Research Article

Age-Related Decline in Learning Deterministic Judgment-Based Sequences

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Abstract

Objectives: Because sequence learning is integral to cognitive functions across the life span, the present study examined the effect of healthy aging on deterministic judgment-based sequence learning.

Methods: College-aged, younger–old (YO), and older–old (OO) adults completed a judgment-based sequence learning task which required them to learn a full sequence by chaining together single stimulus–response associations in a step-by-step fashion.

Results: Results showed that younger adults outperformed YO and OO adults; older adults were less able to acquire the full sequence and committed significantly more errors during learning. Additionally, higher sequence learning errors were associated with advancing age among older adults, even when controlling for other factors known to contribute to sequence learning abilities. Such impairments were selective to learning sequential information, because adults of all ages performed equivalently on postlearning probe trials, as well as on learning simple stimulus–response associations.

Discussion: This pattern of age deficits during deterministic sequence learning challenges past reports of age preservation. Though the neural processes underlying learning cannot be determined here, our patterns of age deficits and preservation may reflect different brain regions that are involved in the task phases, adding behavioral evidence to the emerging hypothesis of frontostriatal declines despite spared hippocampal function with age.

Keywords: Aging, Deterministic sequence learning, Judgment-based learning
on at least some blocks. In these types of tasks, learning is often measured as participants’ decreased reaction time on trials that follow a sequential pattern as compared with those presented in randomly determined locations. Results generally show that younger and older adults perform equivalently when sequences are deterministic (i.e., when event locations can be perfectly predicted from previous events; Gaillard, Destrebecqz, Michiels, & Cleeremans, 2009; D. V. Howard & Howard, 1989, 1992). However, at least one study reported age deficits in learning more complex (i.e., higher-order) deterministic SRT sequences (Curran, 1997), revealing that there may be characteristics of deterministic sequence learning that yield age differences. Perhaps age preservation is unique to those types of deterministic sequence learning tasks that have most commonly been used in the past; that is, those that involve relatively simple, motor-based sequential regularities.

Furthermore, sequence learning is not a unitary concept, nor are its underlying learning processes. Seger (1997) recognized that sequence learning might be supported by different mechanisms when it involves motor processing versus making judgments about stimuli. Given reports of age deficits in learning judgment-based associations (e.g., Frank & Kong, 2008; Simon & Gluck, 2013), this raises the possibility that some forms of deterministic sequence learning—ones that require participants to learn sequential events based on judgments—can produce age deficits. One such example task involves a complex (i.e., higher-order) chaining procedure, in which participants learn a full, temporal sequence of behaviors bit by bit using trial-and-error feedback. While the chaining of stimulus–response associations has been identified as an effective method of teaching new skills to older adults, including how to get up after a fall (Reece & Simpson, 1996), no one to our knowledge has directly evaluated the effects of healthy aging on learning these types of deterministic sequences.

Here, we administered a judgment-based sequence learning task (Shohamy, Myers, Grossman, Sage, & Gluck, 2005) to healthy younger and older adults. The goal of this task is to lead a character through a series or “chain” of rooms leading to reward. Using feedback, the correct chain of behaviors is learned in a sequential step-by-step fashion. The participant starts by learning the correct final response, and then moves backward through a sequence concluding with the first step, until the full chain has been mastered. Learning is typically measured as the total number of errors over the course of learning sequential (“chained”) associations. Notably, a response occurs on every trial, thereby providing an on-line measure of learning similar to what is done in motor-based sequencing tasks (as opposed to relying on the learner’s judgments in a subsequent test).

Though this task has previously only examined patient populations (Herzallah et al., 2013; Kéri et al., 2008; Nagy, Kéri, et al., 2007; Polgár et al., 2008; Shohamy et al., 2005), examination of younger and older adult control data initially hints at age equality in learning, in line with traditional motor-based sequencing findings. Specifically, younger adult controls (aged in mid- to late-30s) typically make an average of six errors (Herzallah et al., 2013; Nagy, Kéli, et al., 2007; Polgár et al., 2008) and older adult controls average around the same (Nagy, Kéri, et al., 2007). Additionally, all older adult controls in one study (Shohamy et al., 2005) successfully met a minimum performance criterion during learning, which was often not the case among younger adult controls (e.g., Herzallah et al., 2013; Nagy, Kéli, et al., 2007; Polgár et al., 2008), adding the possibility that healthy older adults may even outperform their younger counterparts.

However, a keener look indicates that performance declines with age are more likely. For example, healthy older controls showed equivalent sequence learning to Parkinson’s disease (PD) patients (Shohamy et al., 2005), a result suggesting that older adults might actually be impaired. Though another study revealed that healthy older controls made fewer errors in learning than never-medicated PD patients (Nagy, Kéri, et al., 2007), participants who failed to meet a minimum performance criterion were not excluded from the analysis. Hence, the total errors for PD patients may have been misleadingly inflated, since PD patients are reportedly less able to meet the criterion than healthy controls (Shohamy et al., 2005).

Nevertheless, discrepant findings in comparing healthy older controls across studies may also be reconciled by considering the average age of the participants, which differed by approximately a decade. Previously, studies of complex, motor-based, probabilistic sequences reported age differences among healthy older–old (OO) adults aged 76–80 relative to younger–old (YO) adults aged 65–73 (e.g., J. H. Howard & Howard, 1997) as well as among older middle-aged adults (mean age = 49.43 years) relative to younger middle-aged adults (mean age = 41.42 years; Feeney, Howard, & Howard, 2002).

The present study more directly compared deterministic sequence learning among college-age, YO and OO healthy adults using a complex judgment-based sequencing task. We used this approach to determine whether deterministic sequence learning is broadly preserved across the lifespan, even when learning complex judgment-based chains of associations. However, in the more likely event that we observe age-related declines in learning, particularly among the oldest-old, we provide additional evidence for age deficits in deterministic sequence learning (e.g., Curran, 1997), despite traditional support for age preservation.

Method
Participannts
Participants included 51 college-aged younger adults (M = 20.5 years, SD = 1.6, range = 18–25) and 119 healthy older adults (M = 71.6 years, SD = 9.0, range = 55–89), the latter of whom were divided into two groups using a median split: 62 younger-old (YO) (M = 64.1 years, SD = 4.5,
range = 55–70) and 57 older-old (OO) ($M = 79.6$ years, $SD = 4.8$, range = 71–89). Younger adults (Y) were all Rutgers University students, and YO and OO adults were recruited through advertisements in the local surrounding communities. All participants were in good health, were not color blind, had normal or corrected-to-normal vision, had no existing neurological or psychological conditions, did not use drugs known to influence cognition, and performed within expected age norms on neuropsychological tests (see Table 1 for demographic and neuropsychological outcomes for each age group). All experimental procedures conformed to the ethical standards for research on human subjects delineated in the 1964 Declaration of Helsinki and were approved by the Rutgers University and St. Olaf College Institutional Review Boards. All participants provided written informed consent before commencing any experimental testing and received monetary compensation for participation.

### General Procedure

Participants completed cognitive and neuropsychological tests, as well as demographic and health screening forms, during a single 1- to 1.5-hr visit to our respective laboratories. The neuropsychological test battery (Table 1) was administered before the sequence learning task described subsequently, using a constant ordering of tests across participants.

### Computerized Judgment-Based Sequence-Learning Task

This task was first described in Shohamy and colleagues (2005), though the version used here reflects that described in Nagy, Kéri, and colleagues (2007). The objective of this task is to guide a character, “Kilroy,” through a sequence of rooms leading to a goal, the outside. On each trial, regardless of the task phase, Kilroy faces three doors, each with a colored card on it. The colors of the doors for each participant are selected from a set of 18 discriminable colors. The correct door either leads to the outside or to the next room, whereas the incorrect doors are locked. Participants must use a mouse click to select the door that they think is correct. At first, participants make a guess. If the correct door is selected, Kilroy passes through the door or reaches the outside (the goal). If an incorrect door is selected, the phrase “Locked!” appears, Kilroy shrugs in disappointment, and the participant must try again. The location of the correct door in each room is randomized across trials. The colors of the doors in each room are randomized once for each participant and remain consistently mapped in subsequent trials. A trial is complete when Kilroy reaches the outside, regardless of Kilroy’s starting position.

The task has three phases: sequencing, probe, and retraining. Though the phases are distinct, the transition to a new phase is not signaled to the participant. The task commonly takes 10–15 min to complete; however, the exact duration depends on the number of trials to meet the criterion, as well as the time taken to make a selection in each room.

### Sequencing

The task begins with practice trials, whereby the participant guides Kilroy through a single room to the outside to acquaint the participant with the task. After practice, the participant is told that the task will begin. In the sequencing phase, the participant leads Kilroy through a sequence of four rooms, starting with learning the correct response in the final room (Room 1) that leads to the outside. Once the correct response in Room 1 is learned, the participant is taken into a second room (Room 2) and is required to learn

### Table 1. Demographics and Neuropsychological Performance

<table>
<thead>
<tr>
<th>Demographic and neuropsychological outcomes</th>
<th>Younger adults (Y) ($n = 51$)</th>
<th>Younger-old (YO) ($n = 62$)</th>
<th>Older-old (OO) ($n = 57$)</th>
<th>Comparisons $^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Demographics</td>
<td></td>
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</tr>
<tr>
<td>Age in years</td>
<td>20.49 (1.580)</td>
<td>64.15 (4.526)</td>
<td>79.60 (4.754)</td>
<td>Y &lt; YO &lt; OO</td>
</tr>
<tr>
<td>Gender (F, M)</td>
<td>35, 16</td>
<td>39, 23</td>
<td>41, 16</td>
<td>ns</td>
</tr>
<tr>
<td>Years of education</td>
<td>14.27 (1.294)</td>
<td>15.53 (2.157)</td>
<td>16.86 (2.438)</td>
<td>Y &lt; YO &lt; OO</td>
</tr>
<tr>
<td>Neuropsychological performance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MMSE score</td>
<td>28.65 (1.197)</td>
<td>28.66 (1.200)</td>
<td>28.56 (1.282)</td>
<td>ns</td>
</tr>
<tr>
<td>WMS-III LM I, immediate</td>
<td>19.67 (5.074)</td>
<td>20.40 (6.377)</td>
<td>21.70 (5.223)</td>
<td>ns</td>
</tr>
<tr>
<td>WMS-III LM II, delayed</td>
<td>16.84 (6.201)</td>
<td>16.31 (7.063)</td>
<td>16.58 (5.840)</td>
<td>ns</td>
</tr>
<tr>
<td>WAIS-IV DS, forward $^+$</td>
<td>10.73 (2.281)</td>
<td>9.90 (2.078)</td>
<td>10.88 (2.601)</td>
<td>YO &lt; OO</td>
</tr>
<tr>
<td>WAIS-IV DS, backward $^+$</td>
<td>8.80 (2.191)</td>
<td>8.40 (2.564)</td>
<td>9.00 (2.312)</td>
<td>ns</td>
</tr>
<tr>
<td>NAART errors $^*$</td>
<td>30.47 (8.100)</td>
<td>25.74 (11.318)</td>
<td>16.14 (8.725)</td>
<td>OO &lt; YO &lt; Y</td>
</tr>
</tbody>
</table>

Note. All scores are $M$ (SD). DS = digit span; LM = logical memory; MMSE = Mini-Mental State Examination; NAART = North American Adult Reading Test; ns = no significant group differences; WAIS-IV = Wechsler Adult Intelligence Scale—Fourth Edition; WMS-III = Wechsler Memory Scale—Third Edition. $^a$Patterns of significance did not change when we removed 4 Y, 18 YO, and 16 OO who failed to meet practice stage of our task. $^+$Data not available for one participant. $^p < .05$. $^*p < .01$. 

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which door leads to the final room (Room 1). Once inside Room 1, the participant is prompted to choose the correct door that leads to the outside. After this two-step sequence is learned, additional rooms are added to the sequence one at a time. By the end of this phase, the participant should be selecting the correct door in each room from Room 4 to Room 1.

To meet the criterion, the participant must make four consecutive correct responses in each stage of the sequence. If participants fail to meet criterion within 15 trials starting in any given entry room (including practice), they skip the remaining rooms and the probe phase and proceed directly to the retraining phase.

**Probe**
Here, in a total of six trials, Kilroy starts in Room 4, and the participant must guide him through the entire sequence of rooms until he reaches the outside. However, unbeknownst to the participant, the colors of the doors have changed; now, each room contains the correct door, another door that was correct in a different room, and one door that was always incorrect. To successfully complete a trial, the participant must accurately associate the correct colored door with the correct room in sequence. This phase tests whether participants fully learned the chain of associations in the sequencing phase, as intended (i.e., the red door is correct in Room 2), as opposed to more specific stimulus–response relationships, regardless of the sequence (i.e., the red door is correct with no knowledge of the chaining relationships between stimuli). Either approach can support learning during the sequencing phase, but only a participant who learned sequentially can perform well on the probe phase because the sequence of correct stimuli has not changed. In contrast, participants who learned nonsequential stimulus–response relationships would make many errors, as they would have to routinely choose between two doors that were both correct at some point in the sequencing phase.

Three types of errors can occur during probe: a reward error occurs when the participant selects the door that leads to the outside (i.e., the correct response in Room 1) but in the wrong room (Rooms 2–4); a serial position error occurs when the participant selects a door that was correct in a different room, but not in the present room (excluding reward errors); and a distractor error occurs when the participant selects a door that was never correct in any room.

**Retraining**
The retraining phase, which occurs at the end of the task, tests whether deficits during the sequencing or probe phases may be due to fatigue effects on leaning single stimulus–response associations. Here, the participant enters a new room (Room 5) with three new doors and must choose the unlocked door that leads outside. On each trial, the same room with the same three colored doors is presented, but the position of the colored doors is shuffled across trials. This phase ends once the participant has made four consecutive correct responses, so the number of trials is variable to a participant’s performance.

**Results**

**Judgment-Based Deterministic Sequence Learning Task**
Seven participants (1 Y, 6 YO, and 1 OO) could not complete the practice trials and were not included in the analyses below. Moreover, all of the analyses below were rerun after excluding individuals who had a Mini-Mental State Exam (MMSE) score below 27, n = 11 (4 Y, 2 YO, 5 OO), and because patterns of significance were unchanged with these individuals removed, we report the data using the full sample.

**Task criterion**
We first examined the percentage of participants in each age group who reached a minimum performance criterion during sequencing. A 2 (criterion: pass, fail) × 3 (age group: Y, YO, OO) chi-square analysis of the number of participants who learned the full sequence was significant, $\chi^2(2) = 8.85, p < .05$. Post hoc pairwise comparisons revealed that both YO (29.0%) and OO adults (28.1%) had a significantly higher failure rate than Y adults (7.8%) ($p < .01$). Analyses of those older adults (18 YO + 16 OO) who met versus failed criterion indicated that these subgroups did not differ significantly in terms of age, gender, or years of education ($p > .13$). The only neuropsychological differences were numerically small in MMSE (met criterion: $M = 28.8 \pm 1.5$; failed criterion: $M = 28.1 \pm 1.3$) and North American Adult Reading Test (NAART) errors (met criterion: $M = 19.8 \pm 10.7$; failed criterion: $M = 24.7 \pm 11.8$), with all other $p > .30$.

**Sequencing**
Considering only those participants who successfully met the minimum performance criterion ($n = 132$), a one-way analysis of variance (ANOVA) examining age group (Y, YO, OO) on total number of sequencing errors revealed a significant main effect, $F(2, 129) = 8.27, p < .001, \eta^2 = .114$ (Figure 1). Post hoc analyses using Fisher’s least squared difference revealed that Y adults performed significantly better than both YO and OO adults ($p < .05$), and that YO adults made marginally fewer errors than OO adults ($p = .062$). Analysis of the type of errors made during the sequencing phase for all three groups showed that the majority of errors made during learning were in response to new stimuli, presented for the first time in the current phase (Y, 92.6% “new”; YO, 85.0% “new”; OO, 83.0% “new”), as opposed to older stimuli learned in previous phases.

To more fully explore the marginal difference between YO and OO adults, we examined age as a predictor of sequencing errors among only the older sample (YO + OO), which revealed a significant positive correlation ($r(83) = .234, p = .031$), or higher sequencing errors with
advancing age. Previous work has shown that verbal ability and working memory can predict sequence learning differences among older adults in a deterministic sequence learning task (e.g., Bo, Borza, & Seidler, 2009; Cherry & Stadler, 1995) and, as seen in Table 1, our YO and OO samples differed significantly on these measures: verbal ability (education + NAART) and a form of working memory (digit span forward, DS FWD). Thus, to ensure that these neuropsychological differences were not driving our aging effect, we ran a linear regression using age to predict sequencing errors with education, NAART and DS FWD included as covariates. As seen in Figure 2, age remained a significant predictor of judgment-based sequencing ($\beta = .240$, $p = .044$) after controlling for individual differences in education, NAART and DS FWD, and indeed only the model with age as the sole predictor of sequencing errors was significant [$F(1, 82) = 4.51, p = .037$], suggesting a true associative learning error.

Because digit span backward (DS BWD) is often considered a better measure of working memory than DS FWD, we re-ran our model to control for DS BWD (even though YO and OO samples did not differ on this measure). Age remained a significant predictor of sequencing ($\beta = .237$, $p = .045$). Notably, we also observed no significant correlation between DS BWD and sequencing errors among older adults [$r(82) = −.138$, $p = .212$], confirming that working memory did not explain our observed aging effect.

Probe
A one-way ANOVA examining age group on the number of probe errors revealed no main effect, $F(2, 129) = .717$, $p = .490$, $\eta^2 = .011$. Because the absence of an age group effect might have masked differences in the types of probe errors made by each age group, we ran a 2 (age group: Y, YO, OO) × 3 (error type: serial position error, reward error, distractor error) mixed-design ANOVA on mean number of probe errors, which revealed only a significant main effect of error type, $F(1.272, 164.087) = 57.842$, $p < .001$, $\eta^2 = .310$ (see Figure 3). Serial position errors were most common across all participants ($M = 3.26$), followed by reward errors ($M = 1.30$, and lastly distractor errors ($M = 0.48; ps < .01$). Importantly, there was neither a significant effect of age group, $F(2, 129) = .677, p = .510$, $\eta^2 = .010$, nor a significant interaction, $F(2.544, 164.087) = .308, p = .786, \eta^2 = .005$; such successful probe performance overall, across age groups, is taken as evidence that Y, YO, and OO did indeed learn the chain of stimuli sequentially during the sequencing phase as intended.
Retraining

Including only those participants who met criterion during sequencing, a one-way ANOVA examining age group on the total number of retraining errors revealed no main effect, F(2, 129) = .338, p = .714, η² = .005. All age groups performed equivalently (Y: M = 1.28, SD = 1.136; YO: 1.48, SD = 1.372; OO: M = 1.27, SD = 1.533). Similarly, a one-way ANOVA examining age group on the total number of retraining trials revealed no differences, F(2, 129) = .989, p = .375, η² = .001 (Y: M = 5.13, SD = 1.47; YO: 5.43, SD = 1.87; OO: M = 4.95, SD = 1.60), whereby 93% Y, 88% YO, and 90% OO completed retraining within six trials or less. Taken together, this confirms that fatigue effects were not responsible for the observed aging-related impairment in sequence learning as well as age equivalence in learning simple stimulus–response associations.

Discussion

This study was the first to examine the effects of healthy aging on deterministic judgment-based sequence learning, or the ability to learn a predictable sequence of behaviors in a step-by-step fashion. Our results revealed that YO and OO adults not only failed to meet criterion at a higher rate than college-age adults but even those who learned the complete sequence still made significantly more sequencing errors than Y adults. In addition, higher sequence learning errors were associated with advancing age among older adults, even when controlling for other factors known to contribute to performance. This age deficit was selective to the process of learning sequential information because adults of all ages showed similar performance on both postlearning probes, as well as on simple stimulus–response associations that were required during retest. Our finding of age deficits on deterministic sequence learning in a comparatively large sample challenges past reports showing age preservation (e.g., Daselaar, Rombouts, Veltman, Raaijmakers, & Jonker, 2003; Gaillard et al., 2009; D. V. Howard & Howard, 1989, 1992).

To our knowledge, only one previous study reported age deficits on deterministic sequence learning (Curran, 1997) and notably, this study used a more complex higher-order SRT task. Similarly, our task relies on second-order conditioning or learning based on chaining sequences of events leading to reward. Thus, it could be that older adults are unable to learn complex deterministic associations between stimuli and responses that are not contiguous, as predicted by the associative deficit hypothesis (Naveh-Benjamin, 2000). However, on the same complex higher-order SRT task used by Curran (1997), others did not find age differences (Daselaar et al., 2003), or showed that older adults aged 55–70 years performed even better than Y adults (Brown, Robertson, & Press, 2009). Further, previous work has shown persistent age-related deficits on learning probabilistic sequences regardless of task complexity (i.e., first or second-order structure; Stillman, Howard, & Howard, 2016; see also Mutter, DeCaro, & Plumlee, 2009). Taken together, these results indicate that age deficits observed here, and on other deterministic tasks, are not necessarily due to sequence complexity.

In addition, it is unlikely that our observed age deficits in learning reflect general slowing of the aging cognitive processing system (Salthouse, 1996), whereby the products of early processing stages are lost before later processing is complete. For all age groups, the large majority of errors in the sequencing phase were related to learning new stimuli; that is, errors tended to occur on the newest, least-practiced doors (i.e., the first room in a trial) versus well-practiced rooms and doors. Similarly, because learning on our task requires no manual motor sequencing and occurs independent of response speed, we can rule out age-related motor impairments in producing our age differences in sequence learning (such as executing fine motor movements (Smith et al., 1999) or age declines in optomotor performance (Klein, Fischer, Hartnegg, Heiss, & Roth, 2000)). This is consistent with past work showing that age differences in sequence learning are not limited to situations that require learning manual motor sequences (J. H. Howard et al., 2008).

Age impairments on deterministic sequence learning persisted after controlling for verbal ability and working memory. Although lower verbal ability has been associated with poorer deterministic sequence learning (Cherry & Stadler, 1995), our older adult sample was highly educated and demonstrated high verbal ability, making it unlikely that verbal ability would contribute to learning here. The lack of a relationship between working memory and deterministic sequence learning among older adults replicates work showing no correlations between sequence learning using our task and different working memory measures (i.e., Wisconsin Card Sorting, Trail Making, Controlled Oral Word Associations; Kéri et al., 2008; Polgár et al., 2008). That said, evidence shows domain specificity for when working memory influences sequence learning; short-term and span tasks often show no links with sequence learning, as we observed, whereas other measures of working memory do (Janacek & Nemeth, 2013). Future work will need to scrutinize connections between age-related declines in sequence learning and working memory using different measures.

The age-related dysfunction observed here may instead reflect an inability to sequence step-by-step chains of deterministic associations using judgment-based learning processes, including a failure in the gradual process of binding smaller chunks of information into a larger unit (Naveh-Benjamin, 2000). Indeed, previous work on the aging of judgment-based learning processes report age deficits (Fera et al., 2005; Frank & Kong, 2008; Schmitt-Eliassen, Ferstl, Wiesner, Deuschl, & Witt, 2007; Schuck et al., 2018; Simon, Howard, & Howard, 2010), and one study even showed age differences in judgment-based probabilistic learning of sequences (Seaman, Howard, & Howard, 2016).
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Since similar motor-based tasks report age preservation in learning deterministic sequences, this finding leaves open the possibility that motor- and judgment-based tasks are supported by independent mechanisms (Seger, 1997) that may be differentially affected by aging. Then again, J. H. Howard and Howard (2013) argued that age differences on sequence learning are based more broadly on the extent to which learning recruits striatal processes. Because healthy aging brings various frontostriatal circuitry disruptions, including losses to volume (e.g., Raz et al., 2003) or the dopaminergic system (see Bäckman et al., 2000 for a review), age-related deficits in sequence learning may depend only on whether the age-sensitive frontostriatal system is engaged (D. V. Howard & Howard, 2012), regardless of whether the association is judgment- or motor-linked. Future work is needed to test this possibility more directly, especially given that our closest proxy of frontal functioning, DS BWD, did not correlate with learning.

Importantly, dopamine is already known to be critical for learning sequences of stimuli leading to a reward in analogous animal learning paradigms to ours (Schultz, 2002; Tan & Bullock, 2008), such that if one cue reliably predicts an outcome, and another cue predicts that predictive cue, the dopamine response shifts to the earliest predictor of the outcome. Accordingly, previous work on our same task using computational modeling (Guthrie, Myers, & Gluck, 2009), PD patients who have low concentrations of dopamine (Nagy, Kéri, et al., 2007; Shohamy et al., 2005), and healthy adults with low levels of a dopamine metabolite (Nagy, Kelemen, et al., 2007), shows that sequencing relies on the dopaminergic system. Hence, it follows that age-related dopaminergic disruptions could underlie age deficits in deterministic judgment-based sequence learning. This interpretation may even explain the marginal differences in sequencing performance between YO (range: 55–70 years) and OO adults (range: 71–89 years); previous work showed that dopaminergic cells in the basal ganglia of healthy adults more than 70 displayed damage consistent with what is reported in PD (Kravtsev et al., 2006). Still, the link between dopamine availability and learning remains speculative without measurements of dopamine levels to substantiate our claims.

Age deficits occurred only during the acquisition of sequential information; college-aged adults performed equivalently to both Y- and OO adults on postlearning probe trials. Near perfect probe performance across age groups offered insight into how participants approached learning; adults of all ages learned the chain of stimuli sequentially, as intended, as opposed to simply associating each stimulus with a reward, regardless of its place in the sequence. Furthermore, this pattern of age-related impairments on sequencing despite age-preservation during probe compliment double dissociations revealed by patient work using our task (Herzallah et al., 2013; Nagy, Kéri, et al., 2007; Polgár et al., 2008). Specifically, patients with frontostriatal impairments show sequencing dysfunction and intact probe performance whereas patients who have medial temporal lobes (MTL) dysfunction show the reverse (Nagy, Kéri, et al., 2007). Our data may, therefore, add behavioral evidence to the emerging view that healthy aging compromises the frontostriatal system before the MTL (D. V. Howard & Howard, 2012). Though the neural processes responsible for learning cannot be determined here, spared probe performance among older adults fits with reports that the MTL remain stable or decline more slowly until advanced old age (e.g., Pudas et al., 2013; Raz, Rodriguez, Head, Kennedy, & Acker, 2004). Furthermore, older individuals who made fewer probe errors on our task showed significantly better recall on immediate $r(83) = -.243$, $p = .025$ logical memory scores and marginally better recall on delayed logical memory scores $r(83) = -.209$, $p = .055$ [Supplementary Figure 4], the latter of which has been used as a proxy for MTL functioning (Squire & Zola-Morgan, 1996). Of note, neither sequencing nor probe performance related to any of our other neuropsychological measures ($ps > .05$).

Certainly, we do not have biological evidence to address the hypothesized roles of frontostriatal dopamine or the MTL in explaining our findings. Future neuroimaging work is needed to directly assess the neural mechanisms underlying patterns of age-deficits or preservation using our task. Future research should also more directly compare motor-based versus judgment-based tasks in producing age differences given a lack of understanding for the condition under which age differences emerge in sequence learning and why. A better understanding of age-related impairments in the type of judgment-based chaining under study here can prove helpful to older adults recovering after a fall (Reece & Simpson, 1996) and older stroke patients re-gaining reading abilities (Thorsteinsson & Sigurdardóttir, 2007), especially those with basal ganglia stroke who are impaired at chunking sequences (Boyd et al., 2009). Building a more coherent characterization of sequence learning is also necessary to maximize cognitive abilities for adults of all ages, especially considering how integral sequence learning is to cognitive function (e.g., Lashley, 1951).

Supplementary Material

Supplementary data are available at The Journals of Gerontology, Series B: Psychological Sciences and Social Sciences online.

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Conflict of Interest
The authors declare that they have no known conflicts of interest.

References


