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The effect of how to perform movement sequences on absolute and relative timing transfer

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Depending on the difficulty of the task in terms of movement duration and the number of elements forming the sequence, recent research has shown that movement sequences are coded in visual-spatial coordinates or motor coordinates. An interesting question that arises is how a specific manner of performance without a change in such functional difficulties affects the representation of movement sequences. Accordingly, the present study investigated how the way in which a movement sequence is performed affects the transfer of timing properties (absolute and relative timing) from the practised to unpractised hand under mirror (same motor commands as those used in practice) and non-mirror (the same visual-spatial coordinates as those present during practice) conditions in two experiments each with segment movement time goals that were arranged differently. The study showed that after a limited amount of practice, the pattern of results obtained for relative timing differed between the two experiments. In the first experiment, there was no difference between retention and non-mirror transfer, but performance on these tasks was significantly better than that for mirror transfer, whereas in the second experiment, there was no difference between the mirror and non-mirror transfer. For total errors, no significant difference was found between the retention and transfer tests in both experiments. It was concluded that the way in which a sequence is performed could affect the representation of the task and the transfer of relative timing, while absolute timing could purposefully be maintained if necessary.

In general, combining a learned sequence of movements for producing a smooth, efficient action in order to perform a particular task skilfully has been described as a motor skill (Magill, 1993). Certainly, in

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order to achieve this level of learning, the need for physical practice is undoubtedly one of the most influential determinants of the acquisition of motor skills, as supported by the early theories of motor learning (Adams, 1971; Fitts, 1964; Schmidt, 1975). However, the mere physical practice cannot lead to optimal performance and learning. According to Newell (1986), the person who performs the task, the task which is performed and environment and conditions in which the task is performed are crucial factors which influence the performance of motor skills. Therefore, based on this perspective, when researchers examine different variables to understand the processes involved in motor learning, these factors should be taken into account. Accordingly, the present study has tried to manipulate the condition of practice, the condition of transfer, and especially the characteristics of a motor task so that it could be understood whether these issues affect the representation of a movement sequence and the transfer of its features from the practised to unpractised limb. For this purpose, movement timing was evaluated as one of the central issues studied in motor behaviour. Timing has been considered in two separate aspects in the field of motor control and learning, such that the total duration of the movement represents the absolute timing and the proportion of the total time required to produce each segment of the movement is defined as relative timing.

Historically, the concepts of absolute and relative timing have been explained by several different views of motor control and learning. According to Schmidt's schema theory (Schmidt, 1975, 2003), absolute timing is a parameter that a person has the ability to change according to the demands of the current circumstances, whilst relative timing is a shared and invariant feature of a class of movements generated in different conditions and situations in which these movements differ only within the limits of certain parameters, including overall movement time. Some hierarchical theoretical approaches have suggested (Verwey, 2001; Keele et al., 1995) that the two distinct processing mechanisms are responsible for structuring and scaling the movement sequence. Relationships between elements in the sequence are organized at higher cognitive levels, whereas the specific commands required to carry out the planned sequence are developed at lower levels. Therefore, based on these approaches, relative timing appears to be represented in a more abstract, effector-independent manner than absolute timing. In this regard, proponents of the dynamical systems perspective have described relative and absolute characteristics of movement as higher and lower order variables (Fowler & Turvey, 1978), or as essential and nonessential variables (Kelso, Putnam, & Goodman, 1983). From a dynamical systems perspective, there is a repertoire of natural timing preferences (Collier and Wright, 1995) that originate from the stable and functional patterns known as attractor states (Kelso, 1997; Kelso & Zanone, 2002), and new complex timing rhythms are developed by modifying this repertoire through practice.

Considering the general theoretical perspectives in the field of motor learning and control, two distinct and independent processing mechanisms are responsible for organizing and executing motor sequences, placed in two different levels of the nervous system (Keele, Jennings, Jones, Caulton, Cohen, 1995; Schmidt, 1975; Scully and Newell, 1985; Shea and Wulf, 2005; Verwey, 1999). A high-level mechanism of the system is related to the processing of the underlying structures of the sequences, whereas another mechanism that is thought to be processed at lower levels is responsible for organizing the motor elements at effector level. Given the abstract representation of fundamental structures, well-learned movement sequences could be performed with different effectors if their overall shape is maintained (Park & Shea, 2002, 2003 a, b, 2005).

Recent theoretical concepts such as those proposed by Hikosaka et al. (1999, 2002) suggest that, similar to the dual-processing model, two distinct neural networks are simultaneously and independently involved in acquiring movement sequences, one using spatial coordinates (spatial locations of the end effectors and/or sequential stimuli positions) and the other using motor coordinates (activation pattern of the agonist/antagonist muscle - sequential pattern of joint angles). In research on spatial and motor coordinates, non-mirror and mirror transfer tests have been used respectively. In the literature, these tests have been referred to using different labels, representing tests for visual-spatial and motor coordinates (Shea, Kovacs and Panzer, 2011). In the non-mirror transfer test, the visual-spatial coordinates are reinstated, with the result that participants could move to the same spatial locations as those during acquisition but using the unpractised limb. This leads to a new unpractised pattern of muscle activation and joint angles. The mirror transfer test also engages the unpractised limb but with a mirror display of the target positions. This allows the movement sequence to be performed with the same pattern of homologous muscle activation and to attain the same relative joint angles as those achieved during the practice phase, but the spatial locations are altered. Therefore, when performing the mirror transfer test, the motor coordinates are reinstated and the visual–spatial coordinates are altered, whereas when performing the non-mirror transfer test, the visual–spatial coordinates are reinstated and the motor coordinates are altered (Williams & Hodges, 2004). From this perspective it can be inferred that when a movement sequence is learned by a limb, sequence features are transferred to the contra-lateral limb under mirror and non-mirror conditions of the sequence. In the mirror transfer condition, the same pattern of homologous muscle activation and joint angles (motor coordinates) are required as those used during acquisition, while in the non-mirror transfer condition, the visual spatial coordinates are the same as those used in practice, but there is recruitment of unhomologous motor commands (Kovacs, Boyle, Grutmatcher and Shea, 2010; Hayes et al., 2012). The tasks used in Hikosaka's research were key-pressing sequences. As demonstrated by Zelaznik et al (Zelaznik, Spencer and Doffin, 2000; Zelaznik, Spencer and Ivry, 2002; Spencer, Zelaznik, Diedrichsen, and Ivry, 2003), timing behaviour is different in continuous and discontinuous movements. The force used in discontinuous motor tasks seems to be almost the same for each key press, and only the interval between key presses is important, whereas in continuous movements, the entire path of a movement from one point to another has an impact on timing. Consequently, a similar path but with a different execution time is likely to require different movement dynamics. In the tasks used in the present study, which included five-segment sequences, it was necessary to perform each segment in a specified time.

Recent studies have shown that in relatively simple movement sequences (Kovacs, Han, and Shea, 2009; Panzer, Krueger, et al., 2009; Hayes, Andrew, et al., 2012), the transfer of spatial-temporal characteristics from the practised to unpractised limb in the mirror condition is better than the non-mirror condition. Moreover, where post-performance feedback is given during the practice phase, which results in pre-planned control (Kovacs, Boyle, Grutmatcher, Shea, 2010), this allows for better transfer to the mirror condition. Contrary to these findings, in relatively complex tasks (Kovacs, Han, and Shea, 2009; Kovacs, Mühlbauer, Shea, 2009; Panzer, Muehlbauer, et al., 2009; Panzer, Gruetzmacher, et al., 2011), transfer to the non-mirror condition is better than the mirror condition. This also holds true for practice in conditions where concurrent feedback is provided, which encourages on-line control (Kovacs, Boyle, Grutmatcher, Shea, 2010).

Therefore, it appears that in previous studies, different results have been obtained for the visual-spatial and motor representation of simple and complex tasks in terms of duration and the number of components in movement sequences (or number of movement reversals). For example, in the study by Kovacs, Han, and Shea (2009), there was a better transfer to the mirror condition in simple movement sequences and conversely better transfer to the non-mirror condition in complex motor sequences, as well as an effect of the requirements of the task itself on performance and learning based on Newell's constraints-led approach (1986). Accordingly this study aimed to keep constant the overall time and the number of components while the procedure for executing the sequence differed in terms of time ordering of successive segments in two decreasing versus alternating states, an issue that has not yet been investigated. This manipulation in the task causes specific relative relationships between segments, possibly resulting in different perceptual demands of the action, and also requiring unique movements due to biomechanical and task constraints on the organization of movement in the effector.

As previously mentioned with respect to the underlying structures of movement, including relative timing, it can be supposed that transferring the timing structure is likely to be different depending on whether the task is performed under different conditions. According to Newell's constraints-led approach (1986), the task itself, as one of the components influencing the performance of motor skills, can play a determinant role in research results. Taking into account this issue, it is assumed that the performance procedure of the task that is likely to induce different motor dynamics and perceptual demands (as a form of task constraints) can be effective in transferring the structural and metrical characteristics of movement, including movement timing made up of absolute and relative timing. Therefore, in the current study, two versions of a sequential task were used, which, in terms of the order of relatively low and high execution times in the sequence segments we have labelled them as the timed motor sequences with either decreasing or alternating performance, with each of these tasks being examined in a separate experiment. In the alternating task, a person should switch the velocity of movement from fast to slow and vice versa when shifting between fast and slow segments, and it therefore appears that there is a need for more control in motion so that individuals can decrease or increase their speed when approaching the next segment. In the decreasing task, however, the individual moves from relatively slow segments to relatively fast segments, in which only a gradual increase in velocity is required. These assumptions seem to be somewhat consistent with the studies on simple and complex tasks (Kovacs, Han, and Shea, 2009), in which the duration and the number of constitutive elements for the performance of the movement sequence were different. In the present research, the aim was to keep these factors constant whilst varying the way in which the sequence was executed. Previous theories have also supposed that a person can purposely rescale the absolute timing for meeting the specific demands of the task (Schmidt, 1975, 2003), which means performing the movement with the unpractised limb in the same absolute total time as practised if needed. We therefore hypothesized that the following results would be obtain in the present study: 1) In both decreasing and alternating tasks, the performance of absolute timing in the unpractised hand in both the mirror and non-mirror conditions will be similar to that in the retention test, performed with the same hand as that used during the acquisition phase. 2) In the alternating task, there will be no differences in the performance of relative timing for the retention test and non-mirror transfer test, and performance on both will be superior to that on the mirror transfer test. 3) In the decreasing task, the performance of relative timing on the retention and mirror transfer tests will be similar, but superior to that on the non-mirror transfer test.

EXPERIMENT 1

The first experiment examines whether participants, after a limited amount of practice on a continuous movement sequence requiring each segment to be performed within a specific time, can transfer the acquired timing from the trained limb to the opposite, untrained limb under conditions where mirror (same motor commands as those in practice) and non-mirror (same visual spatial coordinates as those in practice) transfer tests are used.

METHOD

Participants. A total of 24 healthy male volunteers aged 22–34 years (mean age: 26.6 ± 2.8), who had no prior experience in similar motor skills and were unfamiliar with the experimental task, took part in this study. They were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants were in good health and had no history of disease or medical treatment that might influence visuomotor functions. The local ethics committee at Ferdowsi University of Mashhad approved the experiment. Informed consent was obtained from all participants.

Apparatus and Task. The apparatus designed for the present study, depicted in Fig. 1, was composed of a wooden square (20 cm × 20 cm). The large square was divided horizontally and vertically by means of two lines of 20 cm, constituting four small squares. Four sensors are located on the four corners of each small square. Thus, a total of 9 sensors are located on the square, separated by a distance of 10 cm. The apparatus was wired so that that the movement time (MT) for each segment (ten-centimetre sides) could be recorded by a millisecond clock. The electronic measuring system works with a frequency of 12 MHz and a precision of 1 ms. This system detects when sensors are touched by the participant and measures the time difference between them. Movement time is obtained by moving the finger from one sensor to another sensor on a movement path. The apparatus is connected to a computer through which the data was collected to be used in subsequent statistical computations. The computer also provides feedback about the time of each segment and overall time. The experimental task required subjects to execute five-segment sequences of these movement paths with the index finger. In this study, depending on the hand used and the various conditions during acquisition, retention, and transfer, the movement path was different, as depicted in Fig. 1. The tasks required the subject to meet specified goal times for each segment. Subjects were provided with their actual goal times after each trial and were encouraged to match these times to specified goal times. The movement time goal for each segment was 460, 1150, 260, 700 and 215 ms respectively which was, in fact, an alternation of relatively high and low execution times between segments (the alternating performance task). These values formed an absolute time goal (ATG) of 2775 milliseconds, which was the time taken to perform the entire movement. Therefore, the relative time goal (RTG) was 16% for Segment 1 (450 ms), 41% for Segment 2 (1150 ms) 9% for Segment 3 (260 ms), 25% for Segment 4 (700 ms), and 8% for Segment 5 (215 ms) (i.e., 450 ms + 1150 ms + 260 ms + 700 ms + 215 ms = 2775 ms). The transfer included the mirror and non-mirror performance of the trained sequence but with the opposite (untrained) hand, similar to the time used for the original task trained in the acquisition phase (Fig. 1).

Procedure. For the acquisition and transfer phases, each subject was tested individually in a quiet and adequately lit room containing a chair and a desk. They were informed that they would be participating in an investigation of basic perceptual–motor processes. Participants were seated on a height-adjustable chair facing the computer and the apparatus placed on the desk. Before entering the testing room, participants were randomly divided into two equal groups of 12, assigned to a left or right limb acquisition condition. The necessary instructions about how to execute movement tasks were given to the subjects prior to the beginning of the practice session by the examiner. Depending on the limb used during the practice phase (right hand or left hand), participants practised the task during an acquisition phase of six blocks consisting of 10 trials each. After each practice trial, the KR related to the execution time of each segment and the difference from criterion values was presented on the monitor. To ensure that participants perceived KR correctly, they verbally explained to an experimenter how their performance differed in milliseconds (ms) and direction [+ (too slow) and − (too fast)] from the ATG and RTG.

Immediately following the practice phase, participants performed a retention test under the same conditions as those of the acquisition phase except that KR was not provided. Subsequently, mirror and non-mirror intermanual transfer conditions were presented using the unpractised hand. Each of the three conditions comprised of 5 trials, without KR, and the order of the transfer tasks were counterbalanced.

Statistical analysis. Performance on the task was evaluated by calculating the root mean square error (RMSE) for each segment (errors in relative timing) and Total error for total movement time (errors in absolute timing). RMSE is measured as the sum of the absolute differences between the goal proportions and the actual proportions for each segment on each trial. Total error is measured as the deviation of the actual overall movement time from the goal movement time on each trial, determining bias and stability of total movement time (Shea & Wulf, 2005). Therefore, the two following formulas were considered for calculating the Total Error and Relative Timing Error: (Total Error) $E^2 = CE^2 + VE^2$, where CE is a measure of response bias, which is computed as the average of the signalled differences between actual total movement time and the ATG, and VE is a measure of response variability, which is computed as the standard deviation of the signalled errors. Relative timing error = $|R1 - 0.16| + |R2 - 0.42| + |R3 - 0.09| + |R4 - 0.25| + |R5 - 0.08|$, where R1–R5 are the proportions of total movement time utilised in Segments 1–5.

Changes in average RMSE and total error across acquisition were assessed by separate 2 (Group: right hand; left hand) × 6 (Block) repeated-measures analysis of variance (ANOVA) with block as the repeated measure and RMSE (and total error) as the dependent variable. There were 15 trials divided into 3 blocks of 5 trials for the retention and two transfer phases. For transfer, the dependent variable (total error and RMSE) was analysed using a 2 (Group: right hand, left hand) x 3 (retention or transfer test) analysis of variance (ANOVA). LSD post hoc tests were employed for inter-block (Blocks 1-6) and inter-phase (retention, mirror transfer, and non-mirror transfer) comparisons when the ANOVA yielded a significant difference. Alpha was set at 0.05 for all statistical analyses.

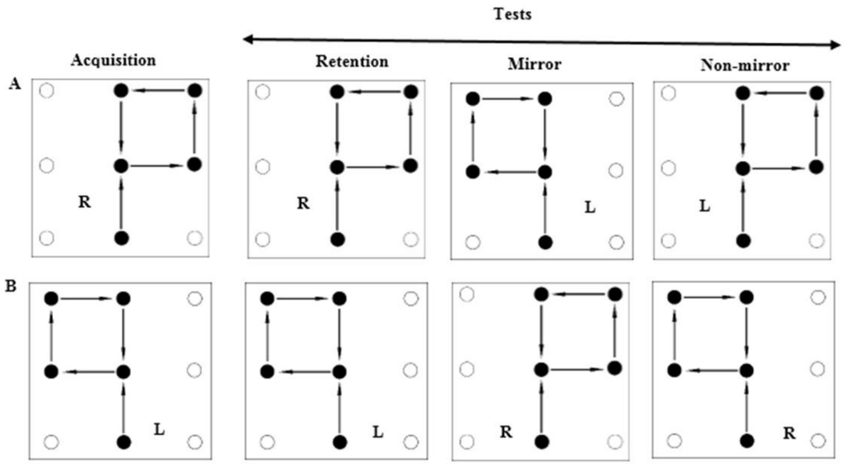

Fig. 1. Schematic representation of the experimental design where the participant was required to practice the task with either the right (A) or left (B) limb and then tested on a retention test which was subsequently followed by two transfer tests (mirror, non-mirror) in a counterbalanced order. The letter inside each quadrangle represents the limb used on those trials.

RESULTS

Acquisition. Total Error and RMSE during acquisition were computed in blocks of ten trials and analysed through a 2 (Acquisition group: left limb, right limb) × 6 (Block: 1-6) Analysis of Variance (ANOVA) with block as repeated measures. The analysis detected main effects for Total Error [$F(5, 110) = 21.121$, $p < 0.001$] and RMSE [$F(5, 110) = 20.954$, $p < 0.001$] only for block, indicating improvement in accuracy and specified temporal relationships during acquisition respectively, as illustrated in Fig 2 A and B. For Total error (Fig. 2A), the LSD test revealed that Block 1 differed from all subsequent blocks (all $P < 0.001$), but no significant difference was observed in the other five blocks (all $P > 0.05$). Concerning RMSE (Fig. 2B), the LSD test revealed that there was a significant difference between Block 1 and 2 ($P < 0.01$) with both being significantly different from all subsequent blocks ($P < 0.01$), whereas Blocks 3 and 4 significantly differed from Block 6 ($P < 0.05$), but did not differ from each other and from Block 5 ($P > 0.05$). No significant difference was found between block 5 and 6 ($P > 0.05$). There was no significant main effect for acquisition group or the Acquisition group × Block interaction for both Total Error and RMSE values.

A
B

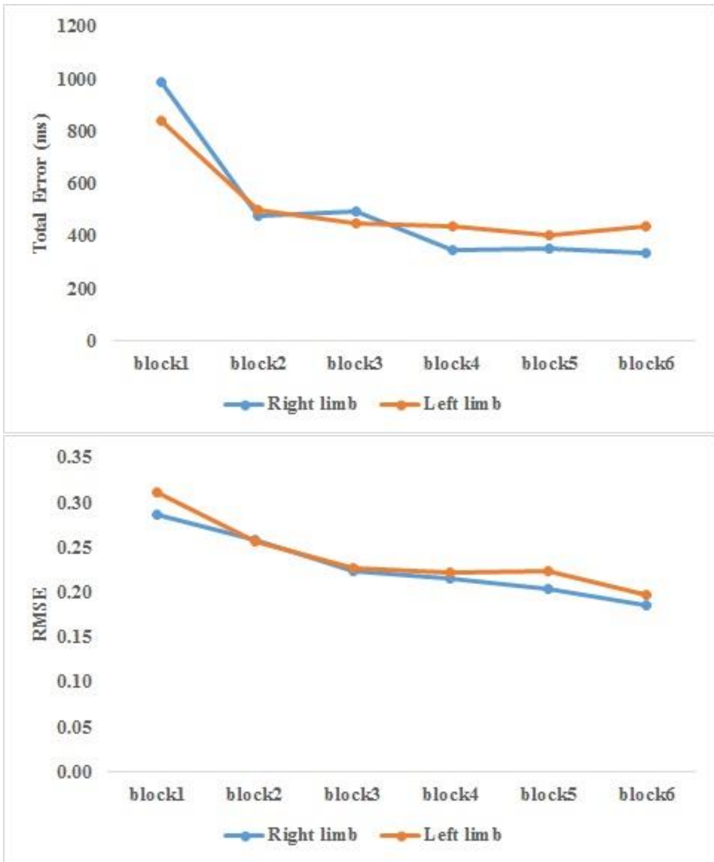

Fig. 2. Mean Total Error (A) and RMSE (B) on acquisition in experimental 1

Retention and transfer. Mean Total Error and RMSE on the retention and transfer tests were analysed using separate 2 (Acquisition group: left, right) × 3 (Test: retention, mirror, non-mirror) ANOVAs with repeated measures on the test. The analysis related to Total Error (Fig. 3A) indicated neither a main effect of group, $F(1, 22) = 2.574$, $p > 0.05$, nor a main effect of test, $F(2, 44) = 1.243$, $p > 0.05$. Further, the Acquisition group × Test interaction, $F(2, 44) = 1.639$, $p > 0.05$, was not significant.

The analysis of RMSE (Fig. 3B) revealed no significant main effect of acquisition group, $F(1, 22) = 1.551$, $p > 0.05$, but revealed a main effect of test, $F(2, 44) = 26.039$, $p < 0.01$. The LSD Post-hoc tests indicated that there were no differences in RMSE on the retention and non-mirror transfer test, and these were significantly lower in comparison with the mirror transfer test. Further, the Acquisition group × Test interaction, $F(2, 44) = 1.647$, $p > 0.05$, was not significant. Since the separate analysis for each group in both Total error and RMSE was consistent with the results of the 2

(Acquisition group: left, right) × 3 (Test: retention, mirror, non-mirror) ANOVAs, these additional analyses were not provided.

A

B

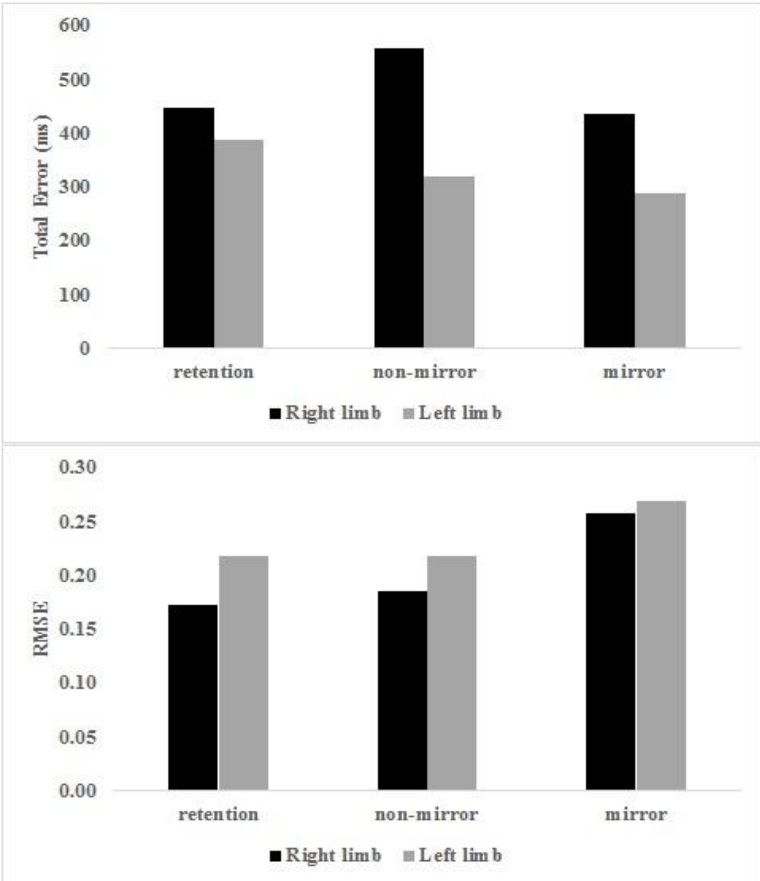

Fig. 3. Mean Total Error (A) and RMSE (B) on retention and transfer in Experiment 1. Right limb and left limb denote the right and left limb acquisition groups.

DISCUSSION

The first experiment examined whether timing characteristics — including absolute and relative timing— learned with a motor sequence can be transferred from the practised limb to the opposite, unpractised limb under conditions where the same visual–spatial coordinates (non-mirror transfer) or the same motor coordinates (mirror transfer) are tested. In the analysis of the acquisition data, no difference was found between the left and right acquisition groups on performance in a movement sequence timing task. The analysis showed that the Total Error in the first block was reduced and this reduction was maintained in the remaining five blocks.

This analysis, however, did detect significant decreases in RMSE across the first three practice blocks with a failure to increase performance on the next two blocks, eventually falling again by the sixth block. Although participants practicing the task with the left or right limb performed the task in the retention phase with the limb used during acquisition, the task was performed using the contralateral limb during the mirror and non-mirror transfer phase. No significant difference in Total Error was found between the retention and the two transfer tests. The RMSE on the retention and non-mirror transfer test was similar but showed a higher level of performance in comparison with the mirror transfer test. The non-mirror transfer test was the same as the original task used during the acquisition phase but was performed with the contralateral limb, exhibiting the same visual–spatial coordinates as those experienced during practice and activating different muscle patterns to those engaged during acquisition. In the mirror transfer condition participants were required to perform the original task used during the practice phase but with the untrained index finger in a mirror path, generating the same pattern of muscle activation as that observed during acquisition.

The results of the total error scores indicated that a motor sequence-timing task could be performed with the unpractised contralateral homologous and non-homologous muscle groups in the absolute timing that had been learned with the practised limb during acquisition. It seems that absolute timing is unaffected by the conditions of the task performance, as verified by the transfer tests. At first glance, this finding appears to be contradictory to concepts that explain absolute timing in terms of a lower-order variable (Fowler & Turvey, 1978) or non-essential variable (Kelso, Putnam, & Goodman, 1983) at lower and less abstract levels (Verwey, 2001; Keele et al., 1995), whilst it also appears to run counter to the concept that absolute timing is a changeable parameter (Schmidt, 1975, 2003). However, it should be noted that in the current study, the participants were purposefully asked to maintain the overall time of movement during all stages of the experiment and in different conditions. In fact, absolute timing is the potential to change, if necessary, and is rescaled to meet the specific demands of the task. Therefore, given the ability of the participants to consciously preserve the overall movement time (maintaining accuracy and stability in the total movement time), it can be concluded that these results are compatible with the above-mentioned concepts, and in line with the results of Hayes et al. (2012) in which the transfer of absolute timing from the practised hand to the unpractised hand in terms of mirror and non-mirror transfer for a physical group was close to 100%.

Importantly, however, the experiment provided interesting evidence that demonstrates a clear dissociation between relative timing performance on the non-mirror and mirror conditions. These results, in comparison with those of the total error scores indicate that different processing mechanisms (Keele, Jennings, Jones, Caulton, Cohen, 1995; Schmidt, 1975; Scully and Newell, 1985; Shea and Wulf, 2005; Verwey, 1999) appear to be involved in relative and absolute timing as distinct and presumably independent variables (Park & Shea, 2002, 2003 a, b, 2005), and are affected differently under conditions where specific experimental manipulations are introduced. However, contrary to these theoretical predictions, relative timing was not similar across the different transfer conditions. The Hikosaka model (1999, 2002) proposes that movement sequences are simultaneously coded in two independent representations in the form of visual–spatial coordinates and motor coordinates. This perspective also suggests that movement sequence is coded in an effector independent manner, represented in visual-spatial coordinates at an early stage of practice, and then with additional practice, the coding develops into a more specific effector system represented in motor coordinates. The data extracted from this experiment demonstrate that the contralateral performance of relative timing acquired from a limited amount of practice depends on the transfer conditions, providing the same visual/spatial characteristics of the sequence or the same agonist/antagonist muscle activation patterns as those present during acquisition. The findings of this experiment confirm and extend the results obtained in previous studies (Kovacs, Han, and Shea, 2009; Kovacs, Mühlbauer, Shea, 2009; Panzer, Muehlbauer, et al., 2009; Panzer, Gruetzmacher, et al., 2011; Kovacs, Boyle, Grutmatcher, Shea, 2010), in which the inter-manual transfer of spatial-temporal features was examined for continuous movement patterns. Although the findings are somewhat inconsistent with evidence obtained from a number of other previous studies (Kovacs, Han, and Shea, 2009; Panzer, Krueger, et al., 2009; Hayes, Andrew, et al., 2012; Kovacs, Boyle, Grutmatcher, Shea, 2010), this seems to be related to the relative difficulty of the sequence (Kovacs, Han, Shea, 2009). It is likely that for this task, with this amount of practice, the response structure is represented in a visual-spatial coordinate system that involves a relatively abstract coding of movement, which leads to effector-independent performance, and therefore the development of effector-specific commands requires extended practice (Park and Shea, 2005). Given the Hikosaka model concerning abstract effector-independent representation of the spatial codes that reflect the extrinsic coordinates of the task, as well as the theoretical perspectives of Keele, Jennings, Jones, Caulton, and Cohen

(1995), Verwey (1994), and Grafton et al. (2002), transfer (both left to right and right to left) was symmetrical, as expected.

EXPERIMENT 2

METHOD

Participants. Twenty-four male students from the Ferdowsi University of Mashhad ranging in age from 22 to 32 years (mean age 26.7 ± 2.8), with no prior experience of similar experimental tasks, voluntarily participated in this experiment. There was no overlap between the subjects of these two experiments. They were all right-handed, as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971) and had no history of disease or medical treatment that might influence visuomotor functions. All participants gave informed consent and the study was approved by the local ethics committee of The Ferdowsi University of Mashhad.

Apparatus, Task, and Procedure. Apparatus, tasks, procedures and statistical analysis were the same as those described in Experiment 1, with the exception that execution durations for each segment of the five-segment timing task were different, such that the task was performed in a decreasing time procedure. The total criterion movement time, like that of the task used in the first experiment, had a duration of 2775 milliseconds and segment criterion movement times were 1150, 700, 450, 260, and 215 ms which were presented in a particular order and were the same segment times as those used in the previous task. The relative-time ratios were obtained by dividing the duration of movement components over the total movement time, including 41, 25, 16, 9, and 8%. The last two segments have almost the same relative time.

Before entering the testing room, subjects were randomly divided into two equally sized groups, practicing with the right hand or left hand. Under a left or right limb acquisition condition in the acquisition phase, subjects performed 60 trials on the task. At the beginning of the session, participants were instructed to simply produce the task at the criterion times presented on screen. The task required an individual to move the index finger continuously on fixed paths (Fig. 1). After each trial, feedback was provided. By comparing the obtained time scores with the criterion scores, the participants could attempt to improve their movement performance.

RESULTS

Acquisition. The 60 trials for each acquisition group (left and right acquisition limb groups) were separated into 6 blocks of 10 trials each, and changes in Total error and RMSE were assessed by 2 × 6 repeated-measures analysis of variance with block as the within-subjects factor. For Total Error, the analysis failed to reveal a main effect of Acquisition group, $F(1, 22) = 1.475$, $p > 0.05$, or an interaction between Acquisition Group ×Block, $F(5, 110) = 1.694$, $p > 0.05$, but a main effect of block, $F(5, 110) = 29.846$, $p < 0.001$, was found (Fig. 4A). LSD pairwise comparisons revealed a statistically significant difference between Block 1 and all subsequent blocks (all $p < 0.001$) and between Block 2 and Block 5 ($p = 0.046$). The other pairwise comparisons did not reveal any significant differences (all $P > 0.05$).

For RMSE, the analysis showed a significant main effect of Block [$F(5,110) = 47.790$, $p < 0.001$], but no main effect of group [$F(1,22) = 2.972$, $p > 0.05$], or a group × block interaction [$F(5,110) = 0.287$, $p > 0.05$] (Fig. 4B). Post hoc LSD tests revealed that there were significant differences among the first three blocks, and also among the subsequent three blocks (all $p < 0.05$) whilst the latter three blocks did not differ from each other (all $p > 0.05$).

A

B

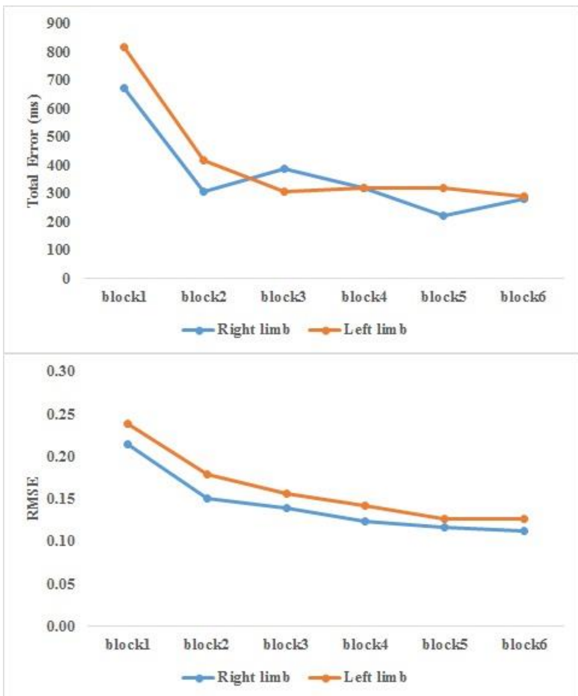

Fig. 4. Mean Total Error (A) and RMSE (B) in acquisition in Experiment 2

Retention and transfer. Two separate 2 (Acquisition group: left, right) × 3 (Test: retention, mirror, non-mirror) ANOVAs with repeated measures on the second factor were conducted on the Total Error and RMSE scores for the retention test and the two transfer tests. In relation to Total Error, the analysis did not reveal any significant main effect for neither Group, $F(1, 22) = 0.729$, $p > 0.05$, nor Test $F(2, 44) = 0.676$, $p > 0.05$, whilst the Acquisition group × Test interaction, $F(2, 44) = 0.295$, $p > 0.05$, also failed to reach significance (Fig. 5A).

In relation to RMSE scores, although there were no significant main effects of Group, $F(1, 22) = 0.006$, $p > 0.05$, or a Test × Group interaction, $F(2, 44) = 2.510$, $p > 0.05$, a significant main effect of Test, $F(2, 44) = 11.398$, $p < 0.001$, was found (Fig. 5B). The LSD Post hoc tests indicated that there were no differences between RMSE scores on the mirror and non-mirror transfer test ($p > 0.05$), but the scores on both of these tests were significantly higher than those on the retention test ($p < 0.01$).

In an additional analysis of variance, conducted on the RMSE scores separately for each group, a significant main effect of Test, [for right acquisition group, $F(2, 22) = 8.145$, $p < 0.01$, for left acquisition group, $F(2, 22) = 4.133$, $p < 0.05$] was again found. However, the pattern of results varied for each acquisition limb group. For the right acquisition limb group, the LSD Post hoc tests indicated that retention was better than both transfer tests ($p < 0.01$), whereas for the left acquisition limb group, retention was only better than the non-mirror transfer condition ($p < 0.05$). Nevertheless, in both groups, there was no difference between the mirror and non-mirror transfer conditions ($p > 0.05$). Furthermore, there was no significant difference between the average RMSE scores across the 6 blocks during the acquisition phase and the transfer tests (Fig. 5B). This analysis failed to reveal main effects of Group, $F(1, 22) = 0.204$, $p > 0.05$, or a Test × Group interaction, $F(3, 66) = 2.068$, $p > 0.05$. However, a significant main effect of Test, $F(3, 66) = 7.490$, $p < 0.001$, was found. The LSD Post hoc tests revealed that when RMSE scores where averaged from six blocks of acquisition, there were no differences between the mirror and non-mirror transfer conditions ($p > 0.05$).

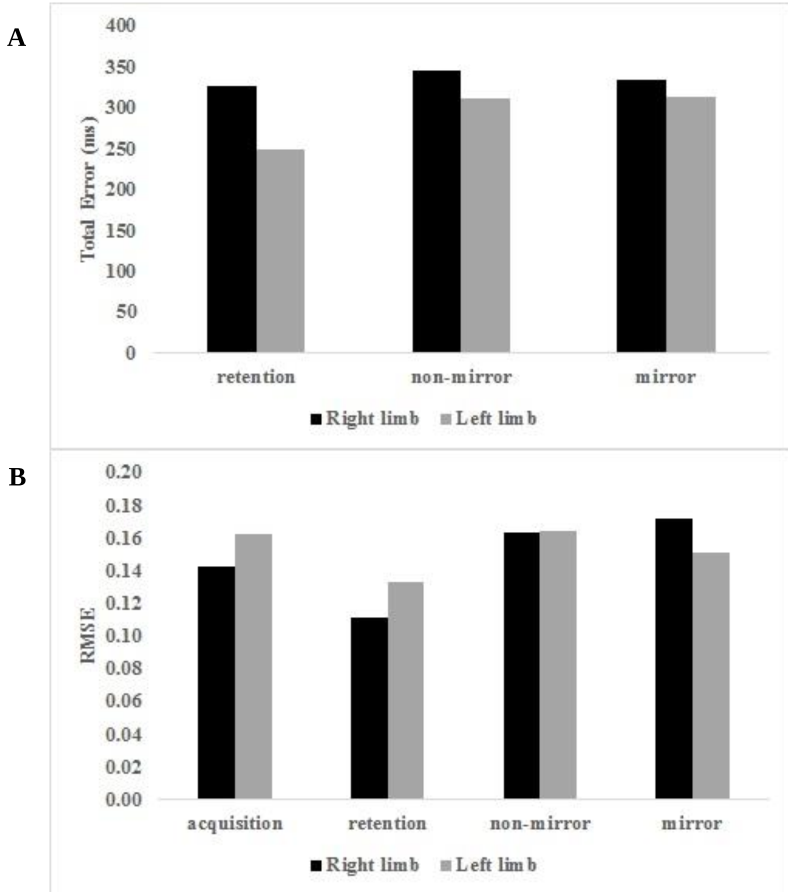

Fig. 5. Mean Total Error (A) and RMSE (B) on retention and transfer in Experiment 2. Right limb and left limb denote the right and left limb acquisition groups.

DISCUSSION

The second experiment aimed to investigate whether the findings of the first experiment could be replicated when the task was performed with a different execution procedure in which the execution speed of sequential segments in the task moves from a relatively slow to a relatively fast velocity (a decreasing time procedure). According to Newell's constraints-led approach (1986) to the role of task characteristics on performance, we assumed that particular execution procedures that are likely to result in specific motor dynamics and perceptual demands affect the transfer of timing, including absolute and relative timing.

During acquisition, absolute timing improved in terms of the Total Error scores after the first block, and this improvement remained constant in the subsequent blocks, with the exception that there were lower Total Errors in the fifth block compared with the second block. Relative timing in terms of the RMSE scores significantly improved up to the fourth block, with performance remaining stable until the final block (sixth block). Therefore, in general, participants became more efficient at performing in terms of both overall goal movement time and relative time allocated to each segment of the movement sequence across the acquisition stage. Nevertheless, absolute timing reached stability faster than relative timing, indicating that time scaling is possibly easier to achieve in comparison with time structuring.

Participants performed the retention test with the same limb as that used during practice, whereas transfer tests were performed with the opposite, contralateral limb under the mirror and non- mirror conditions of the practice task. There was no difference in Total Error between the retention and the two transfer tests, confirming the results of the first experiment. However, the results obtained from the RMSE scores were not in agreement with the findings of the first experiment. These results, indicating failure to find a difference between performance in the mirror and non-mirror transfer conditions whilst succeeding in finding better performance on retention than on both transfer tests, are inconsistent with the findings of previous studies (Kovacs, Han, and Shea, 2009; Panzer, Krueger, et al., 2009; Hayes, Andrew, et al., 2012; Kovacs, Boyle, Grutmatcher, Shea, 2010; Kovacs, Mühlbauer, Shea, 2009; Panzer, Muehlbauer, et al., 2009; Panzer, Gruetzmacher, et al., 2011). After conducting further separate analysis of the data for each limb, it was found that the preceding results were true for the right acquisition limb group, whereas the retention in the left acquisition limb group was only better than non-mirror transfer, with no difference between the two mirror and non-mirror transfer conditions. When the average RMSE of the 6 blocks across the acquisition phase was compared with the RMSE scores obtained on the transfer tests, no difference between them was detected, thus indicating that in any case, there are improvements in the performance of relative timing in the bilateral transfer under the mirror and non-mirror conditions, which confirms the findings of previous studies (Schmidt, 1975, 2003; Park & Shea, 2002, 2003 a, b, 2005). The participants in this study were all right-handed. It is likely that the right hand, on the whole, has more control and better movement dynamics than the left hand. Therefore, it is thought that on the one hand better retention was produced by the right limb practise group, whilst on the other hand, weaker performance generally occurred in transfer tests where the unpractised left hand was employed. However, the results of the left-hand practice group seem to be related to the characteristics of the task, which is in line with the findings of some previous studies (Kovacs, Han, and Shea, 2009; Panzer, Krueger, et al., 2009; Hayes, Andrew, et al., 2012). For instance, Kovacs, Han and Shea (2009) concluded that after a limited amount of practice, relatively more simple sequences are coded more efficiently in a motor representation that requires the same pattern of homologous muscle activation. One issue that remains to be discussed is the difference between the current study and previous research (mentioned above) in relation to the level of difficulty of the motor sequences. While two movement sequences used in other studies had different durations and different numbers of reversals (or segments), the overall time and the number of segments in both tasks used for the two experiments in this study were the same. According to Newell's model of constraints (1986), it is thought that a specific procedure for performing a task, which may induce the individual to adopt different motor dynamics and different perceptual demands, could influence the transfer of the structural characteristics of movement, including relative timing. The same argument, not consistent with recent research results (Kovacs, Han, and Shea, 2009; Panzer, Krueger, et al., 2009; Hayes, Andrew, et al., 2012; Kovacs, Boyle, Grutmatcher, Shea, 2010; Kovacs, Mühlbauer, Shea, 2009; Panzer, Muehlbauer, et al., 2009; Panzer, Gruetzmacher, et al., 2011) but in line with earlier theoretical frameworks (Schmidt, 1975, 2003; Verwey, 2001; Keele et al., 1995) that propose the existence of effector-independent representations of structural features, seems to be able to explain the lack of a difference in performance on the transfer tests under the mirror and non-mirror conditions. When required to carry out the task in a decreasing time procedure (increasing speed), this task seems to make the control of force and the understanding of time relations easier, and as a result the person requires fewer attentional and cognitive resources to execute the task, which in turn results in the ability to perform using both homologous and non-homologous muscles.

GENERAL DISCUSSION

The current study examined the bilateral transfer of relative and absolute timing under conditions in which the visual–spatial coordinates (non-mirror transfer condition) or the motor coordinates (mirror transfer condition) for the contralateral unpractised limb were the same as those used by the practised limb in the acquisition phase. This was conducted in two experiments that used different performance procedures for a movement sequence. The results of both experiments showed that for intramanual transfer of absolute timing from the practised hand to the unpractised hand, no significant difference in retention (in which the hand used was the same as that used during the acquisition phase) was observed between the mirror and non-mirror conditions. This finding is consistent with early theoretical approaches (Keele, Jennings, Jones, Caulton, Cohen, 1995; Schmidt, 1975; Scully and Newell, 1985; Shea and Wulf, 2005; Verwey, 1999) and previous research (Hayes, Andrew, et al., 2012) indicating that individuals are able to perform a movement sequence with different muscle groups and different limbs in specific absolute timing. However, different results were yielded for the intramanual transfer of relative timing in the two experiments. In the first experiment, consistent with the findings of recent studies (Kovacs, Han, and Shea, 2009; Kovacs, Mühlbauer, Shea, 2009; Panzer, Muehlbauer, et al., 2009; Panzer, Gruetzmacher, et al., 2011; Kovacs, Boyle, Grutmatcher, Shea, 2010), the transfer to the non- mirror condition, which did not differ from performance on the retention test, was better than the transfer to the mirror condition, whereas in the second experiment, no significant difference was found between the two transfer conditions. Separate analysis of each left and right limb acquisition limb in the second experiment revealed that in the right-hand practice group, retention was better than both transfer tests, whereas in the left-hand practice group, this difference between the retention and the transfer was only found for non-mirror transfer. The latter result in the second experiment for the left-hand practice group is consistent with the findings from Kovacs, Han and Shea (2009) and Hayes et al. (2012).

According to the Newell model of the constraints-led approach (1986), a movement is the result of dynamic interaction between the individual, task, and environmental constraints, and as a result of changing one of these components, movement performance is affected. Based on the time values given to each segment of the movement sequence, a specific procedure for executing the sequence in the form of a decreasing or alternating order was presented in each experiment as a task constraint, which was the major issue of interest in the current study. The results of the second experiment indicated that the performance procedure was effective on transfer tests, leading to no difference between performance in transfer tests, contrary to the pattern of results found in the first experiment and previous research (Kovacs, Han, and Shea, 2009; Kovacs, Mühlbauer, Shea, 2009; Panzer, Muehlbauer, et al., 2009; Panzer, Gruetzmacher, et al., 2011; Kovacs, Boyle, Grutmatcher, Shea, 2010).

A decreasing procedure, in comparison with an alternating arrangement for performing the sequence, creates different movement dynamics that seem to give rise to different perceptual, cognitive, and motor requirements. These changes appear to have produced a new form of interaction between the task and other constraints, which were held constant in both experiments. Eventually, this new interaction probably allowed the participants to be able to perform the learned sequence while using the unpractised contralateral limb under both the mirror and non-mirror transfer conditions. Although retention performance was better than that shown on the transfer tests, with the exception of the mirror transfer in the left-hand practice group, it should be kept in mind that according to the values obtained for relative timing in the first block of the acquisition phase compared with those obtained on the transfer tests, the transfer has occurred in any case. This finding that performance on retention was better than that on the transfer tests, in which most of this difference was due to better retention in the right-hand practice group, is also a consequence of the particular procedure used to perform the task. It seems that when starting the sequential task with relatively slower-performing segments, there is more time to process and subsequently make decisions to optimally perform the task, and after a limited amount of practice with one hand, a participant is able to use this capability to perform the task with the unpractised hand whilst the homologous or nonhomologous muscle groups are recruited. Another issue is finger movement control for the task performances between the sequence segments. Both tasks were supposed to be performed continuously; however, alternating performance of relatively low and high times requires that the person regulates their speed from the quick segment to the slow segment and vice versa, whereas it appears that moving the finger in a gradual procedure for the whole sequence from slow to fast gradually increases speed and does not require a shift from fast to slow and vice versa. Therefore, a person may have less difficulty in controlling finger movement in a gradual procedure compared with an alternating procedure in the transfer phase, regardless of whether the same motor coordinates or visual-spatial coordinates as those used in practice were employed, and as a result, the cognitive processes involved in producing the relative timing obtained through the practised hand could be transferred to the unpractised hand.

The overall conclusion is that the learner attempts to organize the internal factors in the presence of feedback at the acquisition stage so as to be able to meet external demands, including the particular features of movement performance. The new obtained interaction between the internal factors and external demands is usable in the retention test with no feedback. Then, in the transfer stages, the learner tries to construct a new organization to maintain the discovered relationships between the internal and external factors in the acquisition phase as far as possible, which seems to be dependent on the new conditions. It is thought that in the second experiment, the learner was able to maintain the relative timing acquired in the acquisition phase, while in the first experiment, these adaptations were only useful under certain circumstances (the non-mirror transfer). Therefore, these results indicate that coding and representing relative timing as one of the fundamental movement structures (Schmidt, 1975, 2003; Verwey, 2001; Keele et al., 1995; Fowler & Turvey, 1978; Kelso, Putnam, & Goodman, 1983; Collier and Wright, 1995; Kelso, 1997; Kelso & Zanone, 2002), and its cross-limb transfer, depends on the characteristics of the sequence (Kovacs, Han, and Shea, 2009). In the current study, task characteristics were related to the way in which the sequence was executed. Therefore, according to the constraints-led approach (Newell, 1986), these task-related constraints should be taken into account when investigating movement sequences and examining the effect of different variables on how such sequences are performance under different conditions.

Finally, a very important point regarding the apparent contradiction between our findings and the schema theory (Schmidt, 1975, 2003) should be noted. These discrepancies, can, in fact be explained in two ways. The movements used to investigate this issue have usually been very fast movements, which lasted from 1,000 to 1,500 milliseconds, whereas in the present study the total movement time was 2775 milliseconds, which is likely to follow the rules concerning slow movements. On the other hand, in schema theory, effectors (i.e., the individual muscle or muscle groups) are known as the variant (selectable) characteristics of the motor program, which, according to this theory, learned fast movements can be performed with various effectors. However, the point to note here is that when performing the learned movement with novel effectors, the learner must have have the opportunity to be able to change the overall movement time, so that they could maintain the ratios between the components of movement as invariant features, as shown in early research on the production of a signature with different limbs (Lashley, 1942). In the present study, it was stressed to the participants that the movement sequence had to be performed with the same total time as that used during the practice phase. As a result, this has probably led participants to focus more on the performance of the movement within the required overall time, and in some circumstances, has made them produce more errors in relative timing. More importantly, as can be inferred from the results of this study, participants could in any case perform the relative timing at the phases of retention and transfer when compared with the early phases of acquisition, which in itself supports the schema theory. In this study, considering the limitations of the apparatus used for measurements and the factors affecting representation of movement sequences such as the amount of practice (Kovacs, Mühlbauer and Shea, 2009), the type of feedback (Kovacs, Boyle, Grutmatcher, Shea, 2010) and length of delay between learning and retention (Savion-Lemieux and Penhune, 2005), intermanual transfer of timing was investigated in the mirror (same motor commands as those in practice) and non-mirror (same visual-spatial coordinates as those in practice) conditions, in which the findings were discussed on the basis of behavioural measures from the quantities of time spent for moving in the intervals between the sensors. The results should therefore be interpreted with caution and need to be confirmed and extended in future research where certain factors such as velocity, variability in muscle activity during movement, and joint angles are measured so that we can understand how and what causes possible differences in the representation of motor sequences when these are performed in a variety of ways. In the future, researchers could also use a pattern of spatial-temporal movement sequences similar to those employed in Kovacs et al's research (Kovacs, Han, and Shea, 2009; Kovacs, Boyle, Grutmatcher, Shea, 2010), so that movement reversals could be executed at different speeds, and thus, different combinations of these speeds could provide a specific way of executing the sequence.

Declaration of Conflicting Interests. The Authors declare that there is no conflict of interest.

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