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Motor imagery-based implicit sequence learning depends on the formation of stimulus-response associations

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ABSTRACT

Implicit sequence learning (ISL) occurs without conscious awareness and is critical for skill acquisition. The extent to which ISL occurs is a function of exposure (i.e., total training time and/or sequence to noise ratio) to a repeated sequence, and thus the cognitive mechanism underlying ISL is the formation of stimulus-response associations. As the majority of ISL studies employ paradigms whereby individuals unknowingly physically practice a repeated sequence, the cognitive mechanism underlying ISL through motor imagery (MI), the mental rehearsal of movement, remains unknown. This study examined the cognitive mechanisms of MI-based ISL by probing the link between exposure and the resultant ISL. Seventy-two participants underwent MI-based practice of an ISL task following randomization to one of four conditions: 4 training blocks with a high (4-High) or low (4-Low) sequence to noise ratio, or 2 training blocks with a high (2-High) or low (2-Low) sequence to noise ratio. Reaction time differences (dRT) and effect sizes between repeated and random sequences assessed the extent of learning. All groups showed a degree of ISL, yet effect sizes indicated a greater degree of learning in groups with higher exposure (4-Low and 4-High). Findings indicate that the extent to which ISL occurs through MI is impacted by manipulations to total training time and the sequence to noise ratio. Overall, we show that the extent of ISL occurring through MI is a function of exposure, indicating that like physical practice, the cognitive mechanisms of MI-based ISL rely on the formation of stimulus response associations.

1. Introduction

Implicit sequence learning (ISL) is a process in which an individual learns a sequence without conscious awareness. Implicit sequence learning has been demonstrated in numerous domains (Destrebecqz & Cleeremans, 2001; Dienes, Broadbent, & Berry, 1991; Jamieson, Vokey, & Mewhort, 2015; Lang, Gapenne, Aubert, & Ferrel-Chapus, 2012; Nissen & Bullemer, 1987; Rohrmeier & Rebuschat, 2012; Sævland & Norman, 2016), including the study of motor learning, where ISL has been shown to be critical for the acquisition of motor skills (Nissen & Bullemer, 1987; Schwarb & Schumacher, 2012; Wilkinson & Shanks, 2004; Willingham, Nissen, & Bullemer, 1989). To investigate the cognitive mechanisms underlying ISL, many studies have employed the serial reaction time task (SRTT; for a review see Schwarb & Schumacher, 2012). In the SRTT, an individual repeatedly practices a seemingly random sequence, comprised of both a perceptual cue (e.g., auditory or visual stimuli) and motor response (e.g., a key press) (Robertson, 2007), in which, unbeknownst to the individual, a repeating sequence is embedded (Schwarb & Schumacher, 2012; Wilkinson & Shanks, 2004). As perceptual-motor learning is facilitated with training, reaction times (RT) to the repeating (but not random) sequences decrease. The implicit nature of learning is demonstrated as the reduction in RT to the repeated sequence occurs despite the fact that participants report not being explicitly aware of the repeating sequence (Nissen & Bullemer, 1987; Robertson, 2007; Schwarb & Schumacher, 2012; Wilkinson & Shanks, 2004; Willingham et al., 1989).

The cognitive mechanism underlying ISL is linked to the formation of stimulus-response associations (Schwarb & Schumacher, 2012), in that modifying total training time and/or the ratio of the repeated sequence to noise (i.e., parameters that influence the formation of stimulus-response associations) impacts the extent to which learning occurs.

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Specifically, the total number of trials can be increased or decreased during an ISL task (i.e., changing total training time; for examples see Kantak, Mummidisetty, & Stinear, 2012; Nissen & Bullemer, 1987; Willingham et al., 1989), and/or the number of sequence repetitions relative to random button presses during a training block can be increased or decreased (i.e., changing the ratio of the repeated sequence to noise; for examples see Jiménez, Vaquero, & Lupiáñez, 2006; Kaufman et al., 2010; Sanchez & Reber, 2012). Considered together, total training time and the sequence to noise ratio determines the total number of repetitions performed during training, which we refer to as exposure.

Nissen and Bullemer (1987) first demonstrated that ISL could be detected within a single training block, and further showed that ISL became more robust as total training time increased, as RT to the repeated sequence decreased across subsequent blocks of training. A large body of literature investigating the mechanisms of ISL has since been generated using variations of the SRTT to provide further evidence that, until asymptote is reached, the extent of learning increases with increased training time as shown by a decrease in RT to the repeated vs. random sequences (Destrebecqz & Cleeremans, 2001; Goschke & Bolte, 2012; Kantak et al., 2012; Nissen & Bullemer, 1987; Schwarb & Schumacher, 2012; Wilkinson & Shanks, 2004; Willingham et al., 1989). Further, research has also established that the sequence to noise ratio within a training block also impacts the extent to which learning occurs (Jiménez et al., 2006; Kaufman et al., 2010; Sanchez & Reber, 2012). Using a modified version of the SRTT, in which participants responded at precise times to a seemingly random order of targets moving on the screen, Sanchez and Reber (2012) reduced the sequence to noise ratio by increasing the amount of 'noise' or number of random sequences within a training block. Indeed, only weak learning was observed when the sequence to noise ratio was too low. Thus, reducing the sequence to noise ratio (i.e. increasing the amount of noise while maintaining the equivalent training time) is shown to result in decreased learning (Jiménez et al., 2006; Kaufman et al., 2010; Sanchez & Reber, 2012; Schvaneveldt & Gomez, 1998).

While both total training time and the sequence to noise ratio can be manipulated independently to impact the extent of ISL that occurs, it is suggested that the exposure to the repeated sequence during training can be used to predict the resulting ISL (Reber, 2013; Sanchez & Reber, 2012). In the aforementioned study (Sanchez & Reber, 2012), while learning was shown to weaken when the sequence to noise ratio was too low, it was shown that this effect occurred not owing to the introduction of more noise, but because there were too few repetitions of the repeated sequence practiced during training to adequately facilitate the formation of stimulus-response associations. In support of this conclusion, it was further shown that the rate of ISL is strongly related to the logarithm of the number of repetitions of the sequence to which the participant is exposed to during training (Sanchez & Reber, 2012). In other words, it has been shown that the extent of ISL is best predicted by exposure to the repeated sequence during training.

Collectively, this evidence indicates that ISL results from the formation of stimulus-response associations, and the extent to which ISL occurs is a function of exposure to the repeated sequence, which can be modified by manipulating total training time and/or the sequence to noise ratio. Not surprisingly, our understanding of the cognitive mechanisms of ISL comes from studies employing paradigms in which participants physically execute the SRTT, as physical practice is the primary modality used for acquiring or strengthening motor skills. As shown in past literature, motor imagery (MI), the mental rehearsal of motor tasks, has been demonstrated to be effective for improving performance and facilitating skill learning in numerous domains (Jeannerod, 1995; Wulf, Shea, & Lewthwaite, 2010). Specifically, while MI can be performed a number of ways, kinaesthetic imagery (i.e., imagery performed while emphasizing the sensations of the action during imagined performance) is the form of MI proposed to best facilitate basic motor skill learning (Stinear, Byblow, Steyvers, Levin, & Swinnen, 2006). Further, there is evidence to suggest that kinaesthetic imagery, when performed from the first person perspective, is thought to be more 'functionally equivalent' to motor execution than other types of imagery (Callow & Hardy, 2004; Callow, Jiang, Roberts, & Edwards, 2016; Callow, Roberts, Hardy, Jiang, & Edwards, 2013; Holmes & Collins, 2001; Jiang, Edwards, Mullins, & Callow, 2015), and is thus the focus of the current study. To date, a limited number of studies have investigated ISL achieved through MI-based practice, and as such we lack a general understanding of the cognitive mechanisms that underlie ISL occurring through MI-based practice.

Previous research has shown that ISL can be facilitated through MI (Kraeutner, MacKenzie, Westwood & Boe, 2016; Wohldmann, Healy, & Lyle, 2007). Wohldmann et al. (2007) first demonstrated that practicing novel four-digit sequences through MI resulted in improved typing ability without explicit knowledge of the sequences. Further, our past work showed robust ISL resulting from MI-based practice using training parameters previously shown to facilitate ISL through physical practice (Kraeutner, MacKenzie, et al., 2016). In this study, participants engaged in four blocks of training with a high sequence to noise ratio, via either physical practice or MI-based practice. Equal learning was shown between the practice modalities, in that the degree to which RTs to the implicit vs. random sequences of equal length decreased was similar following both forms of practice (Kraeutner, MacKenzie, et al., 2016). While this previous research provides evidence that MI-based practice can drive ISL, we have very little understanding of the cognitive mechanisms underlying MI-based ISL, in particular the relationship between the formation of stimulus-response associations and MI-based ISL has yet to be explored.

Accordingly, the purpose of this research is to examine the cognitive mechanisms of MI-based ISL. By probing the link between exposure and the extent to which ISL occurs, we aim to demonstrate that MI-based ISL, like that of physical practice, depends on the formation of stimulus-response associations. Specifically, our primary objective is to examine the extent to which ISL occurs following reductions in total training time (defined as number of blocks and thus the total number of trials) and the sequence to noise ratio within a training block. It is hypothesized that while learning will occur across all conditions regardless of reductions in exposure to the sequence during training, there will be a difference in the extent of learning that occurs as evidenced through effect sizes observed for each condition.

As a secondary objective, we seek to further explore the extent to which ISL is achieved through MI as a function of exposure. Specifically, as exposure to the repeated sequence during physical practice-based training has been shown to be a predictor of the resultant ISL (Sanchez & Reber, 2012), it is hypothesized that the exposure to the repeated sequence during training (defined as total number of practiced repetitions of the sequence during training) will be strongly related to the resulting RT difference (dRT) between the implicit vs. random sequences. Ultimately, the current research will add to our understanding of the mechanisms underlying ISL occurring via MI-based practice.

2. Method

2.1. Participants

Seventy-two right-handed subjects (49 females, 23.8 ± 7.2 years) from the local and university community volunteered to participate in the study. Right hand dominance was demonstrated by a score of ≥ 40 on the Edinburgh Handedness Inventory (Oldfield, 1971). All participants were healthy, reported normal hearing, were free of neurological disorders, and each provided written informed consent. Prior to the onset of the study, participants were randomly assigned into one of four groups: 4-High, 4-Low, 2-High, or 2-Low (described below). Prior to beginning the experimental task, all participants verbally confirmed they understood the study instructions. The Dalhousie University research ethics board approved the study.

2.2. Experimental task

All participants underwent MI-based practice of a left-handed ISL task involving MI of button presses in response to auditory cues (Fig. 1). The experimental task was the same as that employed in our previous work (Kraeutner, MacKenzie, et al., 2016), but with manipulations in the total training time and/or to the sequence to noise ratio. Specifically, we employed two different total training times (4 blocks and 2 blocks) and two different sequence to noise ratios (high and low; further detailed below), to create four conditions that allowed us to explore the different variants of exposure: four blocks of practice with a 72:28 sequence to noise ratio (4-High), four blocks of practice with a 60:40 sequence to noise ratio (4-Low), two blocks of practice with a 72:28 sequence to noise ratio (2-High), and two blocks of practice with a 60:40 sequence to noise ratio (2-Low).

The experiment involved first engaging in two or four blocks of training (in accordance with the groups described above). Following the training blocks, participants engaged in a physical test block and completed a verbal report task to determine the implicit or explicit nature of learning that occurred. All participants performed the experiment in a seated position directly in front of a computer screen positioned at eye-level, with the left hand positioned on a keyboard, also in front of the participant on a keyboard tray. Participants were oriented to four keys (V, C, X, Z) numbered 1–4 from right to left, representing the index, middle, ring and little finger respectively. During the MI-based training blocks, participants were instructed to close their eyes and imagine themselves performing the button presses that were cued auditorily through noise-cancelling headphones simultaneously to both ears. The auditory cues consisted of a male voice speaking the number of the key to imagine being pressed (i.e., 1 through 4). If participants responded to the auditory cues by actually pressing a button during the MI-based practice blocks, an error tone was played and the response was recorded. Auditory cues were separated by 1.5 s, and thus each individual trial (i.e., one imagined keypress event) lasted 1.5 s. Each training block consisted of 250 keypresses, with a 5-min rest block provided between each.

During the task, participants were instructed to respond to each auditory cue using MI. However, unknown to the participants, a repeating sequence was embedded within the training blocks consisting of ten digits (constrained such that no two consecutive digits repeated) unique to each participant. For the 4-High and 2-High groups, the repeated sequence was intermixed 28% of the time with random sequences of equal length. Thus, the repeated sequence made up 72% of the total imagined keypress events, amounting to 18 repetitions occurring per training block. For the 4-Low and 2-Low groups, the repeated sequence was intermixed 40% of the time with random sequences of equal length. Thus, in these groups, the repeated sequence made up 60% of the total imagined keypress events, amounting to 15 repetitions occurring per training block. The placement of the repeated sequences within each block was randomized, in that the order the repeated and random sequences appeared to each participant varied.

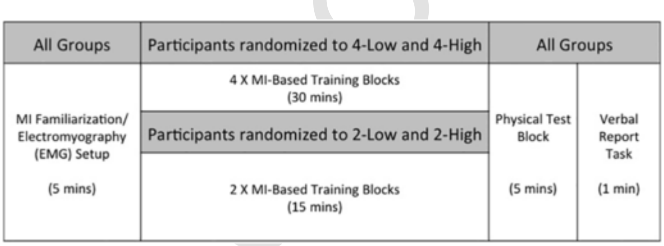

Fig. 1. Timeline of the single experimental session. A reaction time test involving physical performance (i.e., keypresses) of the ISL task and verbal report task followed the MI-based training blocks. Participants either underwent four (4-High or 4-Low) or two blocks of training (2-High or 2-Low), with either a high (4-High or 2-High) low (4-Low or 2-Low) sequence to noise ratio.

2.3. Experimental procedure

The experiment proceeded as in our previous work (Kraeutner, MacKenzie, et al., 2016). In brief, participants first completed the Kinesthetic and Visual Imagery Questionnaire (KVIQ; Malouin et al., 2007) to establish their ability to perform MI, based on achieving a score on the KVIQ within the range previously reported for healthy control subjects (Malouin et al., 2007). Participants then completed a familiarization block prior to undergoing the training blocks, during which they listened to an audio recording describing the type of MI to be performed (kinesthetic), and the task to be imagined (Kraeutner, MacKenzie, et al., 2016).

To monitor muscle activity during MI-based practice, the electromyogram (EMG) was obtained from the left flexor and extensor muscles of the digits (anterior and posterior aspects of the forearm respectively). The EMG signal was acquired using self-adhering electrodes (1×3 cm; Q-Trace Gold; Kendall-LTP, USA) in a bipolar configuration with a 1 cm inter-electrode distance, sampled at 1000 Hz with a bandpass of 25–100 Hz (1902 and Power 1401; Cambridge Electronics Design, UK) and stored for offline analysis.

Immediately following the training blocks, participants performed the two tests to measure performance and determine the nature of learning that occurred. For the physical test block, participants physically performed a shortened version of the experimental task to allow for measurement of RT, wherein the implicit and random sequences of equal length appeared 10 times each (i.e., a 1:1 ratio) for a total of 200 trials. The order that the sequences appeared was again randomized. Conditions were the same as those in the training blocks, except that participants were instructed to respond 'as quickly as possible' by physically pressing the indicated key. In this physical test block, each cue was presented immediately following the previous response. If participants provided an incorrect response (e.g., pressed the '4' key when the '2' key was cued), an error tone was played through the headphones. Responses and the corresponding RTs were recorded for offline analysis. Consistent with the training blocks, participants were not informed about the presence of the repeating sequence in this physical test.

Following the physical test block, participants completed the verbal report task to determine whether or not they were explicitly aware of the repeating sequence. Participants were first informed that there may have been a repeating sequence during training. Participants were then asked to respond "yes" or "no" to the question: "Do you think you learned a sequence during the training blocks"? Importantly, participants were instructed "it was okay if they did not think they learned a sequence". If a participant responded "yes", they were asked if they could report the sequence that they learned (i.e., any of the 10 consecutive numbers). Any numbers the participant reported were recorded and stored for offline analysis to determine whether participants had explicit knowledge of the repeating sequence.

2.4. Data analysis

2.4.1. Identifying explicit learners

Participants that demonstrated explicit learning were excluded from further analysis, as different processes have been shown to underlie explicit and implicit learning (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003). Explicit learning was characterized via the verbal report task as to whether or not participants could correctly identify the sequence (Eimer, Goschke, Schlaghecken, & Stürmer, 1996; Kantak et al., 2012; Rünger & Frensch, 2010). Specifically, participants that answered "yes" to the question of whether or not they thought they learned a sequence and who correctly reported > 50% of the sequence (i.e., 5 consecutive sequence elements), were excluded from further analyses (Ingram, Kraeutner, Solomon, Westwood, & Boe, 2016; Kraeutner, MacKenzie, et al., 2016).

2.4.2. Response analysis

Analysis of the keypress responses made during the training blocks was performed to identify participants who had experienced a degree of physical practice during the MI-based practice. Participants that made responses > 2% (20/1000 or 10/500 responses total for participants engaging in four or two blocks of training respectively) of the time across all MI training blocks were excluded from further analyses, to control for any learning that may have been influenced by physical practice.

2.4.3. EMG analysis

Analysis of the EMG data obtained during MI was performed to further identify and reject participants that demonstrated muscle activity in the left flexor and extensor muscles of the digits during MI, and thus performed physical practice of the ISL task. EMG data was first full wave rectified and a 10 Hz low-pass filter applied. Similar to the approach of Mochizuki, Boe, Marlin, and McIlRoy (2010) and consistent with our prior work (Kraeutner, MacKenzie, et al., 2016), the average amplitude across 15 s envelopes of the EMG signal during each training block was calculated and each envelope was compared to a 15 s envelope acquired during the familiarization block (during which participants were at rest). Participants were excluded if > 15% of the comparisons exceeded a pre-determined threshold, defined as the average rest amplitude plus 2 standard deviations, relative to their baseline (resting) muscle activity (Kraeutner, MacKenzie, et al., 2016; Mochizuki et al., 2010).

2.4.4. Performance analysis

Following the work of Wohldmann et al. (2007) and our previous work (Kraeutner, MacKenzie, et al., 2016), the first element of each sequence within the physical test block was omitted from analysis due to its role in motor initiation vs. motor execution (i.e., the first element of a sequence is a perceptual cue for the movement about to be performed; Wohldmann et al., 2007). Trials with RTs < 100 ms or > 1300 ms were also removed from analysis to control for anticipatory and outlier responses (Rüsseler, Hennighausen, & Rösler, 2001). Lastly, RTs for trials in which an incorrect response was provided were also removed from analysis. The RTs for all remaining trials as well as error rates were then averaged for both the implicit and random sequences for each individual participant. The difference in RT (dRT) between the implicit and random sequences (average RT random minus average RT implicit) was also calculated for each participant.

2.4.5. Group analysis

Shapiro-Wilk and Bartlett's tests showed that data across groups for each sequence met assumptions of normality and thus, to confirm ISL had occurred, a 2 (sequence type) × 4 (group) ANOVA was conducted to compare the RTs for the random and repeated sequences across groups. To explore the extent of learning in each of the four conditions (i.e., our primary objective), effect sizes were calculated between the RTs to the implicit and random sequences of equal length (Kraeutner, MacKenzie, et al., 2016). To explore the extent to which learning occurred as a function of exposure (i.e., our secondary objective), a regression analysis was conducted with the logarithm of the total amount of exposure to the sequence (defined as total number of practiced sequence repetitions) as the predictor variable, similarly to Sanchez and Reber (2012). In addition to the data from the current study, a fifth condition was added using data from Kraeutner, MacKenzie, et al. (2016). Briefly, this fifth condition consisted of 24 participants completing the same ISL task over 4 blocks of training (1000 trials total) with a sequence to noise ratio of 80:20 (i.e., 80 total practiced sequence repetitions). Participants in this fifth condition had a dRT of 49.7 (95% CI [29.2, 70.3]) ms. To replicate previous findings demonstrating that ISL increases according to a log-linear curve, we also conducted a regression analysis using the total amount of exposure to the sequence (i.e., actual number of practiced sequence repetitions; Sanchez & Reber, 2012) to examine whether this model better predicted the magnitude of the dRT. We then conducted a regression analysis using both the total training time and sequence to noise ratio to examine whether this model better predicted the magnitude of the dRT.

3. Results

3.1. Participants

Given the criteria outlined above, 27 participants were excluded from analysis (Fig. 2). Twenty-two participants were excluded for demonstrating explicit knowledge (Fig. 2). From the remaining implicit participants, one participant was excluded (from the 4-High group) for performing 54 keypress responses during MI training, exceeding the 2% threshold as outlined above. Two participants were excluded for the presence of muscle activity during the MI training blocks (one participant each from the 4-High and 4-Low groups) that exceeded the aforementioned threshold. Two participants (one each from the 4-High and 2-Low groups) were also excluded owing to a technical error related to the EMG recording that resulted in a loss of the markers denoting onset/offset of the training blocks. In addition, one participant from the 2-Low group was identified as an outlier, as RTs observed for this participant did not fall within 3 SDs of the overall and group mean and excluded from analysis. Overall, 44 participants total (28 females, aged 23.9 ± 6.8 years) were included in the final data analysis (4-High, $n = 11$; 4-Low, $n = 10$; 2-High, $n = 13$; and 2-Low, $n = 10$; Fig. 2). Importantly, participants across all groups demonstrated scores for visual and kinesthetic imagery within ranges previously reported for healthy controls (Malouin et al., 2007; Table 1).

3.2. Reaction time

The 4-High group had mean RTs of 617 ± 68 and 658 ± 79 ms for the implicit and random sequences respectively. The mean error rate (%) for the 4-High group for implicit and random sequences were 1.2 ± 1.0 and 1.9 ± 1.7. The 4-Low group had mean RTs of 599 ± 70 and 635 ± 49 ms for the implicit and random sequences respectively. For the 4-Low group, the mean error rate for implicit and random sequences was 1.4 ± 0.52 and 2 ± 1.4. In the 2-High group, mean RTs of 636 ± 97 and 667 ± 95 ms were observed for the implicit and random sequences respectively. For the 2-High group, the mean error rate for the implicit and random sequences were 2.5 ± 2.7 and 4.4 ± 3.3. Finally, in the 2-Low group, mean RTs of 590 ± 51 and 604 ± 49 ms were observed for the implicit and random sequences respectively. The mean error rate for the 2-Low group for implicit and random sequences was 1.1 ± 1.3 and 2.7 ± 2.0.

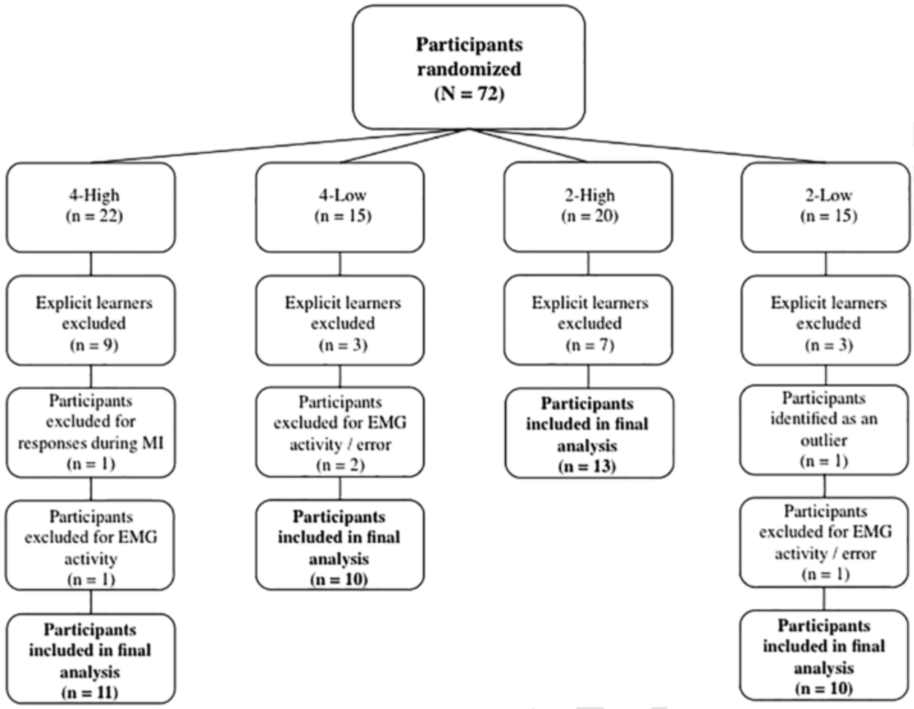

Fig. 2. Summary of participant inclusion and exclusion process. Following application of our exclusion criteria, 28 participants were excluded leaving a total of 44 participants across the four groups.

Table 1
Mean KVIQ Scores for each group. Previous scores reported from healthy controls (Malouin et al., 2007) are included for reference.

Group	Mean Visual MI Score (SD)	Mean Kinaesthetic MI Score (SD)
Malouin et al., 2007[a]	18.5 (4.3)	16.3 (4.2)
	17.7 (3.9)	16.1 (4.4)
4-High	17.9 (4.2)	20.4 (4.3)
4-Low	17.7 (3.3)	20.4 (4.3)
2-High	19.1 (5.0)	19.3 (4.8)
2-Low	21.2 (2.9)	21.4 (4.5)

[a] Scores from a test, re-test paradigm of healthy controls.

3.3. Group comparisons

There was a significant main effect of sequence type [F(1, 40) = 35.60, $p < 0.001$], in that participants were faster to respond to the repeated compared to the random sequence, demonstrating ISL. No main effect of condition was found [F(3,41) = 1.24, $p = 0.31$], and there was no significant interaction between sequence type and condition ([F(3, 40) = 1.15, $p = 0.34$].

Effect sizes were calculated for comparison of RTs for the implicit and random sequence within each group to further characterize the extent to which learning occurred (Cumming, 2014; Kelley & Preacher, 2012; Table 2). Moderate effect sizes were observed for the groups that engaged in a greater amount of total practice time (4-High and 4-Low; Table 2; Fig. 3). Overall, we observed effect sizes for the groups engaging in 4 blocks of practice similar to those observed in previous research ($d = 0.59$; Kraeutner, MacKenzie, et al., 2016) employing four blocks of training with a 80:20 sequence to noise ratio. Small effect sizes were observed within the two block groups (Table 2; Fig. 3).

A regression analysis of the logarithm of the amount of total exposure by resultant mean dRT for each condition (see Fig. 4), performed similarly to Sanchez and Reber (2012), demonstrated that exposure was strongly related to the extent of learning [F(1, 3) = 18.16, $p = 0.024$, SE = 15.16, adjusted $R^2 = 0.81$]. Further, the logarithm of exposure predicted the magnitude of the dRT better than the actual

Table 2
Mean difference between repeated and random sequences (ms; mean dRT and 95% CIs), and corresponding effect sizes for each learning condition, and thus group, as a function of total training time and sequence to noise ratio.

Total training time	4 blocks		2 blocks	
Sequence to noise ratio	High (72:28)	Low (60:40)	High (72:28)	Low (60:40)
dRT [95%CI]	41.0 [12.7, 69.3]	36.0 [6.3, 65.7]	31.46 [16.1, 46.8]	14.45 [− 4.8, 33.7]
Effect size (Cohen's d)	0.56	0.60	0.33	0.29

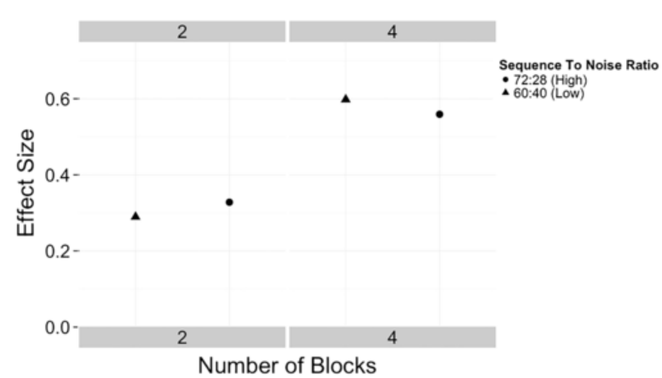

Fig. 3. Effect size of the difference in reaction time (dRT) between the random vs. repeated sequence across groups. The magnitude of the dRT differed across groups, in that smaller effect sizes were observed following reductions in exposure to the repeated sequence during training (i.e., in the 2 block groups) regardless of sequence to noise ratio.

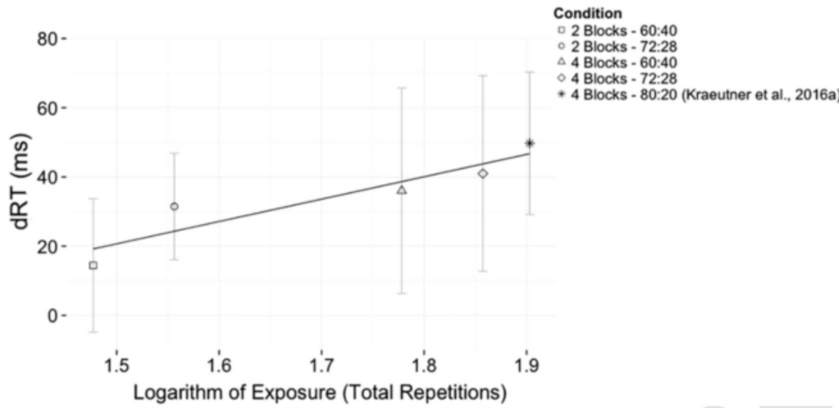

Fig. 4. Scatterplot of the resultant dRT (and 95% CIs) by the logarithm of exposure (total number of sequence repetitions) for each condition. Data from Kraeutner, MacKenzie, et al. (2016) is included as a fifth condition, in which participants completed 4 blocks of training (1000 trials total) with an 80:20 sequence to noise ratio (i.e., 80 total practiced repetitions of the sequence across four blocks of training). The magnitude of the dRT is strongly related to the logarithm of exposure, and learning is shown to increase as a log-linear curve.

number of practiced sequence repetitions [$F(1, 3) = 16.42$, $p = 0.027$, $SE = 0.14$, adjusted $R^2 = 0.79$], or both total training time and sequence to noise ratio [$F(1, 3) = 12.07$, $p = 0.076$, $SE_{(training\ time)} = 2.50$, $SE_{(ratio)} = 2.66$, adjusted $R^2 = 0.85$].

4. Discussion

The primary objective of this study was to examine the cognitive mechanisms of ISL occurring through MI by manipulating parameters that impact the formation of stimulus-response associations. Specifically, we examined ISL under four learning conditions, involving manipulations of total training time (four or two blocks) and the sequence to noise ratio (72:28 or 60:40). While there was an overall decrease of RT to the implicit vs. random sequences of equal length in each group, the extent to which learning occurred was dependent on the parameters that influence the formation of stimulus-response associations, and overall the exposure to the repeated sequence. Specifically, our results show that the logarithm of the total number of sequence repetitions was strongly related to the magnitude of the dRT. Findings from the current study ultimately inform on the cognitive mechanisms of ISL through MI. Below we discuss these findings in the context of physical practice-based ISL and the nature of MI.

4.1. ISL through MI and physical practice

Collectively, our findings demonstrate that, similar to physical practice-based ISL (Nissen & Bullemer, 1987; Schwarb & Schumacher, 2012; Wilkinson & Shanks, 2004; Willingham et al., 1989), modifying parameters that influence the formation of stimulus-response associations impacts the extent to which ISL occurs through MI. Consistent with past physical practice-based ISL investigations (Kantak et al., 2012; Nissen & Bullemer, 1987; Willingham et al., 1989), modifying total training time in our MI-based ISL paradigm impacted the extent to which learning occurred. Modifying the total duration of training while maintaining a constant sequence to noise ratio resulted in lower dRT values and effect sizes for the groups undergoing two vs. four blocks of training. Specifically, comparing the 4-High to 2-High and 4-Low to 2-Low groups yielded dRTs separated by approximately 10 and 22 ms respectively.

Modifying the sequence to noise ratio also impacts the extent to which ISL occurs, akin to findings from physical practice-based ISL investigations (Jiménez et al., 2006; Kaufman et al., 2010; Sanchez & Reber, 2012). Comparing the impact of reducing the sequence to noise ratio while maintaining a greater total duration of training, we observed similar dRTs for the 4-High and 4-Low groups, although the dRT in the 4-Low group (i.e., the group with a reduced sequence to noise ratio) was lower (approximately 41 and 36 ms for the 4-High and 4-Low groups respectively). We observed a similar pattern of a lower dRT value following reductions in the sequence to noise ratio over two blocks of training (approximately 31 and 14 ms for the 2-High and 2-Low groups respectively).

4.2. Training time vs. sequence to noise ratio, and exposure

In accordance with our primary objective, we demonstrate a link between the formation of stimulus-response associations and the extent to which ISL occurs via MI-based practice. Evidence supporting this link was derived through modifications of the parameters that influence the formation of stimulus-response associations, namely total duration of training and the sequence to noise ratio. Specifically, learning is most robust when total training time and the sequence to noise ratio are high enough to result in adequate exposure to the repeated sequence. Conversely, we see that when training parameters (training time and sequence to noise ratio) are set such that the exposure is too low, robust learning is not observed. Given that the combination of total training time and sequence to noise ratio comprise exposure, we hypothesized that exposure would be a strong predictor of the ISL that occurred. Such a finding would be in line with work exploring ISL resulting from physical practice, including the work of Sanchez and Reber (2012), who showed that the logarithm of exposure (i.e., the total number of practiced sequence repetitions) strongly related to the magnitude of the resultant dRT, and that learning was shown to increase accordingly to a log-linear curve.

Results from our regression analysis supports the direct link between the exposure to the repeated sequence during training and the extent to which ISL occurs through MI, in that the extent to which ISL occurs through MI increases as a function of exposure. Similar to ISL occurring via physical practice (Schwarb & Schumacher, 2012), this finding further supports the notion that the cognitive mechanism underlying MI-based ISL is the formation of stimulus-response associations.

4.3. Mechanisms of ISL and the nature of MI

As previously indicated, ISL (through physical practice) results from both the improved recognition of the stimulus and the resulting mapping of these perceptual cues to movement goals, as well as from more readily activated and efficient execution of the movement (the key press) and accompanying sensory feedback (Robertson, 2007). However, while the sensorimotor system uses sensory feedback to update the motor plan based on an error detection and correction mechanisms, leading to improvements in performance (Blakemore & Sirigu, 2003;

Körding & Wolpert, 2004; Therrien & Bastian, 2015), there is no sensory feedback associated with MI-based practice. Thus, whether or not MI can also contribute to the improvements in the execution of the movement without accompanying sensory feedback, and therefore the exact mechanism through which ISL is facilitated via MI remains unknown. Although investigating the extent to which ISL through MI is impacted due to the lack of feedback is out of the scope of the current research question, we turn to research regarding the nature of MI to further shed light on the cognitive mechanisms through which ISL is facilitated through MI.

Interestingly, the nature of learning through MI is suggested to be fundamentally different from that of physical practice. Specifically, MI is suggested to facilitate the perceptual vs. motor component of learning to a greater extent relative to physical practice (Amemiya et al., 2010; Ingram et al., 2016). This observed difference stems from previous research employing sequence tasks investigating learning transfer (i.e., switching the effector or perceptual modality for the test phase) following physical practice vs. MI-based practice (Amemiya et al., 2010; Ingram et al., 2016). Specifically, MI-based practice has been shown to lead to a greater increase in performance with the untrained hand vs. physical practice (Amemiya et al., 2010) and perceptual vs. motor transfer is shown to disrupt the learning that occurs through MI to a greater extent (Ingram et al., 2016). Further, MI is demonstrated to rely on areas involved in visuospatial processes, and damage to these areas is shown to impair MI (Kraeutner, Keeler & Boe, 2016; McInnes et al., 2016; Oostra et al., 2016). Thus, learning through MI is thought to be more perceptual in nature relative to physical practice (Amemiya et al., 2010; Frank, Land, & Schack, 2015; Frank, Land, Popp, & Schack, 2014; Ingram et al., 2016; Kraeutner, MacKenzie, et al., 2016; Kraeutner, Keeler and Boe, 2016) in that it relies more on the mapping of perceptual cues to movement goals (Ingram et al., 2016). While MI-based ISL indeed relies on the formation of stimulus-response associations, we therefore suggest that perhaps MI-based ISL is facilitated via generating and strengthening the link between the stimulus and the response rather than updating this association via feedback following the actual execution of that response.

4.4. Contextualizing the findings – training parameters

While we demonstrate that exposure impacts the extent to which ISL is achieved through MI, we acknowledge that the current task does not address a complete range of possible combinations of total training time and sequence to noise ratio manipulations that ultimately determine exposure. Specifically, as exposure itself can be held constant as total training time or the sequence to noise ratio is modified, it is unknown whether or not maintaining exposure regardless of modifications to these parameters would facilitate learning to a similar extent.

For instance, here we show robust learning following 72 repetitions of the sequence (i.e., a sequence to noise ratio of 72:28 over four blocks of training). Yet, it is unknown whether 72 repetitions of the sequence (i.e., the same exposure) would facilitate learning to a similar extent over a longer duration of training with a lower sequence to noise ratio (e.g., sixteen blocks of training with a sequence to noise ratio of 18:82). While we can only infer the extent to which learning would occur in this scenario, our findings, in conjunction with Sanchez and Reber (2012) suggest that similar amounts of exposure during training would result in similar degrees of learning as it is shown that learning occurs as a function of exposure. We can conclude however that there appears to be a lower bound of exposure at which ISL did not occur, in that the total number of repetitions performed was not adequate to allow for learning. Specifically, the dRT observed in the 2-Low group was shown to be 14.45 ms, 95% CI [− 4.8, 33.7]. In conjunction with the effect size calculated on the dRT ($d = 0.29$), the resulting dRTs from this group are not indicative of robust ISL. In accordance with our objective of advancing knowledge related to the cognitive mechanisms of ISL through MI, we provide evidence linking the formation of stimulus-response associations to the extent to which ISL through MI occurs.

4.5. Limitations

As the concealed nature of MI precludes the ability to definitively conclude whether a participant is performing MI as instructed, it is possible that participants may have employed alternative strategies, such as verbal rehearsal and/or rote memorization, which have previously been shown to facilitate improvements in performance of a sequence task (Saimpont et al., 2013). Use of these alternative strategies is more likely to result in explicit learning, whereby participants are consciously aware of and able to describe the repeating sequence following training. By excluding participants who explicitly learned the repeating sequence from final analyses, we ensure not only that solely implicit learners were included the analysis (in line with the study objective), but also that these participants were less likely to have used alternative learning strategies such as rote memorization. Further, the familiarization session employed in the study was designed to orient the participant to kinaesthetic MI, in a consistent manner across participants, as described above.

4.6. Conclusion

The current study informs on the cognitive mechanisms underlying MI-based ISL by demonstrating that the extent to which ISL occurs through MI is impacted by manipulations to total training time and the sequence to noise ratio during training. Further, in alignment with previous physical practice-based ISL research, the amount of exposure to the repeated sequence was shown to strongly relate to the extent to which learning occurs. Taken together, we conclude that MI-based ISL, like that occurring through physical practice, relies on the formation of stimulus-response associations. Interpreting the findings in the context of the nature of learning through MI, we suggest that despite fundamental differences between learning through MI and physical practice, the cognitive mechanisms underlying MI-based ISL parallel that of physical practice. Future research should address how a broader range of parameters that result in similar exposure during training impacts the extent to which ISL through MI occurs.

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