmer (2003) showed that pianists' finger movements did transfer across different rhythmic patterns: pianists could perform novel rhythms with the same finger movements as quickly as the first-learned rhythms. In addition, there was rhythmic transfer: pianists could perform well-learned rhythms with different hand and finger movements as quickly as with the first-learned movements. There was no interaction between rhythmic transfer and motor transfer; the time at which Memory for Music Performance 9 keys were pressed were remembered independently of the motor features that produced them. Similar findings were obtained when pianists transferred from one melody to another that differed in meter and motor movements. No interactions were observed among the temporal (meter and rhythm) and motor structures: retaining temporal structure from one melody to the next facilitated speeded performance more than retaining motor movements, and motor features

played a smaller role in transfer of knowledge across melodies. These findings are consistent with the general view that representations of timing in sequence production are not defined primarily in terms of motoric features (MacKay, 1982, 1987; Semjen & Ivry, 2001), at least for performers with moderate to high levels of musical experience.

D. Mental and physical practice Practice may be the single most important factor that influences memory for performance. Musicians' verbal reports of practice goals incorporate many levels of analysis, including structure, interpretation, and motor aspects of technique (Chaffin, Imreh, Lemieux, & Chen, 2003). Several studies suggest that deliberate rehearsal accounts for skill differences among music performers (Ericsson, Krampe & Tesch-Romer, 1993; Sloboda, Davidson, Howe & Moore, 1996). More recently, comparisons have been made of the efficacy of physical practice with mental practice. When musicians practice the motor movements for performance in the absence of their physical instrument, they often make other overt movements, such as drumming fingers or tapping feet under the table, suggesting that motor features of performance are important for practice. If mental practice has effects on performance similar to those of physical practice, is it due to motor or non-motor components of mental practice? Are the thought processes underlying mental practice similar to those underlying physical practice? Mental practice has been defined as the mental rehearsal of a specific task in the absence of actual physical movement (Coffman, 1990; Driskell, Copper & Moran, 1994). Mental practice is distinguished from other mental techniques such as analytical study, general mental imagery, imitation, or self-arousal. Measurement of mental practice effects typically include improvement in accuracy or time to complete a task relative to some control task (such as no practice or normal practice). Meta-analyses of mental practice effects (Driskell et al, 1994; Feltz & Landers, 1983) indicate two consistent findings. First, normal (physical) practice exceeds mental practice alone, which exceeds no practice (Coffman, 1990). Second, physical practice plus mental practice instructions exceed physical practice alone (Rubin-Rabson, 1937; Ross, 1985). These findings suggest that improvement with practice in general is due to two components: a physical (motor) component and a mental (nonmotor) component. The meta-studies interpret differences among mental practice findings as indicating that tasks with heavier cognitive requirements (memory, attention, symbol manipulation) show greater effects of mental practice than tasks with high-motor requirements (coordination, endurance, strength).

Memory for Music Performance 11 Examples of high-cognitive load tasks include maze-learning and card-sorting. Examples of low-cognitive load tasks include balancing and dart-throwing. Two common theoretical explanations of mental practice effects include the cognitive (symbolic) hypothesis and the psychoneuromuscular hypothesis. The cognitive hypothesis states that mental practice effects apply to the cognitive components of a skill: those that can be represented symbolically or visuospatially (Feltz & Landers, 1983). In contrast, the psychoneuromuscular hypothesis (which grew out of the ideomotor view) holds that mental practice effects apply to the physical components of a skill, such as low-gain innervation of muscles used in the physical enactment of the skill (Jacobson, 1930; Shaw, 1938). However, potential problems with mental practice studies make conclusions difficult. Instructions to participants that define mental practice often vary or are absent. In addition, mental practice conditions are often accompanied by some kind of physical practice, either overt, such as foot-tapping (Wollner & Williamon, 2004) or covert, such as throat muscle movements (Jacobson, 1932). As a result, the components of mental practice that are considered cognitive or motor are often determined a priori by experimenters. Although mental practice effects have been examined in many behavioral tasks, fewer studies have compared types of mental practice in the context of music performance. Coffman (1990) showed that pianists' mental practice improved their performance compared with no practice. Pianists' mental practice with an auditory model **Memory for Music Performance 12** showed

advantages over mental practice alone (Lim & Lippman, 1991; Theiler & Lippman, 1995). Rubin-Rabson (1937) showed that analytical pre-study of the score often aided performers' memorization of unfamiliar music; this analytical study may involved auditory or motor imagery (Lim & Lippman, 1991). Mental practice may help musicians learning unfamiliar music by facilitating the creation of an auditory and/or motoric image. Comparison of different practice conditions showed that listening to a performance was an effective aid to learning to perform unfamiliar music (Rosenthal, 1984; Rosenthal, Wilson, Evans, & Greenwalt, 1988). Not all studies show a facilitation of mental practice, however; Rosenthal et al (1988) found that silent analysis (similar to mental practice, without explicit instructions) followed by sight-reading was not more effective than sight-reading alone. An indirect source of evidence for mental practice is the lack of detrimental effect that removal of auditory feedback causes to performers, once they have learned a musical piece well. Finney and Palmer (2003) measured the amount of time performers took to play a familiar piece from memory on a silent electronic piano; total performance durations were within 5% of the durations when the pianists played the same piece with normal auditory feedback. This result was not specific to well-learned pieces; after playing a novel musical piece 10 times, the removal of auditory feedback caused no change in the duration of the performance. However, when auditory feedback was removed during the initial practice session, pianists' later performances (with auditory Memory for Music Performance 13 feedback) were significantly slower and more errorful (Finney & Palmer, 2003). Thus, the absence of auditory feedback during practice of an unfamiliar piece did not affect pianists' accuracy while the music notation was in front of them, but the absence of auditory feedback during practice did impair their later performance from memory. Ross' (1985) study of trombonists indicated that normal practice conditions with both auditory and kinesthetic feedback present allowed musicians to correct and adjust their performances; that ability decreased as feedback was removed during practice. In sum, these studies suggest that pianists can substitute mental feedback for auditory feedback, once they have practiced the music sufficiently to form a mental representation. Highben and Palmer (2004) contrasted mental and physical practice, in terms of auditory and motor feedback, to determine their role in how pianists learn to perform unfamiliar music. Comparisons were made of different types of mental practice by replacing auditory or motor feedback with instructions to imagine the missing feedback: how the piece sounds, or how the finger movements feel, during practice. In a Normal practice condition, pianists moved their fingers on the keys and heard themselves play over headphones during practice. In a Motor Only practice condition, the pianists moved their fingers on the keys but auditory feedback was removed; they were told to imagine what the piece would sound like. In an Auditory Only practice condition, motor feedback was removed (the pianists held their fingers in loose fists) and auditory feedback was present in the form of a computer-generated recording of the piece, and pianists were Memory for Music Performance 14 told to imagine what the finger movements would feel like. In a Covert practice condition, both motor feedback and auditory feedback were removed during practice (pianists held their fingers in loose fists and heard silence), and they were given both sets of instructions. Each participant performed in each condition with a different musical piece; a within-subject design was considered important to control for individual differences in mental practice abilities. After performers practiced from a musical score, the score was removed, and pianists performed from memory under normal feedback conditions. Two independent measures of mental imagery ability were collected: one for motor imagery and one for auditory imagery, for comparison with the effects of mental practice. Both auditory and motor forms of practice facilitated pianists' subsequent performance from memory of unfamiliar music. Removal of auditory or motor feedback at practice caused significant memory deficits in later performance, despite the presence of both types of feedback at test. Physical practice

conditions (in which auditory and/or motor feedback were present) led to better performance recall than conditions with mental practice. Recall was best following normal practice conditions, and worst when both auditory and motor feedback were removed during practice. Furthermore, pianists who scored higher on the aural skills test performed better from memory following the absence of auditory feedback during practice, compared with pianists who scored lower on the aural skills test. Thus, it is likely that performers with high aural skills were better able to use auditory imagery during learning than other performers (Highben & Palmer, *Memory for Music Performance* 15 2004). Whereas previous studies demonstrated the overall efficacy of mental practice in music performance (Coffman, 1990; Ross, 1985), Highben and Palmer's (2004) findings suggest specifically that auditory and motor forms of mental practice can aid performers' learning of unfamiliar music. In addition, the presence of a motor component of mental practice that facilitates memory for performance indicates that explanations of mental practice effects based solely on symbolic, videospatial, or other cognitive (non-motoric) forms of representation are not sufficient to explain memory for performance. Individual differences in imagery abilities that are related to memory differences have implications for brain imaging studies as well as for behavioral studies. Most comparisons of mental practice methods rely on cross-group comparisons (see Driskell, Copper & Moran, 1994; Feltz & Landers, 1983), for which any correlated memory differences are not measured. The presence of individual differences suggests that within-subject designs -- those that allow comparisons across all conditions within individual performers -- combined with independent measures of behavioral correlates, may be important controls for memory differences that result from mental imagery abilities. E.

Anticipatory behavior in music performance One of the hallmarks of memory for performance is anticipatory planning: the preparation of events prior to their execution (Rosenbaum, 1991). Anticipatory behavior is evidenced in occasional errors that reveal events intended for the future, and also in *Memory for Music Performance* 16 movements during the production of correct events that reveal trajectories toward future events. Studies of speech and music performance show anticipatory behavior in the types of errors people make (such as a speaker producing "I took the store - " instead of the intended "I took the car to the store", Garrett, 1980). One of the main factors influencing anticipatory behavior is practice. Drake and Palmer (2000) compared anticipatory behaviors of child and adult pianists of various skill levels. The percentage of anticipatory pitch errors (compared with perseveratory errors, or produced pitches that were intended for earlier in the sequence) increased with both age and experience (Drake & Palmer, 2000; Palmer & Drake, 1997). Practice effects on anticipatory behavior are found in many domains. Speech errors suggested that with more practice, speakers were more likely to anticipate a phoneme that was intended for later in the utterance (Dell, Burger, & Svec, 1997). As overall error rate decreased, speakers' percentages of anticipatory errors increased. Palmer and Pfordresher (2003) also found a consistent increase in anticipatory behavior with practice in piano performance, and a general relationship between overall error rate and anticipatory behavior: as pianists' pitch error rates decreased, the percentage of anticipatory errors increased. Furthermore, pianists' pitch errors were likely to span sequence distances of 3-4 events, termed the "range" of planning: the faster the performance, the smaller the range over which anticipatory behavior was evidenced (Palmer & Pfordresher, 2003). Analyses of finger movements in piano performance also display evidence of *Memory for Music Performance* 17 anticipatory behavior. One of the earliest studies of musical motion (Ortmann, 1929), using photographic techniques, documented finger movements during piano performance. Ortmann's records indicated anticipatory interactions among finger movements (movement of the second finger before the third finger strikes a key), as well as anatomical measures (arm weight, finger length, hand position) relevant for piano performance (such as role of forearm bone length on

rotation during production of tremolo). Ortmann (1929) documented general principles that are still the focus of movement research today: there are multiple routes to reach any key on the piano (the degrees of freedom problem), and the way in which each key is struck is influenced by the ways in which preceding and subsequent keys are struck (coarticulation). Current techniques of measuring motion rely on optoelectronic systems. One type includes active markers or sensors that are placed on joints with wires and emit infrared signals “captured” by cameras. Another motion capture technique uses passive markers that reflect light generated from a separate source that is detected by cameras. Both systems pinpoint the 3-dimensional coordinates of each marker at each point in time. Engel, Flanders and Soechting (1997) used an optoelectronic system to measure the degree of anticipatory behavior of fingers as pianists performed short musical excerpts that began with the same pitches but diverged in the middle of the excerpt. Pianists’ finger motions changed about 160 to 500 ms prior to the point of notated divergence in the musical score. Because performances differed in tempo, they were normalized with Memory for Music Performance 18 respect to time and anticipatory times were not reported in number of events. Palmer and Dalla Bella (2004) measured anticipatory movements in piano performance of simple melodies performed at a range of specified tempi. Pianists’ finger motions were recorded with a Vicon-8 system with passive 3mm markers placed on a pianist’s right hand, as shown in Figure 1, and 14 cameras placed around the pianist recorded light reflected from the markers. This system, also applied to violin bowing (Visentin & Gongbing, 2003), has the advantage of requiring no wires on pianists’ hands. An example of a pianist’s trajectory of motion of the fifth finger of the right hand is shown in Figure 2, during a performance of the simple melody shown at the top. The position, velocity, and acceleration graphs below refer to the position of the marker placed on the tip of the fingernail (the finger position of greatest motion) in the vertical plane (height above the keyboard). The top panel shows the finger height; minimum values indicate where the piano key was pressed. The middle panel shows the velocity of the finger motion, and the bottom panel shows the acceleration. In this melody, the pianist’s fifth finger pressed the keys on note events 6, 8, and 10. The pianists’ trajectories of motion indicated changes in velocity and acceleration patterns of each finger prior to its arrival on a key. The key arrival (indicated by minimum finger height, top panel) is marked by peak finger acceleration (bottom panel). Anticipatory motion is evidenced in the finger heights (top panel) during the event prior to the key arrival (events 6, 8, 10). As shown in Figure 2, the pianists’ fingers reached peak amplitudes usually within Memory for Music Performance 19 one event prior to a keypress. However, the trajectories of each finger began to change in velocity and acceleration 1-3 events prior to the anticipated key arrival by that finger; by 4 events prior, the trajectories showed the same amount of change in velocity and acceleration as when the finger had no upcoming keypress (resting level) (Dalla Bella & Palmer, 2004). This anticipatory behavior in finger trajectories is consistent with findings of memory retrieval occurring 3-4 events before the keypress (Palmer & Pfordresher, 2003); finger trajectories toward keypresses must require some information about the arrival location prior to the execution of the movement. Furthermore, the faster the tempo, the less time for anticipatory movements, consistent with the memory retrieval model. Although statistical (morphometric) techniques that identify consistencies in shape and structural time-patterns have not yet been applied to musical movement, motion capture techniques offer promise for rigorous measurement of coarticulation properties (how finger movements are influenced by subsequent and preceding fingers) and other shape/time constancies in musicians’ movements that were first identified long ago (Ortmann, 1929). F. Summary Research in music performance is beginning to document the nature of memory for the motor aspects of performance. Performers’ hand and finger movements, as well as conceptual intentions, are encoded in memory for performance and tend to have independent effects on pitch accuracy.

Performers' memory for melodies (specific pitch Memory for Music Performance 20 sequences) and finger/hand movements generalize in transfer tasks; furthermore, the motor and melodic information transfer independently. Skilled performers show more transfer of learning across melodies that required different motor movements than novices. Mental practice shows evidence of motor components that facilitate memory for performance. Finally, motion capture techniques of measuring music performance are beginning to document the timecourse of anticipatory movements. One ramification of these findings is that memory for performance is flexible; performers can apply what they know about motor movements to different performance situations, and behavioral and neural changes result, as seen in the plasticity with which nonmusicians learn aural-motor associations. Flexibility of motor movements is essential to the interpretive nature of music performance; otherwise, significant additional practice would be necessary before a musician could perform a familiar piece with an alternative interpretation. A second ramification is that performers differ in their individual abilities, as evidenced in interpretive effects on memory, in transfer of learning from one melody to another, and in mental practice benefits. Mental practice is appropriate for study of brain states, measured in EEG, fmri, and MEG studies, because of its avoidance of motion "artifacts". Scientific interest in applying imaging methods and motion capture techniques to music performance suggests that answers may soon be found to the interesting question of how motor aspects of music performance are represented in memory.

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Memory for Music Performance 30 Figure Captions Figure 1. Picture of reflective markers on pianist's right hand fingers and piano keys from Palmer and Dalla Bella (2004). Figure 2. Pianist's fifth finger height above keyboard in terms of position (top panel), velocity (middle panel), and acceleration (bottom panel) during a single performance of the melody shown at top, at a moderate tempo (bpm = 120). Vertical lines indicate time of each keypress (as recorded on MIDI keyboard). Memory for Music Performance 31 Memory for Music Performance 32

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Focus of Attention Affects Performance of Motor Skills in Music Robert A. Duke¹, Carla Davis Cash², and Sarah E. Allen³

Abstract

To test the extent to which learners performing a simple keyboard passage would be affected by directing their focus of attention to different aspects of their movements, 16 music majors performed a brief keyboard passage under each of four focus conditions arranged in a counterbalanced design—a total of 64 experimental sessions. As they performed the test passage, participants were directed to focus their attention on either their fingers, the piano keys, the piano hammers, or the sound produced. Complete MIDI data for all responses were digitally recorded by software written specifically for this experiment. Consistent with findings obtained in tests of other physical skills, the results show that performance was most

accurate and generalizable when participants focused on the effects their movements produced rather than on the movements themselves, and that the more distal the focus of attention, the more accurate the motor control. Keywords motor learning, focus of attention, music skills

The skillful execution of complex motor behavior requires efficient processing of sensory feedback, which facilitates moment-to-moment adjustments in the parameters of movements that skilled behaviors comprise. Of course, the nature of skillful movement changes over time, as learners become more familiar with movement structures and more accurate in their performance. In tasks as varied as riding a bicycle, hitting a baseball, and playing the piano, there are numerous sources of sensory feedback, Downloaded from jrm.sagepub.com by Robert Duke on February 12, 2011

2 Journal of Research in Music Education XX(X) including proprioception. The development of skill is a process by which learners come to notice and respond to external variables that matter and ignore variables that are superfluous, shifting their focus of attention from proximal, near-term goals to more distal, long-term goals (Beilock, Bertenthal, McCoy, & Carr, 2004; Ford, Hodges, & Williams, 2005; Wulf, Shea, & Matschiner, 1998). Learning where to devote limited attentional resources is an obvious challenge for novices. Depending on the extent to which movements in a novel skill resemble those commonly practiced in everyday motor behavior, focusing attention on movement goals (i.e., the effects that movements produce) may be more advantageous than focusing on the movements themselves (i.e., the movements of limbs and fingers; for a review, see Wulf, 2007). This topic has been of interest to researchers studying motor behavior and procedural memory for several decades. Their findings seem particularly germane to applications in music performance, but as yet no one has researched the topic of attentional focus in terms of its effects on the motor behavior of musicians, whose physical movements produce auditory feedback. Investigations of musicians' practice have begun to reveal aspects of practice structure and learner cognition that contribute to the effectiveness of practice by experts (Chaffin & Imreh, 1997, 2001, 2002; Chaffin, Imreh, Lemieux, & Chen, 2003; Duke, Simmons, & Cash, 2009; Gruson, 1988; Maynard, 2006; Williamon, Valentine, & Valentine, 2002) and novices (McPherson, 2005; Miksza, 2007; Rohwer & Polk, 2006). Other research in music education has begun to connect work performed in related disciplines to the learning and teaching of music skills, adopting experimental procedures that have proven effective in illuminating fundamental principles of human learning and procedural memory formation (Cash, 2009; Duke, Allen, Cash, & Simmons, 2009; Duke & Davis, 2006; Simmons & Duke, 2006). The study of attentional focus in the performance of music skills likewise may contribute to a deeper understanding of music learning. The learning of a given movement structure, especially one that is highly complex like many of the skills involved in music performance, seems to benefit from different attentional foci at different stages of skill acquisition and refinement. Thus, teachers may facilitate learning by optimally directing learners' attention to strategically selected points of focus, a notion that is not unfamiliar to teachers of music, who often direct learners' attention to various components of sound production. As one might imagine, the execution of novel motor skills necessarily involves the recruitment of long-practiced movement structures that have become highly automatized by the time the new skills are introduced. Learning to dance, for example, recruits procedural memories related to balance in movements like walking and running; learning to sing recruits procedural memories related to speaking; and learning to play baseball recruits procedural memories related to grasping, reaching, and aiming at targets. Attending to body movements that have become highly automatized over a lifetime of experience can disrupt the performance of well-practiced skills. It has been demonstrated repeatedly that increased attention to the movement of limbs (e.g., focusing on a leg movement in a soccer kick, as opposed to focusing on the intended

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trajectory of the ball), whether self-initiated or in response to instructions or feedback, interferes with the automatic control processes usually engaged during execution. Attending to movement goals (external focus) rather than on movements themselves (internal focus) has been shown to result in more rapid skill acquisition and more accurate performance (Beilock, Carr, MacMahon, & Starkes, 2002; Shea & Wulf, 1999; Wulf, Höß, & Prinz, 1998; Wulf & Prinz, 2001; Wulf, Weigelt, Poulter, & McNevin, 2003). The implications of these and similar results for instruction are clear: Optimally directing learners' focus of attention may enhance the acquisition and refinement of motor skills. In several experimental settings with simulated slalom skiing and balancing tasks, for example, participants who were directed to focus on the effects of their body movements (e.g., the force exerted on either side of a ski-simulator platform) generally performed better than did those who were directed to focus attention on the movements of their feet and better than those given no focus directions (Wulf, Höß, et al., 1998). It is important to note that the term focus in this research does not refer to visual focus but to focus of attention (i.e., what one is thinking about). In fact, in much of the laboratory research in this domain, participants look at a visual fixation point throughout all of the experimental conditions. The effectiveness of an external focus of attention also has been observed in more naturalistic settings outside the laboratory. Wulf and colleagues demonstrated, for example, that golfers who were instructed to focus attention on the swing of their arms (internal focus) made less accurate shots than did those who focused on the motion of the club head (Wulf, Lauterbach, & Toole, 1999). When learners focus on movement goals, the skills they develop tend to transfer more readily to similar tasks that have not been explicitly practiced (Maddox, Wulf, & Wright, 1999; McNevin, Shea, & Wulf, 2003; Totsika & Wulf, 2003). For example, Maddox and colleagues (1999) found that participants who first practiced a backhanded tennis swing while focusing on the trajectory of the ball were later more successful at forehanded swings than were participants who focused on the ball-racket contact point. Both groups executed similar movements, but learners who attended to the movement goal—the ball's trajectory—produced more accurate shots during practice and retention sessions. The effects of attentional focus are not independent of the skill levels of learners. Learners who are first introduced to novel skills of moderate to high complexity produce more consistent and accurate performances when initial instructions focus attention on body movements (internal focus). In contrast, learners who are more skillful or who in the past have practiced skills similar to a new skill being learned tend to benefit more from instructions that focus attention on movement goals (Beilock et al., 2002; Castaneda & Gray, 2007; Perkins-Ceccato, Passmore, & Lee, 2003). Of course, a given movement may result in more than one observable effect, which raises the question of which of several effects should be the focus of learners' attention. McNevin et al. (2003) speculated that focusing on effects of movements that are in close proximity to the body may not be distinguishable from focusing on body movements themselves and that the advantages of external focus are enhanced as the distance increases between the external cue and the body. In many instances, as the focus of attention moves farther from the body, improvements are seen earlier in the learning process (Maddox et al., 1999; McNevin et al., 2003; Totsika & Wulf, 2003; Wulf, McNevin, Shea, & Wright, 1999). Yet, there seems to be an optimal distance at which external cues are most beneficial. Movement goals that are too far removed from movements themselves, such as the landing point of a golf ball, may be so distant from the actual movement structure as to provide no meaningful information to the learner (McNevin et al., 2003; Wulf, McConnel, Gartner, & Schwarz, 2002). Wulf, McNevin, and Shea developed what they termed the constrained action hypothesis to explain comparative benefits of external over internal attentional focus (McNevin et al., 2003; Wulf, McNevin, & Shea, 2001). According to this view, learners who

direct attention to their bodies begin to consciously control movements that have long ago become automatized and require little conscious effort. When the motor system is constrained by this contrived attentional focus, processes that would have occurred automatically may be inhibited. The constrained action hypothesis is supported by findings demonstrating the differing attentional demands of a balancing task. Wulf and colleagues (2001) observed that learners standing on a balance platform who were instructed to keep marks on either side of the platform level were significantly faster in reacting to an unrelated auditory cue than were learners who were instructed to keep their feet level. The shorter reaction times indicated reduced attentional demands in the external focus condition. Additionally, those in the external focus group showed more frequent balance adjustments and adjustments of smaller magnitude, indicating greater use of automatic processes that implement quicker and more refined movements (Wulf et al., 2001). Differential effects of attentional focus have been demonstrated at the neuromuscular level as well (Vance, Wulf, Töllner, McNevin, & Mercer, 2004). Using electromyography (EMG) to measure electrical activity from muscle contractions, Vance and colleagues (2004) found higher levels of muscle activity when participants who lifted a curl bar focused on the movements of their arms than when the same participants focused on the movement of the bar, a result that demonstrates the increased physical efficiency obtained when automatized movement processes are engaged. The development and refinement of skills in music undoubtedly involve many of the processes described in the extant research reported above. But as yet there has been no systematic research conducted with experienced musicians in music contexts. In this experiment, we tested the extent to which learners' focus of attention affects the evenness of motor movements on a piano keyboard. Unlike many of the motor skills investigated to date, music performance includes an auditory component that provides immediate feedback to the player. We wanted to learn whether directing performers to focus on their body movements, the movements of the piano keys and hammers, or the sound of the keyboard would affect motor control. Downloaded from jrm.sagepub.com by Robert Duke on February 12, 2011 Duke et al.

5 Method Participants were 16 music majors (8 males) enrolled in various programs in the Sarah and Ernest Butler School of Music at The University of Texas at Austin. All were between the ages of 25 and 57 and volunteered to participate. Twelve (7 males) were nonpianists who had extensive training in orchestral instruments; 4 (1 male) were advanced pianists. Participants played a 13-note sequence composed of alternating sixteenth notes (see Figure 1) using the index and ring fingers of the right hand on a Roland KR-4700 digital piano. To compare the effects of different attentional foci, participants were directed to focus on either their fingers, the keys, the piano hammers, or the sound produced. All participants performed in all four conditions. The orders of conditions were arranged in a counterbalanced design, and order was randomly assigned to participants. Testing took place in a small room, free of distractions. Throughout the procedure, participants wore Bose QuietComfort 2® noise canceling headphones through which we transmitted all demonstrations, metronome start signals, and the sounds of the digital piano as they played. Customized software written specifically for this experiment using Max/MSP (Puckette & Zicarelli, 2004) controlled all aspects of the experiment and data collection.¹ Each participant performed the test skill at a speed that was 75% of his or her maximum speed. To determine their maximum speeds, participants alternately played the notes A and F “as quickly and evenly as possible” until they were instructed to stop. We used 75% of this speed as the performance tempo for all subsequent trials in that session. Participants established a maximum tempo at each session of the experiment. Sessions comprised (1) a test of maximum tempo, (2) four training blocks, (3) a retest of performance on the trained task, and (4) a transfer test as described below. Two computerized demonstrations of the sequence at the participant's target tempo were played prior to the start of the training session. Each trial began with a visual (written text) and

auditory (spoken) prompt reminding participants of the intended focus of attention (e.g., “Think about the keys”), followed by a metronome sound clicking at the target tempo. The metronome continued until the participant played the first note of the sequence, after which the metronome stopped. Each trial ended with the participant’s 13th key press. Participants’ instruction during the training session was to perform the sequence “as evenly as possible” in the tempo set by the metronome. There was a 2-sec delay before the beginning of the subsequent trial. Throughout the entire Figure 1. Test sequence as presented to participants

Downloaded from jrm.sagepub.com by Robert Duke on February 12, 2011 6 Journal of Research in Music Education XX(X) experiment, participants directed their visual gaze to the computer screen in front of them, on which was displayed the attention cue in text prior to the start of the metronome (e.g., “Think about the keys”), which was replaced by a large letter X in the center of the screen during the trial. Training sessions for each of the four focus conditions consisted of four blocks of 10 trials each. Training blocks were separated by 30-sec rest periods. The fourth block of training was followed by a 5-min delay, after which participants performed a retest, which comprised an additional block of 10 trials under the same conditions. A transfer test consisting of one 10-trial block of the sequence in inversion (starting and ending on F4) was administered 2 min following the retest. All 16 participants completed each of the four focus conditions after rest periods of a minimum of 5 min to avoid fatigue. We assessed evenness in terms of both the evenness in timing and evenness in volume among tones in the sequence. To assess temporal evenness, we calculated the standard deviation of the interonset intervals, in milliseconds, between consecutive tones in each sequence (IOI SD). We assessed evenness in loudness by calculating the standard deviation of the difference scores between the key velocities (the downward rates of travel of individual keystrokes) of consecutive tones in each sequence (KV SD). To obtain an accurate measure of participants’ sustained motor control, we used only the inner 10 tones of each sequence in our data analyses, excluding the 1st, 2nd, and 13th tones. Results We found that temporal evenness (IOI SD) was differentially affected by focus of attention, which is consistent with results obtained in the contexts of other motor behavior. This is the first instance in which focus on an auditory goal (in this experiment, the sound produced by the piano) has been shown to produce an effect on motor behavior similar to that produced by focusing on distal physical goals. We found no consistent differences in KV SD attributable to the experimental conditions, however. Although KV SD varied considerably among participants and among conditions, there were no consistent differences that seemed related to focus of attention. We present details of only the timing analysis below. Recall that all 16 participants performed in all conditions in counterbalanced orders— a total of 64 experimental sessions. Upon initial examination of the performance data, we recognized that the responses of the 4 advanced pianists differed markedly from those observed among the 12 instrumental musicians who were less-skilled pianists. We therefore report the pianists’ and nonpianists’ performances separately. Figure 2 presents the mean deviations in IOI (IOI SD) in the four blocks of training, the retest, and the transfer test for the 12 nonpianists. Evenness by condition was measured by calculating the standard deviation of the IOIs in each trial and averaging the SDs for each trial to obtain a mean IOI SD for each block. During training, nonpianist participants showed the greatest improvement between Training Blocks 1 and 2 in every condition, with the sound focus resulting in the largest improvements and most even performances. There was little to no improvement between the second and third training blocks, and Block 4 performances tended to be Downloaded from jrm.sagepub.com by Robert Duke on February 12, 2011 Duke et al. 7 less even than performances in Block 3, perhaps as a result of fatigue. In general, focusing on the sound produced the most even timing across training blocks, although we did not test for differences among conditions at training. At retest and in the transfer test, participants performed more evenly when focusing

on the sound produced than when focusing on the movements of their fingers. The differences among the four conditions at retest, although consistent with other research, were not statistically significant, $F(3, 33) 1.79, p ! .16$; the differences among the conditions in the transfer task were significant, $F(3, 33) 2.92, p .05, \eta^2 .21$. In the transfer performances in particular, attentional foci more distal to the performer (hammers, sound) produced more even movements than did more proximal foci (fingers, keys). Post hoc comparisons (LSD) indicate that the mean IOI SD for the fingers condition was not significantly different from the keys condition ($p ! .97$) but was significantly higher (indicating greater unevenness) than the mean IOI SDs for the hammers ($p .05$) and sound ($p .05$) conditions, which were not significantly different from one another. Analyses of the four expert pianists' performances indicated no differences among conditions, irrespective of the focus of attention to which they were directed. Their mean IOI SD throughout all sessions was approximately 40% lower than the mean IOI SD for the 12 nonpianists in the study.

Training Block	Mean Interonset Interval (IOI)	Standard Deviation (IOI SD)	Fingers	Keys	Hammers	Sound
1	12	13				
2	11	12				
3	11	12				
4	11	12				
Retest	14	11				
Transfer	14	11				

Figure 2. Mean interonset interval (IOI) standard deviation for each condition at four blocks of training, retest, and transfer

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Discussion Our purpose in this study was to test whether the motor behavior of musicians would be affected by directing their attention to different aspects of their performance. We in fact found significant results that are consistent with those observed in the study of other motor skills that do not involve auditory feedback. We did not observe significant differences among conditions in the retest, which was separated from training by a 5-min rest interval; only in the transfer test were participants' performances affected by their focus of attention during training. In discussing the results of their investigation of attentional focus in a balancing task, McNevin et al. (2003) explained that even though increasing the distance of the effect from the action producing it did not produce immediate performance improvements (a trend for immediate performance benefits was only seen for the far inside condition), the present results were clear in showing that increasing the distance of the effect from the action producing it, through the attentional focus manipulation, enhanced learning. (p. 27) Whereas the retest in the present investigation may have been too close to the training blocks to reveal effects of differential focus conditions on performance of the trained task, the transfer task, which required participants to perform a movement structure that was sufficiently different from the training task, may in fact have served as a measure of learning. Further investigations are needed to clarify these speculations. The sizes of the effects observed are relatively small and may have no direct application to pedagogical prescriptions, but the results are informative with regard to the cognitive organizational structure of motor behavior in music. Our results support Wulf et al.'s (2001) constrained action hypothesis. It seems that in this limited example of a music performance skill, participants performed more effectively when they were able to recruit automatized components of long-practiced motor behavior by focusing on the effects that their movements produced, rather than focusing on the movements themselves. This seems to be the most important aspect of our findings and the basis for continued research. The fact that the advanced pianists were unaffected by the instructions is entirely consistent with this interpretation. The finding that pianists performed consistently more evenly than nonpianists, yet failed to improve over time, suggests that perhaps pianists' motor movements are so practiced that pianists tend to play the same way, despite their attentional focus. Or, perhaps pianists are so accustomed to attending to different aspects of their body, the instrument, or the sound while playing that our instructing them specifically to do so made no difference in their performance. These pianists' results are unlike those obtained by Beilock et al. (2002), Perkins-Ceccato et al. (2003), and Castaneda and Gray (2007), who found that higher skilled learners benefited from externally focused

instructions. Further research is clearly needed on the interaction between expertise and attentional focus in music. Downloaded from jrm.sagepub.com by Robert Duke on February 12, 2011 Duke et al. 9 Because all participants were able to hear the sound in every condition, irrespective of the instructions given, it is difficult to know how the presence of this feedback affected their performance. Several participants reported having difficulty not reacting to the sound feedback while they were playing, which is understandable since musicians who have been the beneficiaries of excellent training have learned to listen to the sounds they produce and make adjustments as they play. This may have made it difficult and perhaps unnatural for our participants to attend to something other than the sound. Fatigue and boredom were undoubtedly a consideration in the four training session blocks. Although participants were aurally and visually reminded before each trial to focus their attention on the target, it is impossible to determine to what extent they were successful at maintaining this focus. Several participants reported having difficulty in maintaining concentration in the last few trials of each block. Future studies may benefit from arranging training blocks of fewer than 10 trials each. It is now widely accepted, based on the results of a number of published investigations, that the recruitment of automated control processes in the learning of novel skills increases both the efficiency and transferability of learned skills. Our results demonstrate that the sound produced by a musical instrument, under the control of a performer, seems to function as a movement goal similar to physical movement goals that have been studied previously. This result is an important part of understanding motor control in the context of music performance. Of course, the admonition to “listen to your sound” is commonly heard in the lessons of musicians at all levels of experience and expertise, but the results of this and previous research deepen our understanding of why this functions as an effective strategy. All teachers and students are interested in maximizing efficiency in learning. The evidence from this and other research indicates that focusing attention in ways that exploit the long-practiced aspects of motor control may optimize the acquisition and refinement of skills. Future investigations that look more specifically at aspects of motor control involved in tone production and the movements of fingers and limbs on wind and string instruments promise to provide further insight into the processes of music learning.

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Note 1. Max/MSP is an interactive programming environment that allows users to design software that controls various aspects of auditory and visual events. The software was designed origiDownloaded from jrm.sagepub.com by Robert Duke on February 12, 2011 10 *Journal of Research in Music Education* XX(X) nally for electronic composition. For this study, a programmer created the software that provided real-time recording of all MIDI data from the digital keyboard, as well as a graphic interface (screen that participants viewed), pre-taped audio instructions, and a timer that alerted participants to the start of each trial.

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