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# Age related differences in the neural substrates of motor sequence learning after interleaved and repetitive practice

Chien-Ho (Janice) Lin <sup>a,b,1</sup>, Ming-Chang Chiang <sup>c,1</sup>, Allan D. Wu <sup>a,b</sup>, Marco Iacoboni <sup>b,d</sup>, Parima Udompholkul <sup>a</sup>, Omid Yazdanshenas <sup>e</sup>, Barbara J. Knowlton <sup>e,\*</sup>

- <sup>a</sup> Department of Neurology, David Geffen School of Medicine, University of California, Los Angeles, 710 Westwood Plaza, Reed A-134, Los Angeles, CA 90095, USA
- b Ahmanson-Lovelace Brain Mapping Center, University of California, Los Angeles, 660 Charles Young Drive South, Los Angeles, CA 90095, USA
- <sup>c</sup> Department of Biomedical Engineering, National Yang-Ming University, Taiwan
- <sup>d</sup> Department of Psychiatry and Biobehavioral Sciences, University of California, Los Angeles, CA 90095, USA
- <sup>e</sup> Department of Psychology, University of California, Los Angeles, 6623 Franz Hall, Los Angeles, CA 90095, USA

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#### ABSTRACT

Practice of tasks in an interleaved order generally induces superior retention compared to practicing in a repetitive order. Younger and older adults practiced serial reaction time tasks that were arranged in a repeated or an interleaved order on 2 successive days. Retention was tested on Day 5. For both groups, reaction times in the interleaved condition were slower than the repetitive condition during practice, but the reverse was true during retention on Day 5. After interleaved practice, changes in M1 excitability measured by paired-pulse TMS were greater than after repetitive practice, and this effect was more pronounced in older adults. Moreover, the increased M1 excitability correlated with the benefit of interleaved practice. BOLD signal was also increased for interleaved compared to repetitive practice in both groups. However, the pattern of correlations between increased BOLD during practice and subsequent benefit of the interleaved condition differed by group. In younger adults, dorsolateral-prefrontal activity during practice was related to this benefit, while in older adults, activation in sensorimotor regions and rostral prefrontal cortex during practice correlated with the benefit of interleaving on retention. Older adults may engage compensatory mechanisms during interleaved practice such as increasing sensorimotor recruitment which in turn benefits learning.

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#### Introduction

Previous studies have shown that introducing manipulations that make performance more difficult during practice may nonetheless improve long-term retention and transfer (Schmidt and Bjork, 1992). The notion of "desirable difficulties" suggests that challenges for learners such as context shifts and retrieval during study result in enhanced learning and should be introduced into skill practice (Christina and Bjork, 1991). An example of a *desirable difficulty* is the contextual interference (CI) effect where practice context is manipulated by presenting multiple tasks in either a repetitive (blocked) order or an interleaved (random) order (Shea and Morgan, 1979). Practicing tasks in an interleaved order generally induces inferior practice performance but leads to superior retention compared to practicing in a repetitive order (Brady, 2008). This differential effect of practice condition during practice and retention phases is an example of the distinction between performance and learning.

The CI effect was initially demonstrated in the verbal learning literature (Battig and Berry, 1966) and was subsequently studied in learning of motor tasks (Shea and Morgan, 1979). Shea and Morgan's results demonstrated that during practice, a more difficult condition (interleaved practice) resulted in worse performance but leads to better retention and transfer compared to a less difficult condition (repetitive practice). The poorer performance during interleaved practice implies that greater effort expended in a more difficult condition may facilitate long-term retention.

Despite the age-related decline in accuracy or speed at making fine movements (Spirduso et al., 2005), healthy older adults remain readily able to acquire new skills and procedures (Kausler, 1994). Studies of motor sequence learning have demonstrated similar levels of sequence learning in older and younger adults (Fraser et al., 2009; Howard and Howard, 1989), although sequence-specific learning in older adults may be slower (Daselaar et al., 2003; Lin et al., 2010), may show less transfer (Seidler, 2006), and may not consolidate as effectively (Brown et al., 2009; Nemeth and Janacsek, 2011). Another similarity in sequence learning for older and younger adults is the finding that both groups benefit equally from interleaved practice on a delayed retention test (Lin et al., 2010). These findings underscore the generality of the CI effect,

<sup>\*</sup> Corresponding author at: Department of Psychology, University of California, Los Angeles, 6623 Franz Hall, Los Angeles, CA 90095-7332, USA.

E-mail address: knowlton@psych.ucla.edu (B.J. Knowlton).

 $<sup>^{1}\,</sup>$  Contributed equally to this work.

and demonstrate that variable practice has a beneficial effect on neural plasticity in healthy aging.

Recent neuroimaging studies have demonstrated that even when behavioral performance is matched, younger and older adults show different brain activation patterns (Morcom et al., 2003). Some activation patterns in older adults are related to optimal performance, suggesting compensatory potential in the aging brain (Cabeza et al., 1997; Lin et al., 2011). There is also evidence suggesting that encoding-related activation patterns that predict subsequent successful retrieval in older adults are different from those that are associated with subsequent retrieval in young adults (Morcom et al., 2003). These data suggest that older adults may engage different neural circuitry from young adults to reach the same behavioral endpoint.

The present study was designed to address two main questions. First, does interleaved practice of sequences result in increased neural activity compared to repetitive practice in older adults, a similar pattern we have previously identified in younger adults (Lin et al., 2011)? Second, is increased neural activity during interleaved practice associated with enhanced learning and whether aging may modulate this correlation? In this study, our measures of neural activity are blood-oxygen-level-dependent (BOLD) signal and cortical motor excitability as assessed by paired-pulse transcranial magnetic stimulation (ppTMS) (Kujirai et al., 1993). As such, we were also able to relate changes between these two measures of neural activity with each other.

Participants were scanned using fMRI during 2 days of practice of a sequence learning task and during a retention test on Day 5. Neurophysiologic changes in primary motor cortex (M1) excitability were evaluated by ppTMS offline (while participants were at rest) before and after each fMRI practice session and before the fMRI retention test. Based on our previous work and the prediction of desirable difficulties in CI, we anticipated that for both age groups, practicing sequences in an interleaved order would result in inferior performance during practice but would induce superior sequence-specific learning compared to practice in a repetitive order (Shea and Morgan, 1979). We anticipated that within each age group, the desirable difficulty effect of CI will manifest as greater sensorimotor activity (measured by BOLD signal) and M1 excitability (measured by ppTMS) during interleaved compared to repetitive practice given that increased task complexity typically results in increased BOLD signal during practice (Kuhtz-Buschbeck et al., 2003; Verstynen et al., 2005). However between age groups, BOLD signal during practice will be greater in older than younger adults based on previous findings showing aging-related hyperactivation on cognitive tasks (Gutchess et al., 2005). For the same reason, increased M1 excitability associated with interleaved practice was expected and that may be maintained at the retention test given that enhanced excitability associated with motor practice may constitute a necessary precursor for inducing plastic changes within the motor system (Koeneke et al., 2006; Pascual-Leone et al., 1995). Furthermore, we anticipated that for both younger and older adults, increased sensorimotor BOLD activity and M1 excitability during interleaved practice would correlate with the level of skill learning (Tamas Kincses et al., 2008). However, the brain regions that show functional correlations with enhanced learning may differ between the two age groups.

To our knowledge, this is the first study that combines fMRI and paired-pulse TMS measures as biomarkers to examine age-related changes in neuroplasticity. Our use of the CI paradigm, which has been shown to benefit learning of motor skills, allows us to identify how aging may modulate the neural mechanisms of optimized learning.

#### Materials and methods

#### **Participants**

Sixteen younger (9 men and 7 women, mean age  $26.4\pm3.1$ ) and sixteen older (7 men and 9 women, mean age  $66.2\pm4.7$ ) righthanded adults were enrolled in the study. Participants were recruited from the University and adjacent community. All participants gave

informed consent using an institutionally approved consent form. Participants were excluded if they had any neuromuscular condition which prevents them from performing the task. Participants were also excluded for any contraindications to TMS or MRI, significant medical, neurological, or psychiatric history, a history of seizure, prescription medications, a family history of uncontrolled epilepsy, uncorrected vision loss, or scored less than 28 on the Mini-Mental State Exam (MMSE; Folstein et al., 1975).

Study design

For both younger and older adults, we applied a within-subject cross-over design with three measurements: behavior (serial reaction time sequence learning task, Fig. 1A) (Nissen and Bullemer, 1987), cerebral hemodynamic responses by functional magnetic resonance imaging (blood oxygen level dependent signals (BOLD), fMRI), and intracortical excitability within the primary motor cortex (M1) by paired-pulse transcranial magnetic stimulation (ppTMS). Therefore, age-group is a between-subjects factor and practice condition is a within-subject factor. The participants practiced the serial reaction time (SRT) task on two consecutive training days (Days 1 and 2, Fig. 1B). To measure the effects of practice on learning, we tested the delayed retention performance on Day 5 (Cahill et al., 2001; Lin et al., 2011; Perez et al., 2005; Shea and Morgan, 1979; Wright et al., 2005) (Fig. 1B). Behavioral and fMRI data were acquired concurrently on each testing day within the MR scanner, while the pairedpulse TMS (ppTMS) was performed immediately before and after each training day and before the retention session on Day 5 in the adjacent TMS laboratory (Figs. 1B and C). ppTMS was applied to evaluate the excitability of intracortical circuits in M1 (Kujirai et al., 1993). The present study did not aim to investigate the difference between implicit and explicit sequence learning, in that the sequences were short and practiced extensively. All participants were informed of the presence of sequences prior to practice. The SRT task was chosen here to study contextual interference because one can readily create multiple sequences that can be learned in either an interleaved or repetitive order. In addition, the SRT finger tapping task is a motor task that is readily adapted to fMRI because it involves minimal motion of the upper body, thus allowing us to assess BOLD signal differences between practice conditions and participant groups.

Participants practiced and learned a variation of the SRT task over the course of 5 days, which consisted of three different four-element sequences, presented in either a repetitive or interleaved order (Fig. 1B, also see "Behavioral task" below for details). In this within-subject cross-over design, each participant started in the first week with either the Repetitive practice (RP) or the Interleaved practice (IP) condition; 2 weeks later, each participant participated in the other practice condition (i.e., Repetitive → Interleaved, or vice versa). The order of the practice conditions and the SRT sequences were counterbalanced across participants.

Functional images were acquired concurrently while the SRT was performed inside the MR scanner. For Days 1 and 2, there were three functional imaging runs on each day (Fig. 1B). Each run consisted of 54 movement trials, where the participants practiced one test sequence in each trial. For Repetitive practice (RP), each of the three test sequences was practiced for 54 consecutive trials (i.e., one fMRI run) before the next sequence appeared, resulting in 162 trials (54 trials×3 test sequences) for each day (Fig. 1B top). The order of the three sequences was counter-balanced across the participants. For Interleaved practice (IP), the three test sequences were arranged in a non-repetitive manner within each 54-trial fMRI run (Fig. 1B bottom), and the same arrangement of the test sequences was applied to all the participants, so that every IP participant performed the same order of test sequences.

On the retention day (Day 5), the participants underwent 3 fMRI runs, with 36 trials per run (Fig. 1B, Day 5). In the first two runs, they were tested with the three sequences they had practiced in the

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