Running head: Motor Sequence Learning in Older Adults

Age-related Declines in Visuospatial Working Memory Correlate with Deficits in Explicit Motor Sequence Learning

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Abstract

Numerous studies have shown that older adults exhibit deficits in motor sequence learning, but the mechanisms underlying this effect remain unclear. Our recent work has shown that visuospatial working memory capacity predicts the rate of motor sequence learning and the length of motor chunks formed during explicit sequence learning in young adults. In the current study, we evaluate whether age-related deficits in working memory explain the reduced rate of motor sequence learning in older adults. We found that older adults exhibited a correlation between visuospatial working memory capacity and motor sequence chunk length, as we observed previously in young adults. In addition, older adults exhibited an overall reduction in both working memory capacity and motor chunk length in comparison to young adults. However, individual variations in visuospatial working memory capacity did not correlate with the rate of learning in older adults. These results indicate that working memory declines with age at least partially explain age-related differences in explicit motor sequence learning.

Introduction

The ability to acquire new action sequences is critical to functional independence with advancing age. Although normal aging does not appear to affect the acquisition of relatively simple motor sequences (e.g. Frensch and Miner 1994; Howard and Howard 1989; Seidler, 2006), numerous studies have reported a decline in the ability of older adults to learn action sequences with complex structure under both implicit and explicit learning conditions (e.g. Curran, 1997; Howard et al., 2004; Shea et al., 2006). For example, Howard et al. (2004) have found that older adults could not learn new sequences where the fixed and random elements were intermixed (alternating serial reaction time task). Curran et al. (1997) have reported that learning-related improvements in the serial reaction time (SRT) task (Nissen & Bullemer, 1987) are less in older than in young adults (YA). The underlying mechanisms of such age-related declines in motor sequence learning remain unclear.

It may be that cognitive declines associated with aging underlie deficits in motor sequence learning. Aging has a detrimental impact on many cognitive functions, including working memory (e.g. Reuter-Lorenz et al., 2000). It has been suggested that declines in working memory capacity may mediate age-related changes in many complex tasks, including sequential behavior (e.g. Cornoldi et al., 2007; Gomez-Perez & Ostrosky-Solis, 2006; Mayr & Kliegl, 1993). In addition, studies have shown that individual differences in working memory capacity play a significant role in explicit motor sequence learning (e.g. Bo & Seidler, 2009; Unsworth & Engle, 2005). It has been shown that older adults rely more on cognitive resources for the performance of simple motor tasks than young adults, such as balance (Huxhold et al., 2006) and walking (Lindenberger et al., 2000). It is unclear how and whether older adults rely on their relatively limited cognitive resources (e.g. Craik & Byrd, 1982) when performing complex motor tasks. Therefore, the current study examined age-related changes in cognitive functions, including working memory capacity and temporal control, and determined whether they are correlated with motor sequence learning deficits in older adults.

To explain the process of sequence learning, Verwey (1996; 2001) has proposed a model including components of “buffer loading” and “dual-processing”, in which sequences are executed by a cognitive and a motor processor. Participants have to rely on the cognitive processor to select individual sequence elements one by one when learning a new sequence. However, once a sequence is learned, the cognitive processor selects a single representation (i.e. a ‘chunk’ of the sequence) while a dedicated motor processor is running in parallel to execute the sequence. Buffer loading may be the engagement of a kind of short-term motor memory (Henry & Rogers, 1960; Sternberg et al., 1978) that allows each chunk to be programmed in advance of execution. Thus, the motor chunks develop as a result of repeatedly filling the motor buffer through the development of inter-element associations (Verwey 1996). Here, we propose that the buffer is not specific to the motor domain, and the size of each chunk is generally determined by short-term memory capacity.

Recently, Shea et al. (2006) have reported that older adults could not develop a clear chunking pattern during sequence learning while young adults did, even though older adults were able to execute the sequence more quickly with practice. However, our recent study in young adults (Bo & Seidler, 2009) as well as other studies on motor sequence chunking (e.g. Kennerley et al., 2004; Verwey and Eikelboom, 2003) show substantial individual differences in chunk development (e.g. the location of chunks varies across participants). Thus, age group comparisons of motor sequence chunking patterns may conceal individual differences.

It has been shown that chunking patterns can be complex and exhibit little consistency across participants (e.g. Kennerley et al., 2004; Sakai et al., 2003; Verwey 2003; Verwey and Eikelboom, 2003; Verwey et al., 2009). It is typical to quantify individual differences in chunking patterns via visual detection of relatively longer inter-element durations, followed by statistical analysis across a group of participants (Kennerley et al., 2004; Sakai et al., 2003). Here, we used a similar technique that defines chunks with at least two elements. Although it is theoretically possible to have a 1-element chunk, it is hard to justify whether no statistical differences among neighbors were actually 12, one-element chunks (12-element sequence in the current experiment); one, 12-element chunk; or no chunks. It is also mathematically possible to have a 10-element chunk (maximum possibility) in a 12-element sequence. Although a 10-element chunk seems quite long based on the literature (e.g. Verwey & Eikelboom 2003), we decided not to put a constraint on the analysis from the outset. Thus, we assume that a chunk is a group of 2 - 10 elements in the current study.

In addition to working memory, temporal control processes may also contribute to the development of chunking patterns when older adults learn new motor sequences. A “central timing mechanism” has been proposed to explain correlations among various tasks that exhibit temporal structures (e.g. Ivry & Hazeltine, 1995). General age-related slowing may affect the pace of the central timing mechanism and thereby limit temporal resolution. In tasks that assess “central timing”, older adults move more slowly and have larger temporal variability than young adults (e.g. Rakitin et al., 2005; Rakitin & Malapani, 2008; Vanneste et al., 2001). Although producing a sequence is not necessarily rhythmic, it is a task that is mainly measured by reaction time. Low temporal resolution and slow speed in older adults can result in slow buffer loading during motor sequence learning. In other words, slow processes for a previous chunk can affect the processes for the next chunk. In addition, multiple brain imaging studies have demonstrated a general timing network including the dorsolateral prefrontal cortex (DLPFC), pre-supplementary motor area (preSMA), supplementary motor area (SMA), and cerebellum (Maquet et al., 1996; Smith et al., 2003). These areas are also engaged during motor sequence learning (Boyer et al., 2005; Doyon et al., 2002; Kennerley et al., 2004). Thus, it is possible that older adults who have impaired temporal control cannot develop consistent motor chunking patterns. The current experiment investigated whether age-related impairments in motor sequence learning might be partially due to declines in temporal control with age as well.

Therefore, the current study examined whether age-related declines in explicit motor sequence learning and the development of motor sequence chunks are related to cognitive declines, particularly in terms of visuospatial working memory and temporal control. To measure the development of motor sequence chunks, we asked young and older adult participants to perform an explicit motor sequence learning task through four learning phases, progressing from a serial reaction time type task to a discrete sequence production task. The last block of training was used to define the final chunking pattern for each participant. To measure working memory capacity, we employed the visuospatial working memory task introduced by Luck & Vogel (1997, exp 1). Lastly, we used the continuous tapping task (Wing A & Kristofferson 1973) to evaluate individuals' temporal control ability. The temporal variability (i.e. coefficient of variation) was calculated using the standard deviation of the absolute tapping interval divided by the mean, then multiplied by 100.

We predicted that older adults would exhibit shorter sequence chunk lengths in comparison to young adults and that they would acquire motor sequences more slowly. Moreover, we expected that individual differences in working memory capacity and temporal control would be positively correlated with the length of motor chunks formed and the rate of sequence learning in older adults. We also expected that older adults would have lower scores on all measures relative to young adults. Finally, because chunking patterns are thought to be represented in an abstract fashion that is not tied to the effector used during training (e.g. Keele et al., 1995; Sternberg et al., 1990; Verwey & Clegg 2005; Young & Schmidt, 1991; but also see Verwey et al., 2009), we predicted that acquired chunk patterns would be maintained when participants performed the same sequence with either hand. We previously found that young adults showed transfer patterns if they developed chunks in the earlier learning phases. In this experiment, we explored whether older adults who developed consistent chunks would show similar patterns when they changed their response effectors.

Methods

Participants

Thirty-two older adults (OA: age range = 65.0-78.7 years, 12 males and 20 females, mean age = 70.6 (± 4.5)) and 27 younger adults (YA: age range = 18.8 – 28.8 years, 12 males and 15 females, mean age = 20.9 (±2.1)) participated in this study. All individuals were right-handed (determined by self-report and the Edinburgh handedness inventory; Oldfield, 1971) with normal or corrected vision. They provided their consent before the experiment and were paid $15 per hour for their participation. The experimental procedures were approved by the Institutional Review Board of the University of Michigan.

Procedure

Participants first completed general health history questionnaires (Table 1). Older adults with a history of stroke, diabetes, alcoholism, arthritis, or neurological disease were excluded from the study. The Mattis dementia rating scale (Mattis, 1988) and the Mini-Mental State Exam (MMSE, Folstein et al., 1975) were administered to screen out older adults with dementia. The CHAMPS physical activity questionnaire for older adults (Stewart et al., 2001) was used to assess how active each participant was during his/her daily life.

Participants were then asked to perform an explicit motor sequence learning task, a visuospatial working memory task, and lastly, a continuous tapping timing task. All stimuli were controlled by a PC using custom software written in E-Prime ™ version 1.0 (Psychology Software Tools, Pittsburgh).

Explicit motor sequence learning task:

Participants were instructed to learn a color-cued 12-element sequence (purple, yellow, blue, purple, red, blue, red, yellow, blue, red, yellow, purple) of finger movements. The colors “red”, “yellow”, “blue” and “purple” were mapped onto the middle and index fingers of the left hand and the index and middle fingers of the right hand to the four adjacent buttons on the keyboard (c,v,b,n above the spacebar) respectively. We selected this sequence because: 1) the probability of each element within the sequence was equally distributed; 2) this sequence did not have a fixed grouping pattern (i.e. no regularity; e.g. ABCD); 3) the sequence did not have runs of three (i.e. triplets) or trills (e.g., ABAB), even when the stimuli were presented continuously in phases 1 and 2 (i.e. no breaks between sequences). To display the sequence while in the learning phase, four visual stimulus boxes were presented side by side on a computer screen. Each square was assigned one of four colors (“red”, “yellow”, “blue” and “purple” from the most left to the most right), which remained ‘fixed’ to that spatial position for the remainder of the experiment. There were 4 *learning* phases and 2 *transfer* phases in the task:

Phase 1: The sequence was presented element by element every 1000 ms (900 ms stimulus duration, 100 ms inter-stimulus delay) and the participants were instructed to press the corresponding buttons as fast as possible after seeing each stimulus. There were no breaks between completions of a sequence and participants were not told where a sequence starts. We used a paced 1000ms inter-stimulus delay because one of our behavioral studies (Bo & Seidler, submitted) showed that older adults were able to show equivalent learning as young adults at this rate and were comfortable with the task. If participants made a response longer than 1000ms, we took that element out of the analysis. A complete sequence (12 elements) defined one trial and 10 trials constituted one block (12 elements * 10 trials). Phase 1 contained 3 blocks (12 element * 10 trials * 3 blocks) of training.

Phase 2: The task was the same as that in phase 1. However, participants had to reach 80% accuracy (to accommodate a potentially large performance range for older participants) on 10 consecutive trials for the last block of phase 2 in order to move on to phase 3. If a participant's accuracy was lower than 80%, they were asked to repeat phase 2.

Phase 3: For this phase, participants were asked to refrain from responding until all 12 elements of the sequence were shown (one element every 500 ms). After presentation of the last element of the sequence in each trial, an instruction screen appeared directing the participant to begin reproducing the entire sequence from memory (i.e. discrete sequence production task). A trial in phase 3 consisted of the visually-presented sequence and the subsequent sequence reproduction generated by the participants. Each trial concluded after the participant had input 12 responses. There were 3 blocks in phase 3 and accuracy feedback was given at the end of each block. If accuracy was lower than 80% at the last block of this phase, participants had to repeat phase 3.

Phase 4: During this phase, participants performed the sequence solely from memory, without visual cues (i.e. they were not shown the sequence) at the beginning of each trial. If they could respond with 80% or higher accuracy for 3 continuous blocks (10 trials each), the sequence was considered learned. The last block of this phase was used to define the final chunking pattern for each participant (see below).

Transfer Phases (5 and 6):

As they had done in phase 4, participants were again asked to generate the acquired sequence purely from memory, but they were asked to use the fingers of only one hand for these trials. Two blocks of responses contained 10 trials each of the sequence, where responding involved the index, middle, ring and little fingers of the right hand in phase 5, and the little, ring, middle and index of the left hand for phase 6. Accuracy feedback was reported at the end of each trial. All participants were asked to perform the two transfer conditions in a counter-balanced fashion (i.e. half of the participants performed the phase 5 first while the other half performed the phase 6 before phase 5).

Visuospatial working memory task:

We slightly modified the visuospatial memory task published by Luck & Vogel (1997, exp. 1) (i.e. we reduced the number of array sizes from 12 to 10 and omitted the array size of 1 to shorten the testing time). Participants viewed a sample array (within a 9” x 9” region) of colored squares (1”x1”) followed by a test array. Then, they had to press the “s” key if the two arrays were identical or the “d” key if the two arrays were different. The arrays consisted of 2-10 (array size) colored squares (drawn randomly from 7 colors: red, blue, violet, green, yellow, black, and white). Each color appeared no more than twice for the 8-10 squares conditions. The sample array was presented for 100 ms, followed by a 900 ms blank screen delay, and then a 2000 ms presentation of the test array. The test array was either the same as the sample array or different in the color of one of the squares. In other words, only one of the colors, not the locations, was changed in the different scenario. The ratio of same to different arrays was 1:1. For each trial, only one of the colors was changed for the test array. Thus, it is possible that the test array contains a color that had not occurred in the sample array on that trial. Therefore, this task relied on detection of a change in color and / or location. We used nine different arrays as the stimulus set, each having between 2 and 10 squares. Each array appeared 5 times in random order.

Continuous Tapping task

Participants wore a pair of over-the-ear headphones and sat comfortably in front of a computer. They were instructed to tap the spacebar using their index finger to coincide with given tones in three interval conditions: 500ms, 1000ms and 1500ms while looking at a fixation cross in the center of the screen. After 15 (audibly paced) tapping responses were recorded, the audible tones ceased and the participants were to continue tapping as consistently as possible for another 30 intervals (unpaced) at the respective interval. Three blocks of five trials were tested for each interval condition. The blocks were presented in a random order.

Analysis

Explicit motor sequence learning:

All error trials were removed for reaction time analyses.

Early learning phases – phases 1 & 2

Data from phases 1 & 2 were treated as the early phase of learning. The *Reaction Time* was the time from the appearance of stimulus to the onset of the response. The mean reaction time for every trial was computed. In our previous study in young adults, we used a power fitting function to evaluate the rate of learning. However, a power function did not provide a good fit to the data for 1/3 of older participants. Moreover, neither did other learning curve functions such as linear or exponential functions (i.e. 8, 12 and 9 older adults' data sets showed R-square values lower than 0.10 using linear, exponential and power functions respectively). Therefore, we computed a *reaction time change score* for each phase as the change in reaction time from the first block (10 trials) to the last block (10 trials) to represent the rate of learning for old and young adults . We did not use accuracy data to calculate the rate of learning because most of the participants attained a high accuracy level after just one or two trials of practice (greater than 90% correct).

Late learning phases – phases 3 & 4

We were interested in observing the motor chunking pattern when participants had to reproduce all the elements of the sequence at once without visual cues in phases 3 and 4. The ***Response Time*** for the first movement in the sequence was defined from the appearance of the go signal to the onset of the first response. Response times for the later sequential elements were calculated between two consecutive responses. All the error trials were removed for further analyses. .

First, we defined the ‘preliminary’ *chunk points*. The last block of phase 4 was used to pre-define these chunking points for each participant, assuming that by this phase the sequence had already been learned and the execution was fluid. A chunk was determined by the number of elements grouped together according to duration in neighboring response times (Kennerley et al., 2004). Longer inter-response times between elements represent the divisions of chunks, whereas shorter inter-response times refer to a strong association within each chunk. We used one-tail paired t-tests, from the 3rd to 11th elements of the sequence, to evaluate whether each element was significantly longer than the element that came before and after it (alpha value was pre-set at 0.2 level). We adjusted the alpha value based on our young adults’ data (Bo & Seidler 2009) and the fact that it was applied for a within subjects analysis only across 10 trials. A chunk is a group of at least 2 elements. So naturally, the 1st and 2nd elements were omitted from the analyses as the 1st element is always the start of a chunk and the 2nd element must fall into the first chunk. Similarly, the 12th element must fall into the last chunk, and was therefore also excluded from the analysis.

Once these pre-defined chunking points were established, we confirmed individual chunk points at the group level using the re-ordering procedure based on that used by Kennerley et al. (2004; see also Bo & Seidler 2009). The individual data were re-plotted according to the longest response time for each chunk. All the chunks were treated equally during the analysis. That is, regardless of the length of the chunks, we aligned all the chunk elements to the longest response time at the beginning of each chunk. Figure 1 illustrates this aligning procedure. The initial analysis identified four chunk points (Figure 1A). Taking the second chunk point as an example, the 4th element of the sequence was labeled as position 0 because the longest response time for that chunk preceded this element. The 3rd and 2nd elements were labeled as -1, -2, whereas the 5th and 6th elements were labeled as 1 and 2 for that particular chunk. The same procedure was used for the rest of the chunks for every participant (Figure 1B). Figure 1C illustrates the same procedure when the lengths of the chunks were different. These two chunks were weighted equally when all the elements were aligned (Figure 1D). After the chunk points were re-organized, we performed a one-way ANOVA on response time (individual participant data) to examine whether the response time at position 0 was significantly longer than the response times at any other positions. Only when the response time at position 0 was found to be significantly higher than the response times at any other positions did we accept the preliminary chunks as the final chunk points. The *Mean Chunk Length* was calculated using 12 (elements) divided by the number of chunks.

Insert Figure 1

Then, we defined *how quickly chunks formed during training*: The mean response time for each element of the sequence was computed for every block in phases 3 and 4. Then, the sequence elements were re-ordered from the longest to the shortest response time for each block. If any earlier block showed the same re-ordered pattern as the last block of phase 4, we marked that block as the beginning of the developed chunks.

<u>Transfer conditions – phases 5 & 6</u>

To evaluate the transfer, we first calculated the mean response times for the first block in phases 5 & 6. Then we used the same re-ordering and matching procedures as described above. If either of the phases showed the same pattern as that in phase 4, the transfer was deemed successful for that participant. Then, we performed a Chi-square test to examine whether transfer was significant for older adults. Finally, a non-parametric independent sample test (Mann-Whitney test) was used to compare transfer effects between young and older adults.

Visuospatial working memory task:

<u>Memory Capacity</u> K = S * (H - F), where S is the size of the array, H is the observed hit rate and F is the false alarm rate (Vogel and Machizawa, 2004). We computed the K value for each array size, and took the average K across all array sizes to represent the visuospatial memory capacity for each participant.

Continuous tapping task:

The mean and standard deviation of the unpaced inter-tap intervals were calculated. Any tapping intervals that were shorter or longer than 2 standard deviations of the mean were excluded from the analysis. The ***Coefficient of Variation*** was calculated using the standard deviation of the absolute tapping interval divided by the mean, then multiplied by 100.

Results

All older participants reached a minimum Mini-Mental State Exam (MMSE, Folstein et al., 1975) score of 27 and a Mattis dementia rating scale (Mattis, 1988) score of 123. Table 1 lists the results of questionnaires and screening tests for older participants.

Insert Table 1

Explicit motor sequence learning:

Results for the young adults have been previously presented in detail (Bo & Seidler, 2009) and are included here as comparison with the older adult data. Seven out of 32 older adults and 2 out of 27 young adults were not able to either remember the sequence (i.e. explicitly expressed that they could not continue the task at any learning phases) or develop chunking patterns (i.e. our statistical procedure failed to identify clear chunking points). We believe that this is one index of poorer sequence learning in older adults. However given the goals of the current study, these datasets were excluded from further analysis.

Early learning phases – phases 1 & 2

Because all the included 25 older adults were able to reach the accuracy cutoff without repetitions in phase 2, we labeled the 1st block of phase 1 as block 1, the 2nd block of phase 1 as block 2, the 3rd block of phase 1 as block 3, the 1st block of phase 2 as block 4, the 2nd block of phase 2 as block 5, the 3rd block of phase 2 as block 6. Figure 2 (A & B) illustrates the overall performance for 60 trials from blocks 1 to 6 in phases 1 and 2. As expected, a mixed ANOVA with block as within-subjects factor and group (young, older) as between-subjects factor revealed that older adults had longer reaction times ($F_{(1,48)}$=133.86, P<0.01) and lower accuracy ($F_{(1,48)}$=19.82, P<0.01) than young adults . Both young and older adults responded faster ($F_{(5,240)}$=61.42, P<0.01) and more accurately ($F_{(5,240)}$=133.86, P<0.01) as they practiced across blocks. A group x block interaction ($F_{(5,240)}$=19.72, P<0.01) on accuracy revealed that older adults had significantly lower accuracy in block 1 and 4 (Bonferroni-corrected post-hoc procedure, all P<0.05) than young adults.

Late learning phases & transfer – phases 3 - 6

Late learning phases – phases 3 & 4

Two of 25 older adults had to repeat phase 3 once due to the accuracy cutoff requirements. Figure 2C & D illustrates the mean response time and accuracy in the last 3 blocks of phases 3 and 4. A mixed ANOVA revealed that older adults had longer response times ($F_{(1,48)}$=55.28, P<0.01), P<0.01) and lower accuracy ($F_{(1,48)}$=24.87, P<0.01) than young adults. Both young and older adults responded faster ($F_{(5,240)}$=28.97, P<0.01) and more accurately

($F_{(5,240)}$=64.02, $P<0.01$) as they practiced across blocks. A group x block interaction on accuracy ($F_{(5,240)}$=6.97, $P<0.01$) revealed that older adults had significantly lower accuracy in all blocks of phase 3 and the 1st block of phase 4 (Bonferroni-corrected, all $P<0.05$) than young adults.

Insert Figure 2

Figure 3A shows the performance of one representative older adult during the last 3 blocks of phase 4. Participant A has divided the whole sequence into 5 chunks: at the 1st, 3rd, 5th, 7th, and 10th elements for the last block in phase 4. Interestingly, the chunking pattern was not the same in the 1st or 2nd block in phase 4 suggesting that the final chunking pattern was not developed until after the 2nd block of phase 4.

Using the methods outlined in the analysis section, we first identified the beginning of each chunk based on multiple paired t-tests for every participant. Then, we confirmed these points at the group level using a procedure modified from Kennerley et al. (2004; see also Bo & Seidler, 2009). A mixed model ANOVA was performed where the position from the predefined chunks was the within-subjects factor and the age group was the between-subject factor. A significant position effect was found ($F_{(8,171)}$=10.66 and 8.73, both $P<0.01$) for both young and older adults. Post-hoc tests (Bonferroni-corrected) showed that the chunk point RT at position 0 was significantly longer than any of the adjacent response times (all $P < 0.01$, Figure 3B), confirming these pre-defined chunk points.

Then, we observed whether the locations of those chunking points were similar across participants. Substantial individual differences were found suggesting that the property of the selected sequence did not evoke particular chunking locations (also see Verwey & Eikelboom 2003).

After all the chunk points were confirmed, a correlation analysis between the chunk length and the response time ratio between and within chunks for the last block of phase 4 was performed to examine whether longer chunks required a longer initial reaction time. While young adults had a significant correlation between the chunk length and response time ratio (R=0.48, P<0.05), no significant correlation was found in older adults (R=0.10, P>0.10). However, when we compared the correlations between young and older adults (Fisher r-to-z transformation to test significance of difference between two correlation coefficients), no group difference was found either (z=1.40, P = 0.16).

Table 2 lists the training block number where the final chunking pattern started to form for both young and older adults. Eighteen of 25 older participants did not show their final chunking patterns until the last block of learning. Two out of these 18 participants had to repeat phase 3, which means that they had 9 blocks of training in phases 3 & 4. Four participants developed their stable chunks at the 2nd block of phase 4. Two participants showed chunks at the 1st block of phase 4. There was only one older adult who had his final chunks at the 2nd block of phase 3.

Transfer conditions – phases 5 & 6

Using the methods outlined in the analysis section, the results for the transfer conditions with “Y” representing positive transfer and “N” representing no transfer were listed in Table 2. Twenty out of 25 older adults did not keep the same pattern of chunking when they changed the response effector. Three older adults appeared to have a consistent chunking pattern regardless of the response effector (full transfer: transfer to both left and right fingers), and the remaining two showed partial transfer (i.e. transfer to either left or right fingers). A Chi-square test revealed that the older group did not show transfer (*Chi-square* = 14.44, $P < 0.01$). When we compared the young and older groups, a nonparametric independent sample test (Mann-Whitney test) showed that older adults had significantly less transfer than young adults ($Z = -2.75$, $P < 0.01$). Overall, older adults formed their chunking patterns later than young adults ($t_{(48)}=3.01$, $P<0.05$) and were less successful at transfer.

Comparing between young and older groups, significant differences were found in the mean chunk length (12 elements divided by number of chunks, $t_{(48)}=3.59$, $P<0.01$, Figure 3C), overall response time at the last block of phase 4 ($t_{(48)}=-6.04$, $P<0.01$, Figure 3E) and the number of the training block that first started to show the final chunk pattern ($t_{(48)}=-2.93$, $P<0.01$ Figure 3D). In brief, older adults had shorter chunk lengths, required a longer time to reproduce the sequence and formed their final chunking pattern later compared to young adults during the sequence learning.

Insert Figure 3, table 2

Visuospatial working memory:

The overall performance for the visuospatial working memory task showed a similar pattern between young and older adults: the accuracy for arrays of size 2-4 items was relatively higher than that for sizes greater than 4. Comparing between young and older adults, older adults had significantly lower visuospatial working memory capacity than the young adults ($t_{(48)}$=6.00, P<0.01, Figure 4A).

Continuous tapping task:

The average coefficients of variation (CV) were 3.7, 3.9 and 3.6 for young adults and 5.3, 5.5 and 6.8 for older adults during the 500, 1000, and 1500ms conditions, respectively. A mixed ANOVA revealed a significant condition x group interaction ($F_{(2,144)}$=4.28, P<0.01) and group main effects ($F_{(1,144)}$=55.35, P<0.01), while the condition effect approached significance ($F_{(2,144)}$=2.85, P=0.06). Post-hoc analysis suggested that while young adults did not show differences across the three intervals (suggesting a general timing ability), older adults increased temporal variability as the interval increased from 500 to 1500ms (Figure 4B). In addition, we ran correlations among CV500, CV1000 and CV1500 to examine whether older adults who had higher CV in one interval would also show higher CV in other intervals. Similar to young adults, significant correlations on the CV among these three intervals were found in older adults

(*R*=0.70, *P*<0.01; *R*=0.57, *P*<0.01; *R*=0.81, *P*<0.01 for CV500 and CV1000; CV500 and CV1500; CV1000 and CV1500 respectively).

Relationships among working memory, temporal consistency and sequence learning measures

In our previous work in young adults, we found a correlation between working memory capacity and rate of sequence learning, as defined with power function coefficients (Bo & Seidler, 2009). Since a power function did not provide a good fit for each individual older adult's data, we computed the reaction time change scores to represent the rate of learning. No correlation between the rate of learning and working memory capacity was found. When we analyzed the young adults data in the same way, there were a trend for a correlation between reaction time change scores within phase 1 and mean chunk length (*R*=0.36, *P*=0.08), and the correlation between reaction time change scores within phase 2 and working memory capacity (*R*=0.38, *P*=0.06). In addition, no correlations were found between any of the timing measures and the rate of learning for all sequence learning phases in both young and older adults.

Figure 4C depicts the scatter plot for individuals' memory capacity and mean chunk length for both young and older adults. Significant positive correlations between working memory capacity and mean chunk length were found in both groups (*R*=0.78, 0.54 for young and older adults respectively, both *P*<0.01) suggesting that the number of items participants could accurately retain in working memory predicted the temporal pattern of the acquired sequence regardless of age. That is, participants with low working memory capacity formed shorter chunks while high capacity participants had relatively longer chunks. Comparing the correlations between working memory and chunk length, there was no difference between young and older adults ($z = 1.46$, $P = 0.14$).

Similar to young adults, no other correlations were found in any combinations between the temporal measures, memory capacity, chunk length and overall response time (all $P>0.05$) in older adults.

Insert Figure 4

Discussion

In our previous study, we found a positive correlation between visuospatial working memory capacity and both the rate of early motor sequence learning and the length of motor chunks that young adult participants formed (Bo & Seidler, 2009). In the current study we report that older adults exhibited an overall reduction in both working memory capacity and motor chunk length in comparison to young adults. Moreover, there was a positive correlation between older adults' visuospatial working memory capacity and the length of motor chunks. However, in contrast to young adults, older adults did not show a correlation between working memory capacity and the rate of learning. Thus it seems that older adults may rely on visuospatial working memory during early sequence learning in a manner similar to young adults, but other factors also influence the overall rate of learning.

It is important to note that seven out of 32 older participants were not able to remember the sequence (n = 4) or develop a consistent chunking pattern (i.e. the statistical procedure used in the current study failed to identify any chunk points, n = 3). When we compared the visuospatial working memory capacity for these seven older adults with the remaining 25 successful older adults, we found that 6 out of these 7 were below the mean capacity. These results provide further evidence for some motor sequence learning deficits in older adults and highlight the substantial individual differences that exist. In addition, these excluded cases suggest that not all the participants had successful explicit learning.

Twenty-five out of 32 older adults were able to develop clear chunking patterns, suggesting that this ability is primarily not impaired by normal aging. However, using the 25 data sets from the older participants who did develop a consistent chunking pattern, we found that the length of motor chunks was significantly shorter than those seen in young adults. This result is different from those of Shea et al (2006), who reported that older adults could not develop a consistent movement sequence structure. We believe that this discrepancy arose due to several experimental differences between the two studies. First, we used only the successful participants’ data when measuring chunks while Shea et al (2006) compared group performance between all their older and young adults. Second, we used a key-press version of the discrete sequence production task while Shea et al (2006) used an arm aiming version of the task where participants had to move a lever to different target locations in a sequential order. Our task required finger press movements while their task involved more complex multi-joint movements. Third, we explicitly instructed the participants to remember the sequence while Shea et al (2006) did not, although all participants developed explicit knowledge of the sequence by the end of the experiment. Thus, our study forced participants to use an explicit memory strategy to remember a sequence of items throughout the whole learning process while participants in the Shea et al. (2006) study gradually developed explicit awareness from the early to the late learning phase. It is possible that the older adults in the Shea et al. (2006) study would have gone on to develop consistent chunks as participants did in our study if they were given more practice. In addition, the older adult participants in Shea et al. (2006) were younger than ours. It is not clear how this could have lead to the differences, however, given that presumably these younger individuals would have less working memory impairment. Lastly, we focused on individual differences while they only performed a group comparison. The current study revealed that most older adults could develop a consistent chunking pattern during motor sequence learning, although they needed additional practice to remember a new sequence and had shorter chunk lengths when producing a learned sequence.

Since most of the older participants developed consistent chunks at the last block of the training phase, one may question the stability of these patterns. Although it is possible that the chunking pattern may have changed with more practice, our statistical procedure at least ensures that the pattern is consistent across the last block. Previous studies have judged chunk boundaries based on visual inspection of reaction times (e.g. Kennerley et al., 2004; Shea et al., 2006).

In other words, as long as one interval was relatively longer than the neighboring intervals, that interval was defined as the boundary of a chunk. This “relatively longer interval” could be easily biased by one or two trials, however (i.e. a lack of consistency). To address this, we developed and used a statistical procedure (Bo & Seidler 2009) to test whether one “relatively longer interval” was significantly longer than its two neighbors’ at the .2 alpha level. Because of this statistical cutoff, we rejected the data from three of the 32 older adults even though they exhibited some patterns of “relatively longer” and “relatively shorter” intervals. Thus, we ensured that at least most of the trials within the last training block were exhibiting the same chunking pattern.

We previously found that the pattern of motor chunks was not always transferable (Bo & Seidler 2009). Young participants who formed their chunking patterns earlier in the experiment exhibited better transfer of the pattern to new response effectors. Comparatively, it seems older adults had a similar pattern where they had less successful transfer and later development of consistent chunking patterns. These results suggest that chunking patterns are initially effector-dependent, and then become more abstractly represented with additional practice.

It is perhaps not surprising that older adults showed lower visuospatial working memory capacity and poorer temporal control in comparison to young adults, given that several other studies have reported these effects as well (e.g. Baudouin et al., 2004; Gunstad et al., 2006; Jonides et al., 2000; Nordahl et al., 2006; Reuter- Lorenz et al., 2000; Stebbins et al., 2002). However, it was an open question whether older adults would still engage these limited cognitive resources to perform explicit motor sequence learning. The positive correlation between visuospatial working memory capacity and mean motor chunk length that we observed suggests that older adults were able to use their working memory during learning. Awh et al. (2007) have argued that mean working memory capacity represents a fixed number of items that people can hold in short-term working memory regardless of object complexity. This claim is quite consistent with our previous finding in young adults: the ratio between mean motor chunk length and working memory capacity was very close to 1 (3.81/3.18). It is surprising that the ratio between these two variables was even higher for older adults (2.97/1.76). It seems that older adults may have been employing other memory strategies. In addition, older adults might have also relied upon other memory domains (i.e. auditory, verbal etc). In the current study, we did not measure other domains of working memory, though. Thus it remains an open question as to whether and how they would relate to motor sequence learning. An alternative explanation for the result that the chunk length was longer than what was predicted by working memory capacity in older adults might relate to the additional involvement of motor components at the later learning phases. Hikosaka et al. (1999) argued that both spatial and motor components are involved in sequence learning and that the motor component develops more slowly than the spatial one. This implies that there might be a decreasing correlation between working memory and sequencing with practice.

One may question our interpretation of working memory contributions to motor sequence learning in older adults because we did not find a significant correlation between working memory capacity and the rate of sequence learning. In young adults, the power fitting method reasonably represented rate of change for each individual. In contrast, learning patterns were so variable for older adults that we could not select a single fitting method that would provide a reasonable fit to the data of each participant (8, 12 and 9 older adults' data sets showed R-square values lower than 0.10 using linear, exponential and power functions respectively). Such results do not indicate that older adults were not learning the sequence, however. Indeed, our results showed that 25 out of 32 older participants had not only learned the sequence but also developed clear chunking patterns. Rather, the older adults were highly variable in the shape of their learning curves across participants. It may be that individuals engaged different learning strategies during the early learning phase. In addition, the lack of correlation between the rate of learning and working memory capacity suggests that older adults were engaging resources other than visuospatial working memory to perform the task. In a study of implicit motor sequence learning, Frensch & Miner (1994) found that digit span performance correlated with the magnitude of implicit learning that occurred, for both young and older adults. While it is hard to extrapolate from implicit to explicit learning conditions, it may be that older adults in the current study were also engaging some (potentially less effective) verbal strategies.

We also predicted that age-related declines in temporal control ability (e.g. Rakitin & Malapani, 2008) would interrupt the development of motor sequence chunking patterns in older adults. In contrast to this hypothesis, we did not find a correlation between individual differences in temporal control and the motor sequence chunking patterns. In combination with our previous findings in young adults (Bo & Seidler, 2009), these data suggest that a “common timing” mechanism does not play a significant role in the temporal structure of acquired motor sequences. In addition, there was no evidence to suggest that older adults engaged temporal control resources to compensate for declines in visuospatial working memory in order to optimize learning.

One may question the sensitivity of the current study to detect correlations, given declines in working memory and temporal control abilities in older adults. However, the fact that we found strong correlations between working memory capacity and mean chunk length, as well as positive correlations among the three temporal conditions, argues against this criticism. Another potential limitation of the current study is whether the correlation between working memory and chunk length was skewed by one or two extreme points due to the limited range of chunk length data, particularly for the older participants. In our older adult data set, one older participant had a mean chunk length of 2, five had a mean chunk length of 4, eight had a mean chunk length of 2.4 (i.e. 12 elements / 5 chunks) and the remaining eleven had a mean chunk length of 3. After removing the one participant with a chunk length of 2, a significant correlation was still observed ($R=0.47$, $P<0.05$), supporting the robustness of our findings.

In summary, we found that older adults exhibited an overall reduction in both working memory capacity and motor chunk length in comparison to young adults. Furthermore, we found a positive correlation between visuospatial working memory capacity and mean motor chunk length, suggesting that older adults relied on working memory resources to maximize motor sequence learning.

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Figure Captions:

Figure 1: Illustration of the chunking realignment procedure. Panel A depicts 4 initial chunking points identified for one representative participant. Panel B shows the plots realigned with respect to each chunk point in the sequence. Panel C depicts two initial chunking points with different chunk lengths for another participant. Panel D shows the plots realigned to each chunk point for the example in Panel C.

Figure 2: A) The mean reaction times for each block in phases 1 and 2; B) The mean accuracy for each block in phases 1 and 2; C) The mean response times for each block in the last 3 blocks of phases 3 and 4; D) The mean accuracy for each block in the last 3 blocks of phases 3 and 4.

Figure 3: A) The response time from the three blocks of phase four of sequence training are depicted for one representative older participant; B) Group mean response time data (last block of phase 4), after re-plotting with respect to each older adult’s initially determined chunk points; C) Mean chunk length for young and older adults; D) Block at which participants formed their final chunking pattern during training in young and older adults; E) Overall response time for completing a learned sequence in young and older adults.

Figure 4: A) Mean working memory capacity for young and older adults; B) Mean CV in 500, 1000 and 1500ms between young and older adults; C) Correlation

between working memory capacity (K) and mean chunk length for young and older adults.

Table 1: Questionnaires and screening tests for young and older adults

	YA		OA	
	M	SD	M	SD
General information				
Age	20.93	2.13	70.58	4.52
Gender	12M/15F	-	12M/20F	-
Year of high education**	2.88	1.33	5.04	2.19
No of medication**	0.20	0.58	3.60	2.00
Screening tests				
Mattis Dementia	143.80	0.58	143.24	0.93
MMSE	29.72	0.74	29.44	0.58
CHAMPS				
KCal/wk. exercise-related activities	5538.09	4305.95	3504.17	2865.15
KCal/wk. moderate exercise-related	4072.55	3566.01	2714.36	2550.98
Frequency/wk. exercise related activities*	21.68	6.61	12.24	5.39
Frequency/wk. exercise related	13.68	8.07	8.76	4.37

*P<0.05 **P<0.01

Table 2a: How quickly the final chunk pattern formed and transfer of the chunking pattern for older adults.

Participant	Repetition of phase 3	Block that showed final defined chunk points	No of blocks of training before forming the final chunks	Transfer Left	Transfer Right
Full Transfer					
11	No	2nd block phase 3	2	Y	Y
6	No	2nd block phase 4	5	Y	Y
5	Yes	3rd block phase 4	9	Y	Y
Partial Transfer					
14	No	3rd block phase 4	6	N	Y
18	No	3rd block phase 4	6	N	Y
No Transfer					
2	No	1st block phase 4	4	N	N
19	No	1st block phase 4	4	N	N
12	No	2nd block phase 4	5	N	N
15	No	2nd block phase 4	5	N	N
24	No	2nd block phase 4	5	N	N
1	No	3rd block phase 4	6	N	N
3	No	3rd block phase 4	6	N	N
4	No	3rd block phase 4	6	N	N
7	No	3rd block phase 4	6	N	N
8	No	3rd block phase 4	6	N	N
9	No	3rd block phase 4	6	N	N
10	No	3rd block phase 4	6	N	N
13	No	3rd block phase 4	6	N	N
16	No	3rd block phase 4	6	N	N
17	No	3rd block phase 4	6	N	N
20	No	3rd block phase 4	6	N	N
21	No	3rd block phase 4	6	N	N
22	No	3rd block phase 4	6	N	N
23	No	3rd block phase 4	6	N	N
25	Yes	3rd block phase 4	9	N	N

Table 2b: How quickly the final chunk pattern formed and transfer of the chunking pattern for young adults.

Participant	Repetition of phase 3	Block that showed final defined chunk points	No of blocks of training before forming the final chunks	Transfer Left	Transfer Right
Full Transfer					
1	No	1st block phase 3	1	Y	Y
6	No	1st block phase 3	1	Y	Y
14	No	1st block phase 3	1	Y	Y
2	No	1st block phase 4	4	Y	Y
5	No	1st block phase 4	4	Y	Y
22	No	1st block phase 4	4	Y	Y
24	No	1st block phase 4	4	Y	Y
Partial Transfer					
19	No	1st block phase 3	1	Y	N
25	No	3rd block phase 3	3	Y	N
9	No	3rd block phase 4	6	Y	N
10	No	3rd block phase 4	6	N	Y
11	No	3rd block phase 4	6	N	Y
No Transfer					
17	No	3rd block phase 3	3	N	N
13	No	1st block phase 4	4	N	N
15	No	1st block phase 4	4	N	N
3	No	2nd block phase 4	5	N	N
8	No	2nd block phase 4	5	N	N
21	No	2nd block phase 4	5	N	N
4	No	3rd block phase 4	6	N	N
7	No	3rd block phase 4	6	N	N
12	No	3rd block phase 4	6	N	N
16	No	3rd block phase 4	6	N	N
18	No	3rd block phase 4	6	N	N
20	No	3rd block phase 4	6	N	N
23	No	3rd block phase 3	6	N	N

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Figure 1

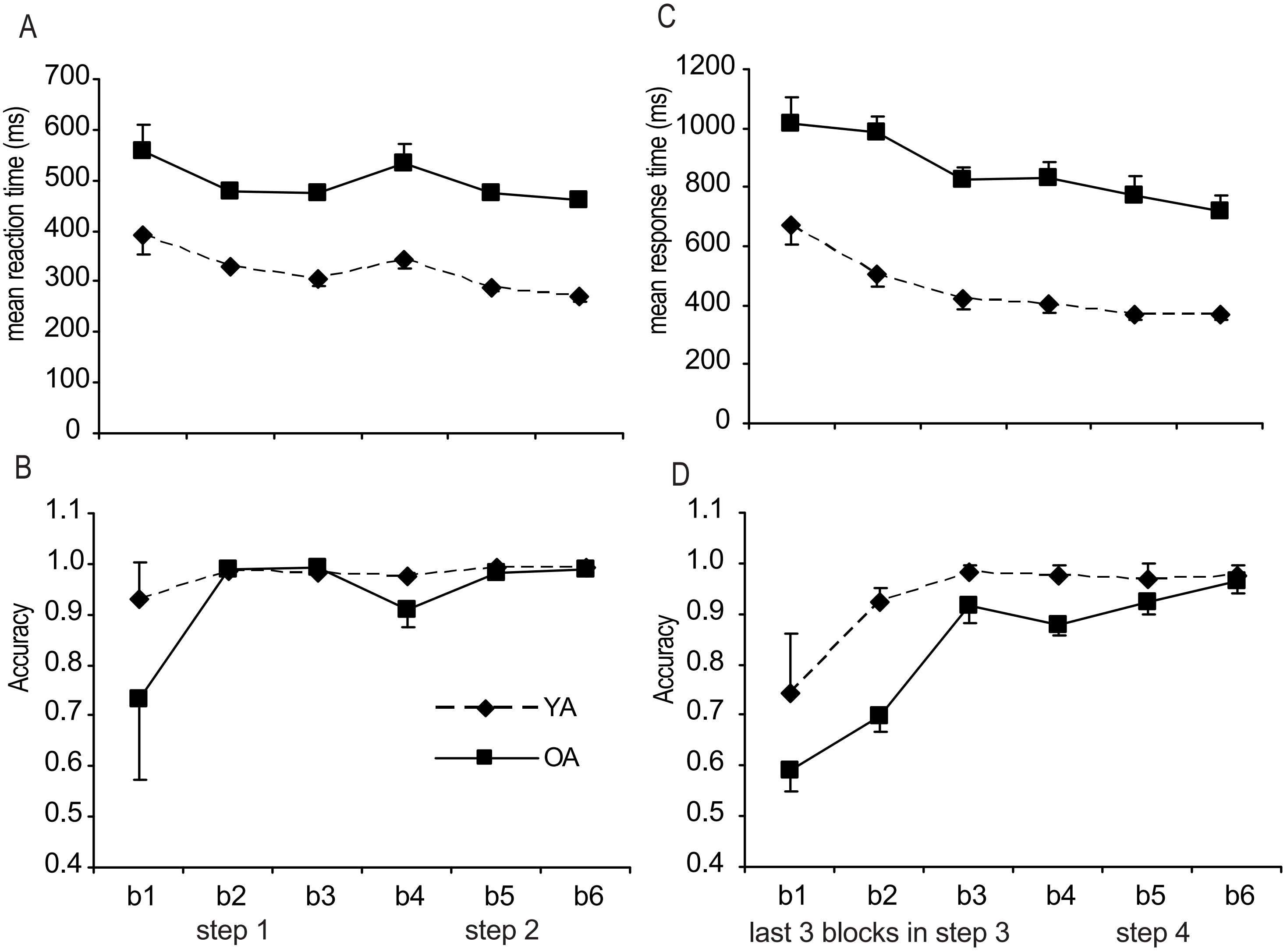

A
700
600
500
400
300
200
100
0
mean reaction time (ms)
C
1200
1000
800
600
400
200
0
mean response time (ms)
B
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
Accuracy
YA
OA
b1
b2
b3
b4
b5
b6
step 1
step 2
D
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
Accuracy
b1
b2
b3
b4
b5
b6
last 3 blocks in step 3
step 4

Figure 2

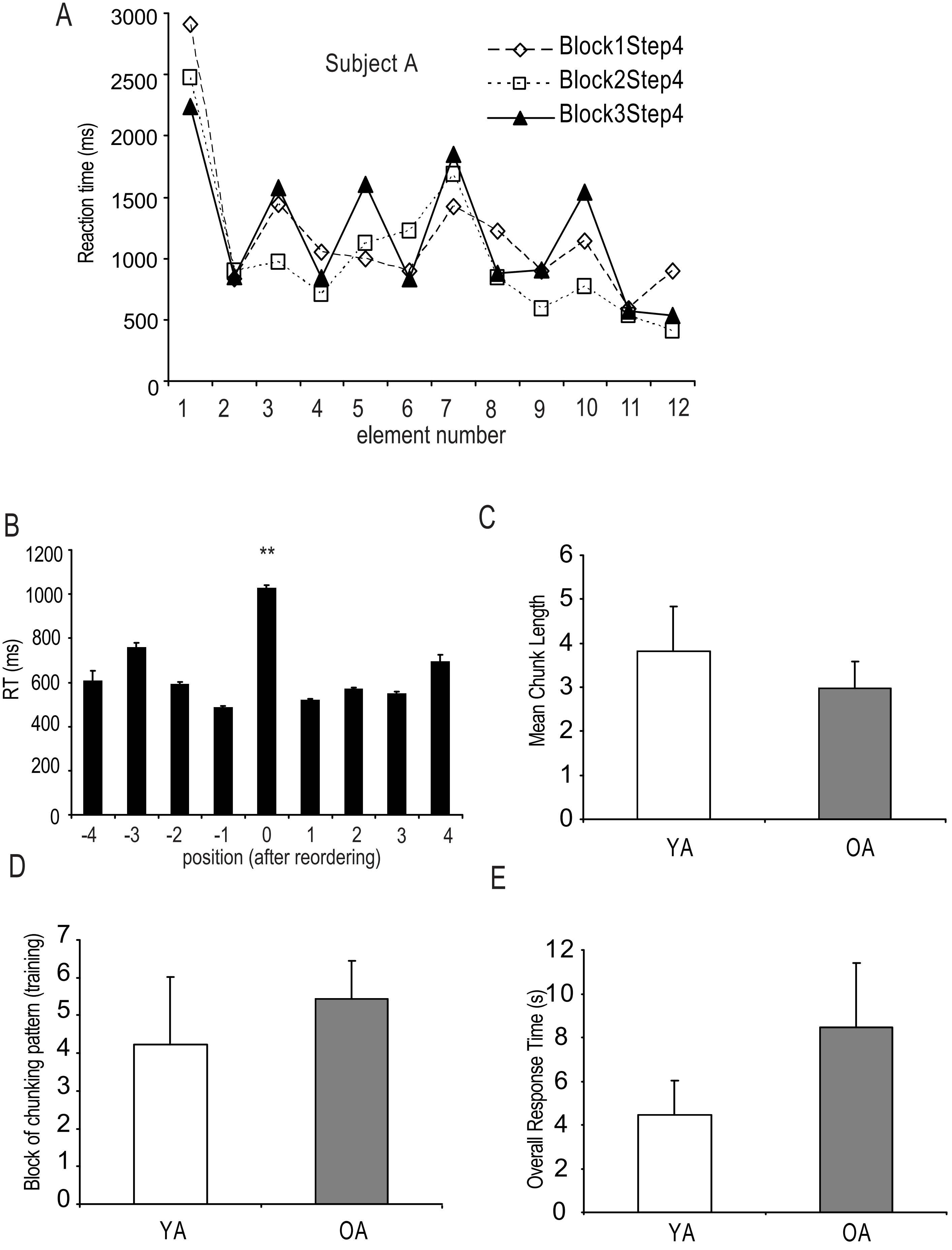

A
Subject A
Block1Step4
Block2Step4
Block3Step4
Reaction time (ms)
3000
2500
2000
1500
1000
500
0
1
2
3
4
5
6
7
8
9
10
11
12
element number
B
RT (ms)
1200
1000
800
600
400
200
0
**
-4
-3
-2
-1
0
1
2
3
4
position (after reordering)
C
Mean Chunk Length
6
5
4
3
2
1
0
YA
OA
D
Block of chunking pattern (training)
7
6
5
4
3
2
1
0
YA
OA
E
Overall Response Time (s)
12
10
8
6
4
2
0
YA
OA

Figure 3

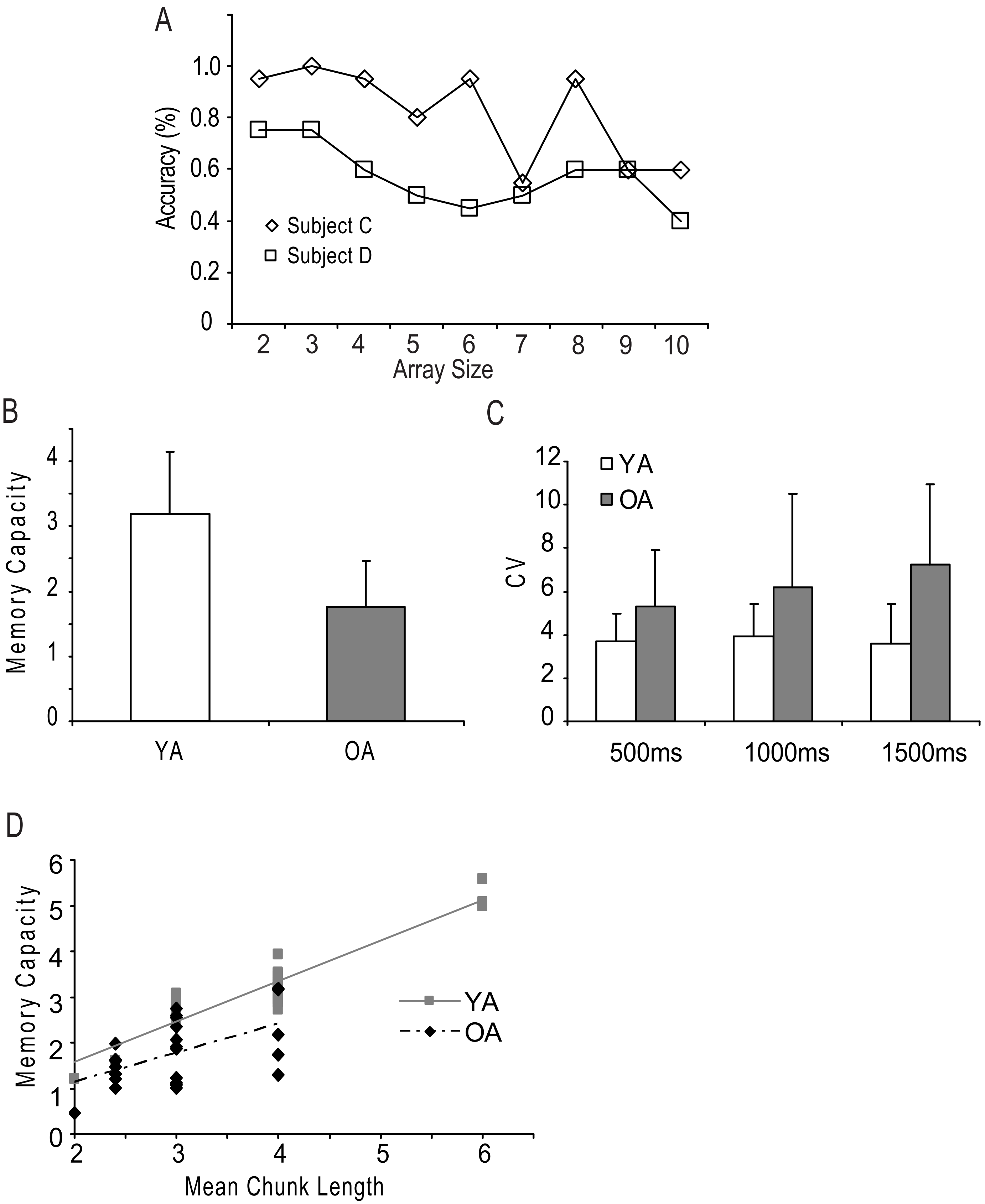
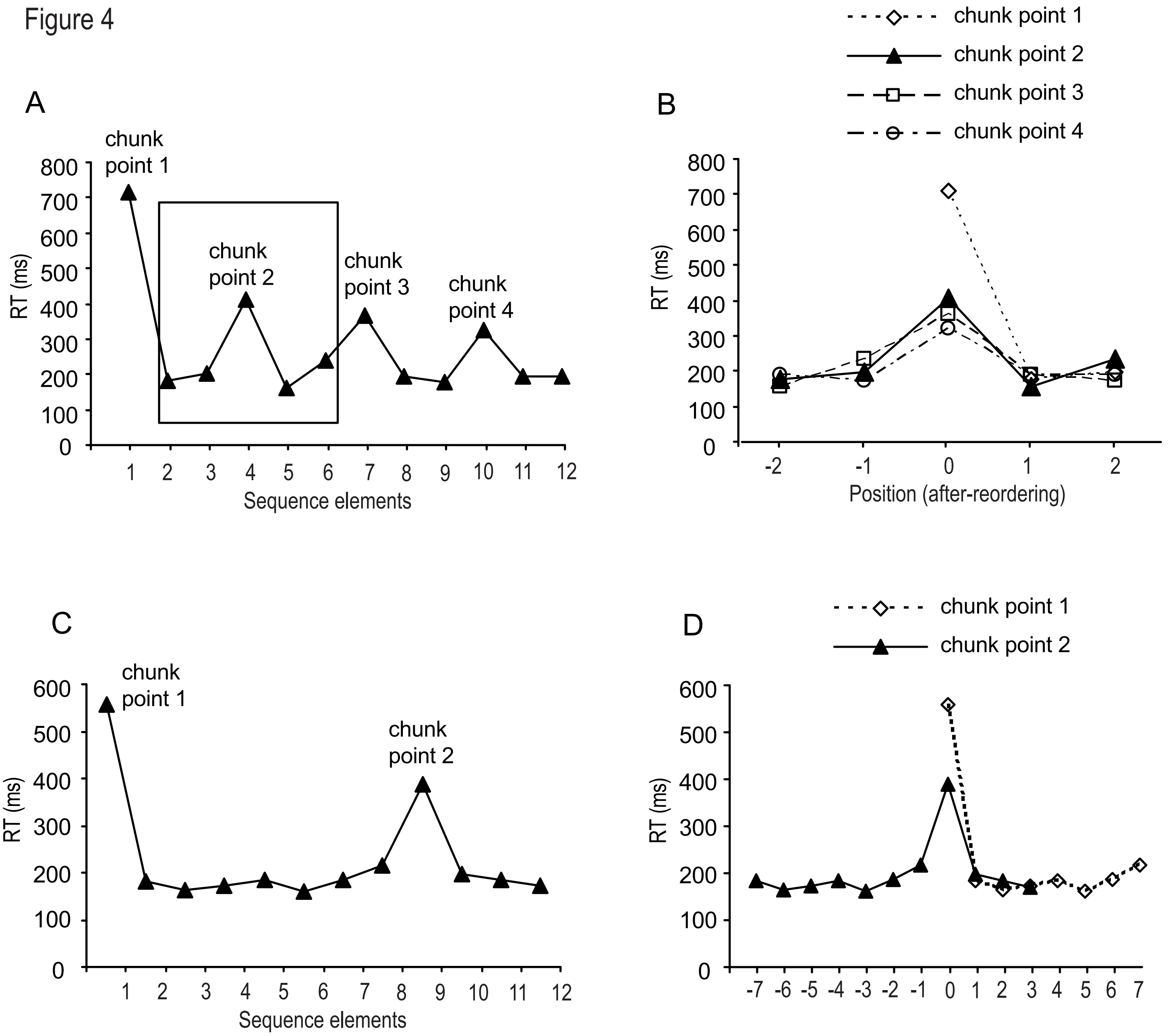

A
Accuracy (%)
1.0
0.8
0.6
0.4
0.2
0
2
3
4
5
6
7
8
9
10
Array Size
◇ Subject C
□ Subject D
B
Memory Capacity
4
3
2
1
0
YA
OA
C
CV
12
10
8
6
4
2
0
□ YA
▨ OA
500ms
1000ms
1500ms
D
Memory Capacity
6
5
4
3
2
1
0
2
3
4
5
6
Mean Chunk Length
YA
OA

Figure 4


A
chunk point 1
chunk point 2
chunk point 3
chunk point 4
RT (ms)
0
100
200
300
400
500
600
700
800
1
2
3
4
5
6
7
8
9
10
11
12
Sequence elements
B
chunk point 1
chunk point 2
chunk point 3
chunk point 4
RT (ms)
0
100
200
300
400
500
600
700
800
-2
-1
0
1
2
Position (after-reordering)
C
chunk point 1
chunk point 2
RT (ms)
0
100
200
300
400
500
600
1
2
3
4
5
6
7
8
9
10
11
12
Sequence elements
D
chunk point 1
chunk point 2
RT (ms)
0
100
200
300
400
500
600
-7
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5
6
7