Title

Children exhibit a developmental advantage in the offline processing of a learned motor sequence

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Abstract

Research that examines changes in a specific behavior across the human lifespan frequently reports an inverted-U trajectory. That is, young adults exhibit optimal performance, children are conceptualized as developing systems progressing towards this ideal state, and older adulthood is characterized by performance decrements. However, not all behaviors follow this trajectory. Notably, there are instances – and in the learning and memory domain in particular – in which children outperform young adults and thus can be considered the model of optimal performance. This study aimed to reveal instances of childhood advantage in the domain of motor learning and memory consolidation. Motor sequence learning data were acquired from 7 to 35 and >55-year-old participants across two experiments via an online data acquisition platform. In Experiment 1 (n=130), participants learned an 8-element, bimanual motor sequence in a single practice session. In Experiment 2 (n=108), participants acquired the same sequence and were retested 5 and 24 hours after initial acquisition, affording the assessment of memory consolidation across offline periods including both wakefulness and sleep. Results from Experiment 1 revealed comparable initial learning dynamics among age groups, but 7- to 12-year-old children exhibited smaller sequence-specific learning relative to adolescents (13-17 years), young adults (18-35 years) and older adults (> 55 years). Interestingly, children tended to demonstrate the greatest performance gains over the short rest epochs interspersed with practice (i.e., micro-offline intervals). Results from Experiment 2 revealed that this developmental advantage was not limited to the micro-offline timescale. Children and adolescents exhibited larger performance gains in the delayed retests, reflecting enhanced “macro”-offline motor memory consolidation. Collectively, these results suggest that children exhibit a developmental advantage in the offline processing of recently practiced motor sequences.

1. Introduction

The ability to learn novel movements is vital to the everyday functioning of individuals across the human lifespan (e.g., from a child learning to ride a bike to an older individual learning to operate a touchscreen). One of the most dominant motor learning paradigms in the field is motor sequence learning (MSL), whereby participants acquire a novel series of interrelated actions (i.e., a motor sequence). MSL has been extensively studied in healthy young adults (~18-35 years), facilitating the development of a framework that characterizes the time course of learning in this age group. Typically, a fast online (i.e., during repeated practice) acquisition phase with substantial performance improvements occurs during an initial training session. This is followed by a slow offline (i.e., in the absence of active task practice) consolidation phase that spans several hours during which the acquired memory trace is stabilized, strengthened and reorganized into a more robust form. Interestingly, recent research has indicated that offline consolidation is also evident on a much shorter timescale. More specifically, young adults exhibit large performance gains over the short rest intervals in between blocks of practice within a session, providing evidence for a fast consolidation process during these micro-offline epochs [Bönstrup et al., 2019; Bönstrup et al., 2020; Buch et al., 2021; Gann et al., 2023; Jacobacci et al., 2020; but see Gupta & Rickard, 2022 for opposing view].

Although previous research has examined motor sequence learning in school-aged children (i.e., between 5 and 12 years), the results are heterogenous. While some studies have reported comparable learning within the initial practice session in children and adults (Du et al., 2017; Salehi et al., 2016; Meulemans , Van der Linden & Perruchet, 1998; Wilhelm et al., 2013), others have shown that children exhibit worse (Adi-Japha et al., 2014; Janacsek et al., 2012; Lukács &

Kemény, 2015; Thomas et al., 2004; Wilhelm et al., 2008) or better learning (Ashtamker & Karni, 2013; Fischer et al., 2007; Janacsek et al., 2012; Juhasz et al., 2019; Savion-Lemieux et al., 2009; Wilhelm, Prehn-Kristensen & Born., 2012). There is a general consensus, however, that children exhibit impaired consolidation of a recently acquired motor sequence over offline periods that include sleep (e.g., Fischer et al., 2007; Wilhelm et al., 2008, 2013; Zinke et al., 2017). Specifically, whereas post-learning sleep is known to boost offline consolidation processes in young adults [see King et al., 2017 for a review], such a beneficial effect is absent in children. Interestingly, there is some evidence suggesting that this degraded consolidation over sleep may be the by-product of enhanced or accelerated consolidation over the wake epochs shortly following initial learning (Adi-Japha et al., 2014; Ashtamker & Karni, 2013; Dorfberger et al., 2007). Specifically, children showed a rapid performance stabilization and enhancement 15 minutes (Adi-Japha et al., 2014) and 1 hour (Ashtamker & Karni, 2013) after learning, which were not observed in young adults. Interestingly, this enhanced offline processing does not appear to be limited to the timescale of hours following initial learning (herein referred to as *macro*-offline intervals) but is also observed on shorter timescales. Specifically, Du et al. (2017) found that young children (i.e., 6-year-olds) showed higher *micro*-offline gains as compared to older children (i.e., 10-year-olds) and young adults. These results collectively suggest that young children may exhibit a developmental advantage with respect to the offline processing of recently practiced motor sequences during wake intervals. This childhood advantage could then be added to the list of examples in which children outperform adults in specific learning and memory behaviors (for review see Gualtieri & Finn, 2022).

At the other end of the lifespan, there is considerable evidence that older adults (> ~60 years) exhibit comparable initial learning of a novel motor sequence as young adults (Bottary et al., 2016; Fitzroy et al., 2021; Fogel et al., 2017; Fogel et al., 2014; Gudberg et al., 2015; Spencer et al., 2007; Vien et al., 2016). And, whereas children appear to have a developmental advantage in the offline processing of recently acquired sequences, older adults are known to exhibit deficits. Specifically, the magnitude of offline gains over macro-offline intervals that include sleep and/or wake is significantly less than those observed in younger adults (Bottary et al., 2016; Fogel et al., 2017; Fogel et al., 2014; Gudberg et al., 2015; Spencer et al., 2007; Wilson et al., 2012).

Although the existing literature suggests that the offline processing of recently acquired movement sequences appears to be superior in children and then declines throughout adulthood, systematic examinations into changes across the human lifespan are relatively limited (see Janacsek et al., 2012; Juhasz et al., 2019 for examples in the initial learning of probabilistic sequences). This study thus aimed to provide an exhaustive characterization of motor learning and memory consolidation behaviors across the lifespan (i.e., in groups of children, adolescents, young adults and older adults). Consistent with Du et al., 2017; Salehi et al., 2016; Meulemans, Van der Linden & Perruchet, 1998; and Wilhelm et al., 2013, we hypothesized that the initial learning of a motor sequence (i.e., within a single training session) would be comparable across the 4 age groups. We expected children to exhibit enhanced micro- and 5-hour macro-offline consolidation, indicative of a developmental advantage in the offline processing of a recently acquired motor sequence across periods of wakefulness. This developmental advantage in macro-offline consolidation was expected to be absent at the 24-hour retest, as previous research has indicated impaired sleep-facilitated consolidation in children (Fischer et al., 2007; Wilhelm et al., 2008, 2013; Zinke et al.,

2017). Last, and consistent with earlier studies, older adults were expected to demonstrate intact initial learning but impaired macro-offline consolidation across both 5- and 24-hour intervals.

2. Methods and materials

The project consisted of two experimental protocols. Specifically, Experiments 1 and 2 examined the effect of age on the initial acquisition of a movement sequence and the time course of motor memory consolidation, respectively. Data collection and analysis plans were pre-registered via Open Science Framework and can be accessed at https://doi.org/10.17605/OSF.IO/WBK9H and https://doi.org/10.17605/OSF.IO/ZMJ75. Any additional analyses that were not included in the pre-registrations are labelled in this text as exploratory. The source data used for the results presented in this text as well as the raw data are publicly available on Zenodo (https://doi.org/10.5281/zenodo.8274119).

2.1 Participants

Healthy volunteers between 7-35 or 55-75 years old of all genders were recruited by advertisements on relevant websites and research databases. Note that as our experiments were conducted through a web-based data collection platform, recruitment was not constrained to a specific geographical region. Individuals interested in participation were sent an online screening questionnaire to assess eligibility, which was subsequently reviewed by a member of the research team. Exclusion criteria were: 1) reported history of medical, neurological, psychological or psychiatric conditions, 2) use of psychoactive or sleep-influencing medications, 3) indications of abnormal or irregular sleep, 4) mobility limitations of the fingers or hands, or 5) considered a professional typist or prior extensive training on a musical instrument requiring dexterous finger

movements (e.g., piano, guitar). All experimental procedures were approved by the local Ethics Committee (IRB_00136894). Adult participants and parents of child participants gave informed consent and participants below 18 years of age provided informed assent. Participants received compensation for their participation.

A convenience sample of 224 individuals met the inclusion criteria and thus initiated participation in an experimental protocol. They were divided into the following four age groups: children (operationally defined as 7-12 years old), adolescents (13-17 years old), young adults (18-35 years old) and older adults (≥ 55 years old). Pre-registered analyses compared differences among these age *groups.* Yet, to provide more fine-grained analyses of age-related trajectories of motor learning and memory consolidation behaviors, we also conducted exploratory analyses with age as a continuous variable (see below for details).

Sample size computations were conducted *a priori* and with the software G*Power (Erdfelder et al., 2007). For the assessment of age-group differences in initial motor sequence learning (i.e., Experiment 1), and to detect an effect size of f = 0.3 (based on the comparison of initial learning between 9-year-olds and young adults in Adi-Japha et al., 2014), with an alpha of 0.05 and power of 0.80, the desired sample size was 128 subjects (32 per group). Data from 7 participants were excluded from data analysis due to a failure to comply to experimental instructions (e.g., repeatedly pressing the same key; n = 3 children), missing data because of software issues (n = 1 young adult), or a failure to correctly perform the motor task (i.e., statistical outliers (> 3SD from group mean) on sequence accuracy; n = 1 child, 1 young adult, 1 older adult). Excluded participants were

replaced and thus the final sample size for analyses consisted of 130 participants (see Table 1 for participant demographics).

For the assessment of age-group differences in macro-offline consolidation processes (i.e., Experiment 2), the detection of an effect size of f = 0.20 (slightly more conservative than group Adi-Japha et al., 2014), with an alpha of 0.05, a power of 0.80 and a correlation among repeated measurements of 0.25, this experiment required a sample size of 108 (27 participants per group). In total, 21 individuals were excluded from data analysis. Specifically, 17 participants failed to comply to experimental instructions (i.e., 4 children repeatedly pressed the same key and 5 children, 2 young adults and 6 older adults did not adhere to the specific schedule of the experimental sessions). Additional exclusions were due to inaccurate data because of software issues (n = 1 older adult), a lack of performance improvements across training (n = 1 young adult, 1 older adult), and an inability to correctly perform the motor task (statistical outliers on sequence accuracy; n = 1 young adult). Similar to above, excluded participants were replaced and thus the final sample for analyses consisted of 108 participants (see Table 2 for participant details). Note that data from the third session of one young adult and the post-learning random data of one adolescent were missing; thus, these individuals were excluded from the contrasts involving these specific task runs only.

Note that the procedures of Experiment 1 (assessing initial motor sequence learning) were identical to the first session of Experiment 2 (assessing macro-offline consolidation). Accordingly, data from a subset of early participants from Experiment 2 (n = 42; 16 children, 19 adolescents, 4 young

adults, 3 older adults) were included in the analyses of Experiment 1. Thus, these participants were included in analyses for both experiments.

Table 1*: Participant demographics, and sleep and vigilance scores for each age group in Experiment 1*

Variable	**Children**	**Adolescents**	**Young adults**	**Older adults**
n	33	33	32	32
Female *(n)*	17	12	23	24
Age (years)	10.2 (1.6)	15.3 (1.3)	26.3 (5.0)	64.4 (5.2)
M/E Preference	2.9 (0.9)	3.3 (0.8)	2.9 (1.0)	2.3 (0.8)
Time of testing (SD in min)	12:47 (172)	12:29 (133)	14:52 (175)	12:05 (169)
Sleep quality	5.1 (0.8)	5.0 (0.7)	4.8 (0.6)	4.8 (0.8)
Sleep duration (hours)	9.8 (0.9)	9.1 (1.4)	8.5 (1.0)	7.7 (1.1)
SSS score	2.0 (0.9)	2.0 (0.8)	2.0 (0.7)	1.5 (0.7)

Numbers represent the mean, with standard deviation in parentheses. Morningness/Eveningness (M/E) Preference was added as an exploratory variable to assess age-related differences in circadian preferences and was defined on a 5-point Likert scale (i.e., 1 = extreme morning person, 5 = extreme evening person). The average time of testing is specified in 24-hour time notation, with the SD in minutes. Sleep quality is defined on a 6-point Likert scale (i.e., 1 = very bad, 6 = very good). SSS = Stanford Sleepiness Scale (Maclean et al., 1992), with higher numbers indicative of increased sleepiness. See Appendix 1 as part of the Supporting Information for corresponding statistical analyses.

***Table* 2:** *Participant demographics, and sleep and vigilance scores for each age group in Experiment 2.*

Variable		**Children**	**Adolescents**	**Young adults**	**Older adults**
n		27	27	27	27
Female *(n)*		16	12	21	18
Age (years)		10.6 (1.6)	15.4 (1.4)	26.6 (4.4)	63.0 (4.4)
M/E Preference		3.0 (0.8)	3.2 (0.9)	3.2 (0.8)	2.4 (0.9)
Session 1	*Time of testing*	11:34 (97)	11:34 (96)	11:39 (82)	11:30 (92)
	Sleep quality	4.9 (0.7)	5.1 (0.6)	5.0 (0.6)	4.7 (0.8)
	Sleep duration (hrs.)	9.7 (1.1)	9.4 (1.2)	8.3 (1.1)	7.7 (1.3)
	SSS score	2.2 (0.9)	2.1 (0.8)	2.0 (0.7)	1.5 (0.7)
	PVT score (ms)	360.9 (81.5)	341.9 (102.3)	320.9 (62.0)	327.5 (75.7)
Session 2	*Time of testing*	16:42 (99)	16:56 (112)	16:43 (89)	16:29 (96)
	Offline period (hrs.)	5.1 (0.8)	5.4 (0.9)	5.1 (1.1)	5.0 (0.7)
	SSS score	2.0 (1.0)	1.8 (0.8)	2.0 (0.7)	1.7 (0.7)
	PVT score (ms)	386.0 (88.4)	318.5 (61.0)	320.3 (69.1)	323.6 (68.0)
Session 3	*Time of testing*	11:57 (148)	12:25 (156)	11:30 (97)	11:24 (109)
	Offline period (hrs.)	24.4 (1.8)	24.8 (1.9)	23.8 (1.4)	23.9 (1.4)
	Sleep quality	5.0 (0.8)	4.7 (0.8)	4.7 (0.7)	4.6 (0.7)
	Sleep duration (hrs.)	10.3 (0.9)	9.3 (1.5)	8.0 (1.3)	7.6 (1.0)
	SSS score	1.9 (0.7)	2.3 (1.3)	2.3 (0.8)	1.5 (0.6)
	PVT score (ms)	378.7 (97.3)	325.8 (74.6)	308.0 (54.4)	306.3 (33.6)

Numbers represent the mean, with standard deviation in parentheses. Morningness/Eveningness (M/E) Preference was added as an exploratory variable to assess age-related differences in circadian preferences and is defined on a 5-point Likert scale (i.e., 1 = extreme morning person, 5 = extreme evening person). The average time of testing is specified in 24-hour time notation, with the SD in minutes. The offline periods represent the time periods between session 1 and sessions 2 and 3, respectively. Sleep quality is defined on a 6-point Likert scale (i.e., 1 = very bad, 6 = very good). SSS = Stanford Sleepiness Scale (Maclean et al., 1992), with higher numbers indicative of increased sleepiness. The PVT score indicates the average simple RT across the 30 trials. See Appendix 1 as part of the Supporting Information for corresponding statistical analyses.

2.2. General Experimental Procedures

After verification of eligibility, participants were contacted via email with the necessary information to continue participation. This email contained a link to a video created by our study team that provided detailed instructions on how to complete our motor learning task (details on

the task are provided in Section 2.3. below). Participants were also provided links to the web-based data collection platform PsyToolkit (Stoet, 2010, 2017). As our experiments were conducted online, participants were free to choose which day(s) to complete experiments but were instructed to complete the protocols on days in which they were well-rested and could adhere to the schedule of the sessions. The precise time-of-day that the experiments were completed was constrained and followed experiment-specific schedules provided below (see Sections 2.4 and 2.5). Participants were instructed to receive a good night of sleep and to refrain from alcohol the night before and throughout the experiment. Compliance to these instructions was verified through a brief questionnaire prior to completion of the motor task. Lastly, parents of the child participants were asked to be present when their child completed the experiments.

For both experiments and at the beginning of each experimental session, a brief questionnaire was completed in which participants reported their sleep patterns in the previous 24 hours and their subjective feelings of alertness (Stanford Sleepiness Scale; Maclean et al., 1992). Additionally, and for Experiment 2 only, participants completed the Psychomotor Vigilance Task (PVT; Dinges & Powell, 1985) to provide an objective measure of vigilance at the time of testing. The PVT required participants to fixate on the middle of the computer screen and press the space bar as fast as possible when a visual stimulus appeared after a varying delay interval. Response time (i.e., time between appearance of stimulus and keypress) was logged and used to assess vigilance (i.e., higher RTs indicative of lower vigilance). We administered a shortened version of the PVT (Basner et al., 2011; Loh et al., 2004) that consisted of 35 trials, the first 5 of which were discarded as participants became familiar with the task.

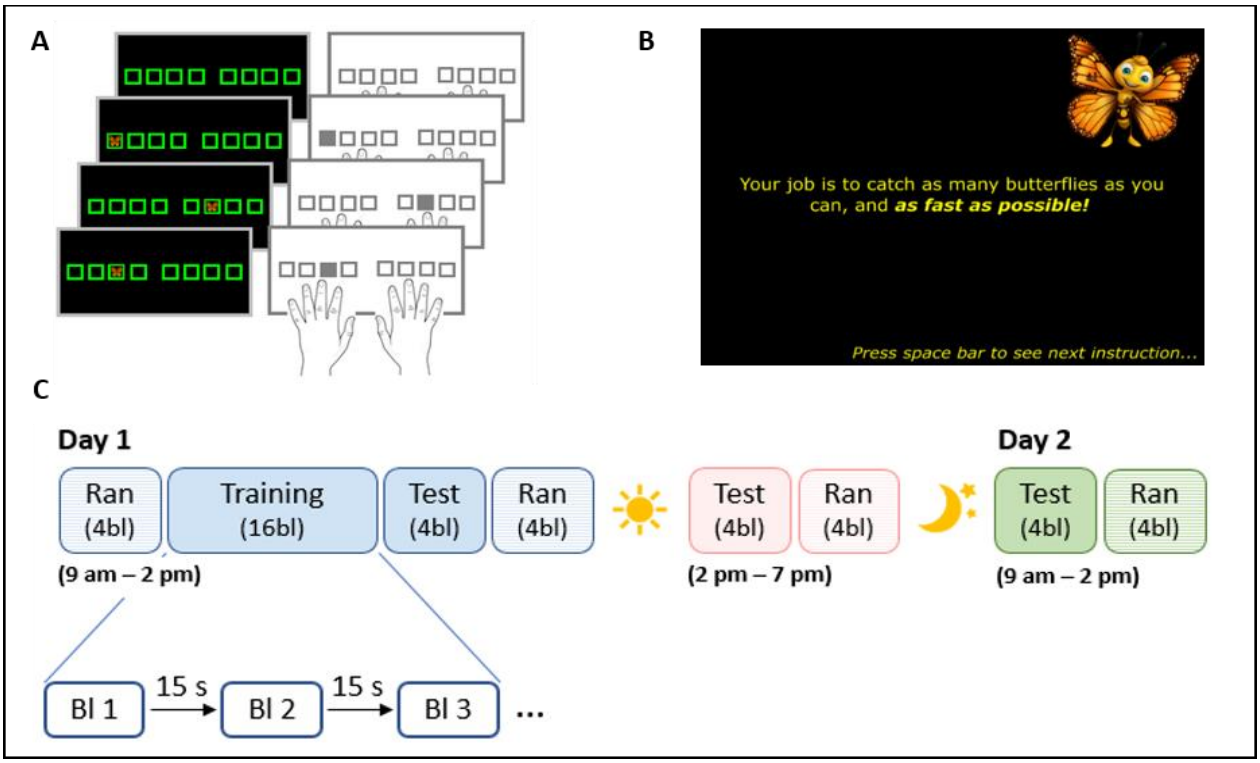

Figure 1. A) *Serial reaction time task (SRTT). A stimulus appeared in 1 of 8 spatial locations and the participant responded with the corresponding key/finger as fast as possible. Stimuli appeared in either a pseudorandom or sequential (i.e., 4-7-3-8-6-2-5-1) manner.* ***B)*** *To increase motivation and attention, the task was built around a story in which participants were asked to catch butterflies.* ***C)*** *Design of Experiments 1 and 2. Experiment 1 consisted of the first session only (i.e., Day 1 in blue) and Experiment 2 of all three sessions displayed. Session 1 included four blocks of pseudorandom SRTT, followed by 20 blocks of sequential SRTT, which were divided into 16 blocks of training and 4 blocks of test after a 1-minute rest. Approximately 5 and 24 hours after session 1, session 2 and 3 were completed, respectively. Both sessions 2 and 3 consisted of 4 blocks of sequential SRTT and 4 blocks of pseudorandom SRTT. Note that the first session of Experiment 2 was constrained between 9am and 2pm to give ample time for the 5hr delayed retest. Those participants in Experiment 1 were instructed to complete the session anytime between 9am and 7pm.*

2.3 Serial Reaction Time Task (SRTT)

All participants performed an adapted version of the explicit Serial Reaction Time Task (SRTT) similar to our previous research (King et al., 2019; Reverberi et al., 2023) which was coded in the online data acquisition platform PsyToolkit (Stoet, 2010, 2017). The task consisted of an 8-choice reaction time task in which participants were instructed to react to cues shown on a screen (see Figure 1A). Eight squares that spatially corresponded to the eight fingers used to perform the task (i.e., no thumbs) and the eight keys on the keyboard were presented on the screen. The color of the

squares alternated between red and green, indicating rest and practice blocks, respectively. During practice, a visual stimulus (i.e., a butterfly) appeared consecutively in one of the squares and participants responded to the visual cues by pressing the corresponding key with the corresponding finger as fast and accurately as possible. The task was presented as a game, designed to increase motivation in child participants, in which participants of all four age groups were instructed to move quickly to catch as many butterflies as possible (see Figure 1B). The visual cues succeeded each other in either a pseudorandom or a sequential order, depending on the experimental run (i.e., pseudorandom SRTT vs. sequential SRTT, respectively). In the sequential SRTT, participants were aware that the stimuli and keypresses followed a deterministic sequential pattern (i.e., 4-7-3-8-6-2-5-1, in which 1 through 8 are the left pinky to the right pinky fingers from left to right), but they were not given any information about the structure or length of the sequence. During the pseudorandom SRTT runs, there was no repeating sequence, but each key was pressed once every eight elements (i.e., no repeating elements). For both pseudorandom and sequential task variants, practice blocks contained 48 key presses (i.e., 6 repetitions of the 8-element sequence in the sequence condition) and were separated by 15-second rest periods.

Measures reflecting performance speed (i.e., response time between visual cue and keypress) and accuracy (i.e., correct or incorrect keypress) of the participants' motor responses were recorded for each trial and used to assess performance on the task. Per our pre-registrations, individual trials (i.e., responses) were excluded from analyses if the measured response time was greater than 3 standard deviations above or below the participant's mean response time for that block. For Experiments 1 and 2, an average of 1.78% (children: 2.03%, adolescents: 1.76%, young adults:

1.68%, older adults: 1.65%) and 1.69% (children: 2.0%, adolescents: 1.83%, young adults: 1.58%, older adults: 1.34%) of trials were excluded from analyses, respectively.

2.4 Experiment 1 Design

The first experiment consisted of a single experimental session in which participants performed both the random and sequential variants of the SRTT (see Day 1 [blue] of Figure 1C). Participants were instructed to complete this session between 9am and 7pm (see Table 1 in the main text and Appendix 1 as part of the Supporting Information (Table S1 and Figure S1) for details on time of testing). The experimental session started with one block of familiarization (pseudorandon; data not analyzed) followed by four blocks of the pseudorandom SRTT (pre-learning random), which afforded an assessment of general motor execution on the task prior to any sequence learning. Subsequently, participants completed 20 blocks of the sequential SRTT. These blocks were divided into two runs: a training run that consisted of 16 blocks and then a post-learning test run of 4 blocks. The post-learning test run was completed approximately one minute after the end of training, affording the assessment of end-of-training performance following the further dissipation of mental and physical fatigue (Pan & Rickard, 2015). Lastly, four additional blocks of the pseudorandom SRTT (post-learning random) were completed, allowing us to assess whether improvements in performance on the sequential SRTT could be attributed to learning of the movement sequence *per se* (i.e., sequence-specific learning) or simply a general improvement in movement speed due to task familiarization.

2.5 Experiment 2 Design

The second experiment consisted of three experimental sessions (see Figure 1C). Participants were instructed to complete the first session between 9 am and 2 pm. This session was identical to what was described for Experiment 1. The second session took place approximately five hours after the first session, allowing the assessment of motor memory consolidation after an interval of post-learning wakefulness. This second session consisted of four blocks of sequential SRTT during which participants again performed the same specific sequence as in session 1, and four blocks of pseudorandom SRTT (post-test random). Finally, the third session was completed 24 hours after the first session, allowing the examination of motor memory consolidation after a night of sleep. Similar to the second session, this third session included four blocks of sequential SRTT and four blocks of pseudorandom SRTT (post-test random). See Table 2 in the main text and Appendix 1 as part of the Supporting Information (Table S2) for details on actual time of testing. For the intervals between sessions, participants were instructed to refrain from napping, consuming alcohol or recreational drugs and to receive a good night of sleep.

2.6 Data Processing and Statistical Analyses

We first describe general data processing and statistical analysis information prior to providing details specific to each of the two experiments. All statistical analyses described below were performed using IBM SPSS Statistics for Windows, version 28 (IBM, Armonk , NY, USA). All statistical tests were performed for both normalized outcome measures (i.e., reaction time and accuracy) and were considered significant when $p < 0.05$. For the sake of completeness, we also highlight those effects when $0.05 < p < 0.1$ as non-significant trends. In the event of a violation of the sphericity assumption, Greenhouse-Geisser correction was applied. All significant main effects

and interactions were followed up by pairwise comparisons and one-way ANOVAs, respectively. Depending on the statistical test, eta-squared, partial eta-squared or Hedges' g are reported as effect size measures. The correspondence among reported p-values, test statistics and degrees of freedom reported in this main text were verified via statcheck (Epskamp & Nuijten, 2018).

To assess potential differences among age groups and experimental sessions in certain demographic/participant characteristics, one-way ANOVAs or chi-square tests (Experiment 1) and two-way ANOVAs (Experiment 2) were performed. These measures included gender, vigilance (both subjective and objective) at the time of testing, self-reported sleep quantity and quality of the night prior to the experimental session(s), and the time of day in which the motor task or session was completed. Any significant effects from these analyses were followed up by pairwise comparisons to determine which age groups or sessions differed from each other. Group means for these dependent measures are provided in Tables 1 and 2 and results from the corresponding statistical analyses can be found in Appendix 1 of the Supporting Information (Tables S1, S2; Figures S1 and S2).

For the SRTT, the averaged response times for correct keypresses and the percentage of correct keypresses were computed for each block and task variant. Additionally, as previous research has indicated age differences in motor performance independent of sequence learning (Bottary et al., 2016; Fitzroy et al., 2021; Kavos Salehi et al., 2016; Meulemans et al., 1998; Sugawara et al., 2014), baseline differences in performance were accounted for by normalizing both movement speed and accuracy of the sequential and post-learning random SRTT runs relative to the outcome variables of the pre-learning random run. More specifically, for each outcome measure and each

block of the SRTT runs, performance was divided by the mean outcome measure across the four blocks of the pre-learning random run. Statistical analyses of these normalized measures are presented in the main text. For completeness, results based on non-normalized performance measures are reported in Appendix 2 of the Supporting Information (Tables S3, S4; Figures S3, S4).

2.6.1 Experiment 1

Sequential learning dynamics (i.e., block-to-block performance changes) were compared among age groups using a mixed ANOVA, with *group* (i.e., children, adolescents, young adults, older adults) as between-subject and *block* (i.e., 16 training blocks or 4 test blocks) as within-subject factors.

To assess whether observed improvements in performance across practice blocks reflected sequence-specific learning (as opposed to general skill learning as a result of familiarization with the motor task), a learning magnitude measure was computed for performance speed. Specifically, the difference between averaged normalized performance across the four blocks in the post-learning test run of the sequential SRTT and the averaged normalized performance in the post-learning random run was divided by the average normalized performance in the post-learning random run. This measure thus reflects the relative difference between the random and sequential task variants at the end of training, affording the assessment of sequence-specific learning. Larger values are indicative of greater sequence-specific learning. The effect of age *group* on learning magnitude was assessed with a one-way ANOVA. To provide more fine-grained analyses of the age-related changes in sequence-specific learning magnitude, we conducted exploratory analyses

with age as a continuous variable. Specifically, we tested five potential fit options (i.e., single exponential, double exponential, linear, quadratic, and power functions) to characterize the relationship between age and learning magnitude. As we did not acquire data from participants between 35 and 55 years of age, separate models were built to characterize age-related changes from 7 to 35 and 55 to 75 years of age. The model with the lowest Akaike Information Criterion value was deemed as the best fitting model and the corresponding results are presented.

Similar to previous research (Buch et al., 2021; Du et al., 2017; Jacobacci et al., 2020), we distinguished between micro-online (i.e., within blocks of task practice) and micro-offline (i.e., across rest epochs in between blocks of practice) performance improvements. Micro-online changes were computed as the difference between the averaged normalized RT for the correct keypresses of the first and last sequence repetitions within each block (i.e., first sequence block n – last sequence block n). For micro-offline changes, the difference between the averaged normalized RT of the last sequence repetition of one block and the first sequence repetition of the subsequent block (i.e., last sequence block n – first sequence block n+1) was computed. These micro-online and micro-offline measures were analyzed with separate *group(4)* x *block(16)* or *group(4)* x *rest block (15)* mixed model ANOVAs, respectively. Moreover, and following the same exploratory procedure as described above for the learning magnitude measure, we assessed age-related changes in these micro measures with age as a continuous variable.

2.6.2. Experiment 2

As in Experiment 1, learning dynamics (i.e., block-to-block performance changes) across training and the post-learning test were analyzed using a *group(4)* x *block(16 or 4)* mixed ANOVAs to

assess potential group differences in initial encoding of the motor sequence within the first session (i.e., before the assessment of consolidation).

The main focus of Experiment 2 was the effect of age on motor memory consolidation across the 5hr and 24hr macro-offline intervals. To this end, and for both the sequential and random SRTT, a macro-offline change measure was computed for each outcome variable and offline interval. Specifically, sequential offline changes were calculated as the difference between the average normalized performance on the sequential SRTT run in the 5hr and 24hr retest sessions and the average normalized performance in the post-learning test run of the first session. Similarly, offline changes for the random task variant were computed as the difference between the averaged normalized performance on the post-test random runs in the 5hr and 24hr retest sessions and the averaged normalized performance in the post-learning random run of the first session. These measures reflect the offline changes in sequential performance and general motor execution from the end of the initial training session to the two retest sessions, respectively. Mixed ANOVAs with *group (4)* as between-subject and *offline period* (i.e., 5-hour and 24-hour offline periods) as within-subject factors were conducted. Consistent with the exploratory analyses described above for Experiment 1, age-related changes in the macro-offline performance gains were also assessed with age as a continuous variable.

Last, and similar to previous research (Bönstrup et al., 2019; Jacobacci, Armony, Yeffal, Lerner, Amaro Jr., et al., 2020), we assessed the relationship between offline changes in performance on the micro- (i.e., during the rest epochs in between practice blocks during training) and macro-offline timescales (i.e., during the 5h and 24h offline periods). Specifically, we performed

exploratory multiple regressions with the micro-offline gains as independent and the 5h or 24h macro-offline gains as dependent variables. To examine how these relationships differed among age groups, we included age group (dummy coded) x micro-offline gains interaction variables in the regression models. The young adult group was selected as the reference group and thus the interaction variables compare the regression slopes of the other 3 age groups with those of the young adults.

4. Results

4.1 Experiment 1: Initial motor sequence learning

4.1.1 Participant characteristics, sleep and vigilance

Group means from participant characteristics, the time of when the experimental session was completed, self-reported sleep quality and duration of the night preceding the experimental session, and a subjective measure of vigilance are provided in Table 1. Results from the corresponding statistical analyses and a brief discussion can be found in Appendix 1 of the Supporting Information (see Figure S1 and Table S1).

4.1.2 Dynamics of Performance Improvements

Normalized performance measures on the SRTT are depicted in Figure 2A and 2B. Performance accuracy remained stable across training, as evidenced by no main effect of block ($F_{(7.011,883.403)}$ = 0.501, p = 0.835, partial η^2 = 0.004), and did not significantly differ among age groups ($F_{(3,126)}$ = 0.322, p = 0.810, partial η^2 = 0.008). Furthermore, no significant group x block interaction was found ($F_{(21.033,883.403)}$ = 0.0.715, p = 0.821, partial η^2 = 0.017). Similarly, no block ($F_{(2.283,287.681)}$ = 1.523, p = 0.217, partial η^2 = 0.012), group ($F_{(3,126)}$ = 1.796, p = 0.151, partial η^2 = 0.041), or

interaction effects ($F_{(6.850,287.681)} = 0.814$, $p = 0.574$, partial $\eta^2 = 0.019$) were found for the post-learning test.

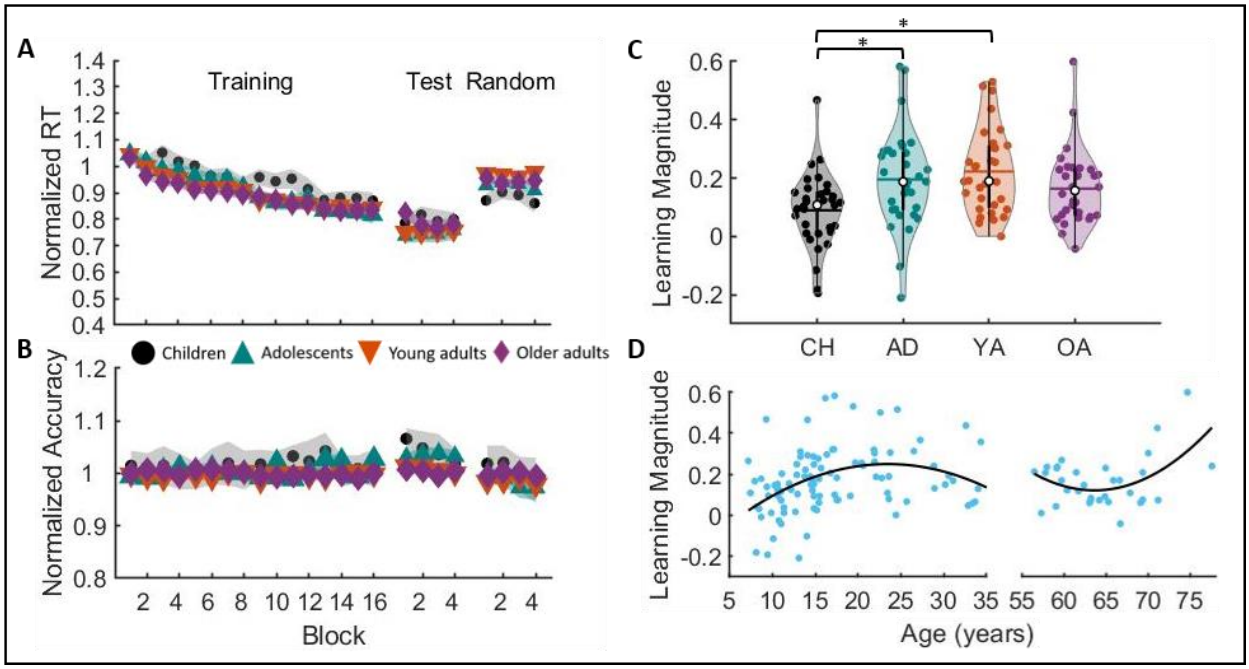

Figure 2. A*) Average normalized response time for both task variants.* ***B)*** *Average normalized accuracy for both task variants. For panels A and B, shaded regions represent standard errors of the mean.* ***C)*** *Average learning magnitude for performance speed per age group. * $p < 0.05$ for pairwise group comparisons.* ***D)*** *Learning magnitude as a function of age. Quadratic fit from childhood into young adulthood: Learning magnitude = $(-0.0008572*age^2) + (0.04021*age) + (-0.2226)$. Quadratic fit for older adults: Learning magnitude = $(0.00157*age^2) + (-0.1996*age) + 6.4675$.*

For an assessment of performance speed, response times significantly decreased across sequential practice blocks, as shown by a main effect of block ($F_{(7.900,995.358)} = 64.246$, $p < 0.001$, partial $\eta^2 = 0.338$). These performance improvements were similar among age groups, as indicated by the lack of a significant group effect ($F_{(3,126)} = 1.578$, $p = 0.198$, partial $\eta^2 = 0.036$) and group x block interaction ($F_{(23.699,995.358)} = 1.337$, $p = 0.130$, partial $\eta^2 = 0.031$). During the post-learning test run, there was no significant block effect ($F_{(2.102,264.890)} = 0.404$, $p = 0.678$, partial $\eta^2 = 0.003$), indicating a performance plateau was reached. Moreover, consistent with the training run, there were no significant differences among groups (Group main effect: $F_{(3,126)} = 1.099$, $p = 0.352$, partial $\eta^2 =$

0.025; Group x Block interaction: $F_{(6.307,264.890)} = 1.148$, $p = 0.335$, partial $\eta^2 = 0.027$). Collectively, the assessment of performance across blocks of practice indicates that the four groups acquired the novel motor sequence and exhibited similar performance improvements.

4.1.3 Sequence-specific learning

A learning magnitude measure was calculated for performance speed that reflects the relative difference between the random and sequential task variants at the end of training and therefore affords the assessment of the magnitude of sequence-specific learning (see Figure 2C). Results revealed a significant group effect ($F_{(3,129)} = 5.440$, $p = 0.002$, $\eta^2 = 0.115$). More specifically, a significantly smaller sequence-specific learning magnitude was observed in children as compared to adolescents ($p = 0.014$, $G = 0.714$) and young adults ($p = 0.001$, $G = 0.970$). Follow-up analyses indicated that the difference in learning magnitude could be attributed to significant group differences in response time for the post-learning random run ($F_{(3,126)} = 5.795$, $p < 0.001$, partial $\eta^2 = 0.121$). Children demonstrated greater improvements in performance speed from the pre-learning to post-learning *random* runs as compared to young ($p < 0.001$, $G = 0.876$) and older adults ($p = 0.022$, $G = 0.591$). Accordingly, a portion of the performance improvements across the sequential training blocks in children can be attributed to general learning of the task that is *not* specific to the sequence.

We also conducted exploratory regression analyses with age as a continuous variable to provide a more fine-grained analyses of the age-related trajectories of sequence-specific learning magnitude. Consistent with the differences among *groups*, age was a significant predictor of learning magnitude from childhood into young adulthood (see Figure 2D; the best fit model was a quadratic

function: $R^2 = 0.156$, $F_{(1,95)} = 8.808$, $p = 0.004$). Specifically, learning magnitude increased across childhood, reaching peak values at approximately 24 years of age, and then decreased thereafter. Age was also a significant predictor of learning magnitude within the older adult group, exhibiting an approximate U-shaped trajectory from 55 to 75 years (quadratic model: $R^2 = 0.247$, $F_{(1,29)} = 4.746$, $p = 0.038$).

4.1.4 Micro-learning across sequential training

For micro-online learning, there was a significant block effect ($F_{(11.524,1429.030)} = 2.358$, $p = 0.006$, partial $\eta^2 = 0.019$) and a non-significant trend for a group effect ($F_{(3,124)} = 2.663$, $p = 0.051$, partial $\eta^2 = 0.061$), but no block x group interaction ($F_{(34.573,1429.030)} = 1.159$, $p = 0.243$, partial $\eta^2 = 0.027$; see Figure 3A). For the sake of completeness, we conducted follow-up pairwise comparisons on the trend for an effect of age group. Results indicated significantly smaller micro-online gains in children as compared to young ($F_{(1,61)} =5.211$, $p = 0.026$, partial $\eta^2 = 0.079$; see Figure 3C) and older ($F_{(1,61)} = 6.240$, $p = 0.015$, partial $\eta^2 = 0.093$) adults. Consistent with these group comparisons, there was a non-significant trend for age being a predictor of micro-online gains from childhood into young adulthood (power model: $R^2 = 0.032$, $F_{(1,96)} = 3.141$, $p = 0.080$; see Figure 3E), but not within the older adult group (power model: $R^2 = 0.045$, $F_{(1,30\}} = 1.424$, $p = 0.242$).

Micro-offline learning also showed a non-significant trend for a group effect ($F_{(3,124)} = 2.490$, $p = 0.063$, partial $\eta^2 = 0.057$), but no rest block ($F_{(11.662,1446.066)} = 1.209$, $p = 0.272$, partial $\eta^2 = 0.010$; see Figure 3B) nor a rest block x group interaction effect ($F_{(34.985,1446.066)} = 0.836$, $p = 0.739$, partial $\eta^2 = 0.020$). Pairwise comparisons following-up on the trend for a group effect indicated that

children exhibited significantly larger micro-offline gains as compared to young ($F_{(1,61)} = 4.829$, $p = 0.032$, partial $\eta^2 = 0.073$; see Figure 3D) and older adults ($F_{(1,61)} = 5.374$, $p = 0.024$, partial $\eta^2 = 0.081$). Similarly, there was a non-significant trend for age being a predictor of micro-offline gains from childhood into young adulthood (power model: $R^2 = 0.029$, $F_{(1,96)} = 2.873$, $p = 0.093$; see Figure 3F), but not within older adulthood (power model: $R^2 = 0.043$, $F_{(1,30)} = 1.362$, $p = 0.252$).

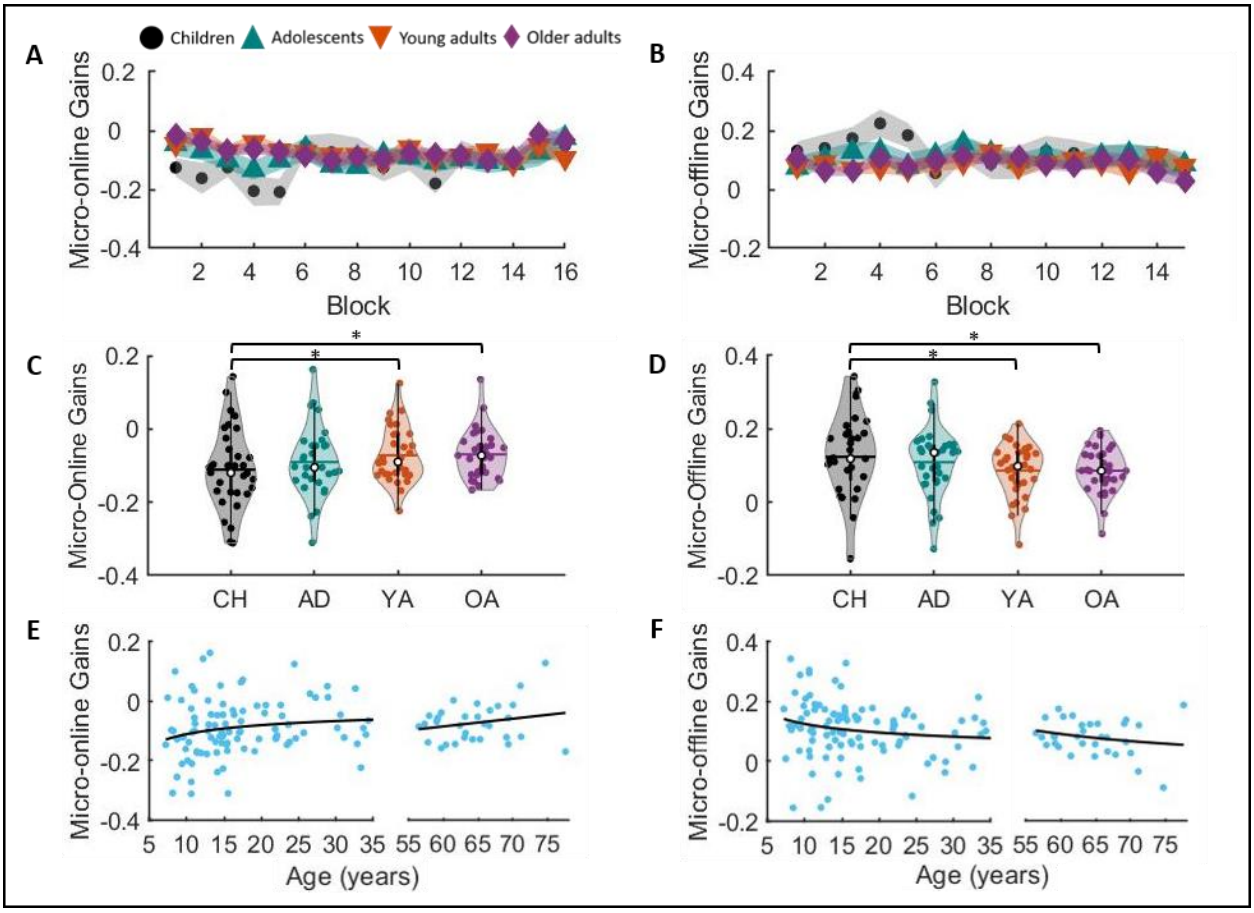

Figure 3. *Micro-online (**left**) and -offline (**right**) gains. Panels A and B depict micro gains displayed as a function of practice blocks. Panels C and D contain violin plots of micro-online and -offline, respectively, gains averaged across blocks. Note that pairwise comparisons in these panels included blocks or rest periods in the statistical models.* $p < 0.05$ for differences between pairs of groups. Panels E and F show averaged micro-online and -offline gains as a function of age from childhood into young adulthood and within older adulthood. Lines of fit childhood into young adulthood: micro-online gains = $(-0.318*age)^{-0.459}$; micro-offline gains = $0.298*exp(-0.377*age)$. Lines of fit within older adulthood: micro-online gains = $(0.003*age) + (-0.238)$; micro-offline gains = $(227.361*age) + (-1.897)$.*

4.2 Experiment 2: Motor memory consolidation

4.2.1 Participant characteristics, sleep and vigilance

Group means for participant characteristics, the times of when the experimental sessions were completed, the duration of the offline periods between sessions, self-reported sleep quality and duration for the nights preceding each experimental session, and subjective (SSS) and objective (PVT) measures of vigilance are provided in Table 2. Results from the corresponding statistics analyses and a brief discussion can be found in Appendix 1 of the Supporting Information (see Figure S2 and Table S2).

4.2.2 Initial learning dynamics

Similar to Experiment 1, we assessed the dynamics of learning during the initial training session of Experiment 2. Normalized performance measures are shown in Figure 4. For brevity, the corresponding statistical results can be found in Appendix 3 of the Supporting Information (Table S7). In brief, the results from the assessment of the initial training session of Experiment 2 largely mirrored those presented above for Experiment 1 (i.e., no differences among age groups in the performance improvements across training blocks).

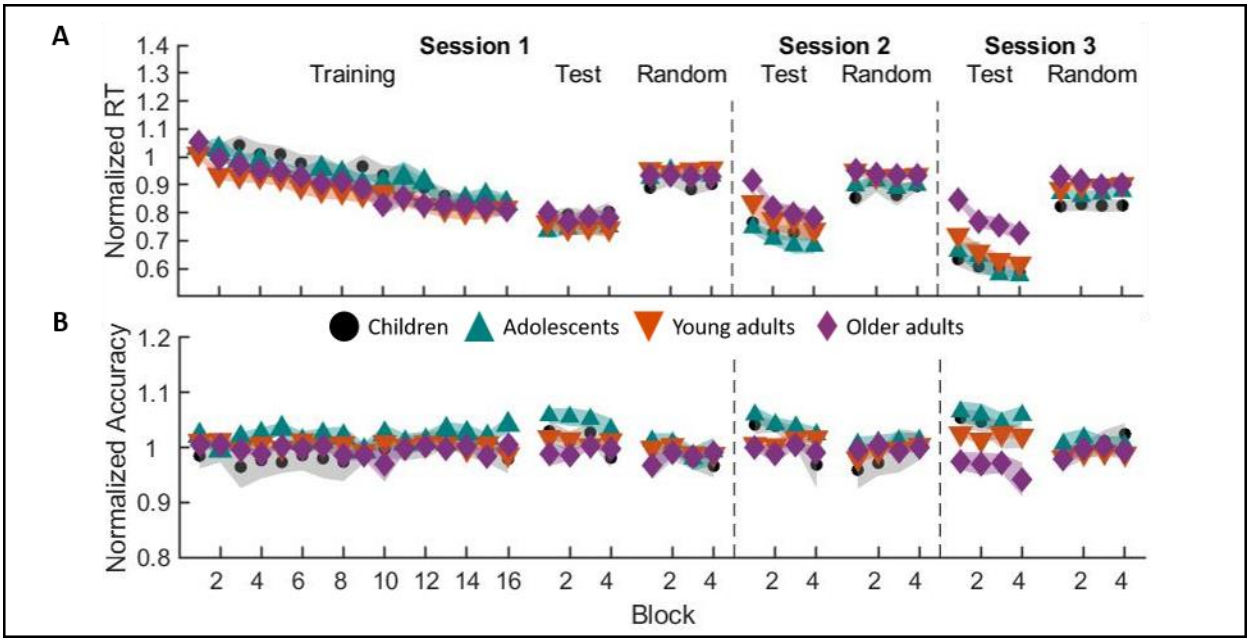

Figure 4. *Average normalized response time (**A**) and accuracy (**B**) for the three experimental sessions and two task variants of Experiment 2. Shaded regions represent standard errors of the mean. Corresponding statistical analyses are in Appendix 3 of the Supporting Information.*

4.2.3 Macro-offline performance gains

Results on the sequential macro-offline changes in performance (Figure 5) revealed both offline period ($F_{(1,104)} = 104.365$, $p < 0.001$, partial $\eta^2 = 0.501$) and group ($F_{(3,104)} = 14.551$, $p < 0.001$, partial $\eta^2 = 0.296$) main effects, as well as a significant offline period x group interaction effect ($F_{(3,104)} = 3.367$, $p = 0.021$, partial $\eta^2 = 0.089$). Follow-up comparisons revealed significant group effects for both the 5-hour ($F_{(3,107)} = 5.764$, $p = 0.001$, $\eta^2 = 0.143$) and the 24-hour ($F_{(3,107)} = 20.577$, $p < 0.001$, $\eta^2 = 0.372$) sequential macro-offline gains. Post-hoc pairwise comparisons indicated that the sequential macro-offline gains after a 5-hour period of wakefulness were higher in children and adolescents as compared to the young ($p = 0.032$, $G = 0.590$; $p = 0.053$, $G = 0.548$, respectively) and older adults ($p = 0.008$, $G = 1.382$; $p = 0.015$, $G = 1.290$, respectively). The children also showed higher 24-hour macro-offline gains in comparison to the young ($p = 0.001$, $G = 1.285$) and older ($p < 0.001$, $G = 2.448$) adults, and the older adults displayed significantly

lower 24-hour macro-offline gains than all the other age groups (adolescents: $p < 0.001$, $G = 1.256$; young adults: $p = 0.002$, $G = 1.237$).

In line with the age group comparisons presented above, our analyses with age as a continuous variable revealed that age significantly predicted the 5h macro-offline gains from childhood into young adulthood (linear model: $R^2 = 0.068$, $F_{(1,78)} = 5.650$, $p = 0.020$; see Figure 5B). Age was not a significant predictor of the 5hr offline gains within the older adult group (quadratic model: $R^2 = 0.117$, $F_{(1,24)} = 1.587$, $p = 0.220$). Lastly, age significantly predicted the 24-hour macro-offline gains from childhood to young adulthood (Power model: $R^2 = 0.157$, $F_{(1,78)} = 14.537$, $p < 0.001$; see Figure 5D) as well as within older adulthood (linear model: $R^2 = 0.139$, $F_{(1,25)} = 4.047$, $p = 0.055$).

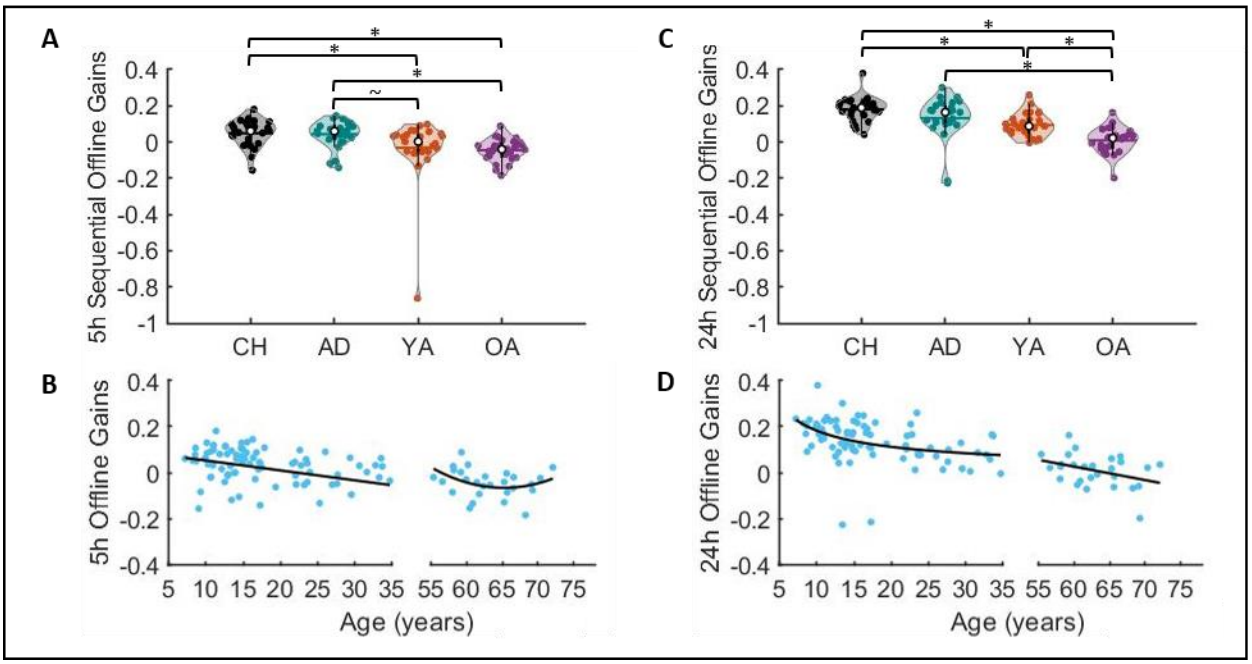

Figure 5. *Sequential offline gains across the 5-hour (**Panel A**) and 24-hour (**Panel C**) offline periods for the four age groups. * $p < 0.05$ and ~ $p < 0.10$ for pairwise group comparisons. Five-hour (**Panel B**) and 24-hour (**Panel** D) sequential offline gains are plotted as a function of age. Lines of fit from childhood into young adulthood: 5h gains = (-0.003 * age) + 0.075; 24h gains = $(0.872*age)^{-0.682}$. Lines of fit within older adulthood: 5h gains = $(0.001 * age^2) + (-0.110 * age) + 3.534$; 24h gains = (-0.006 * age) + 0.377. For*

better visualization of the age-related changes, the scale of the y-axes was set to range from -0.4 to 0.4 and thus the young adult with the outlier 5hr sequential gain (visible in Panel A) is not depicted in Panel B. This individual, however, was included in the fitting procedure. Note that if this individual was excluded from statistical analyses, the pattern of results observed in Panel A remains largely similar, with the exception that the pairwise difference between young and older adults becomes statistically significant (i.e., older adults exhibit worse offline consolidation over a 5hr wake interval as compared to young adults).

4.2.4 Link between the offline performance changes on a micro- and macro-timescale

The regression model assessing the relationship between the micro- and 5h macro-offline gains – independent of age group- revealed a significantly positive relationship between these two offline measures ($b = 0.569$, $p < 0.001$; see Figure S5). This suggests that greater performance changes during the short rest periods throughout training were associated with greater performance gains across the 5-hour offline period of wakefulness following training. We then assessed whether such a relationship differed between pairs of age groups. When age group was modeled, young adults exhibited a steeper slope as compared to children ($b = -1.136$, $p = 0.010$), adolescents ($b = -1.153$, $p = 0.004$) and older adults ($b = -1.358$, $p = 0.005$). This indicates that the relationship between micro-offline and 5h macro-offline gains was strongest in young adults as compared to the other 3 age groups. However, note that these between-group differences were no longer statistically significant if the young adult participant with the extremely negative 5hr offline gain (see Figure 5A) was removed from the analyses.

Micro-offline gains were also significantly and positively related to the 24h macro-offline gains ($b = 0.592$, $p < 0.001$; see Supplemental Figure S6). Specifically, greater performance changes during the short rest periods were also associated with greater performance gains across the 24-hour period following training. This relationship was not significantly different between young

adults and any of the other age groups (children: b = -0.222, p =0.581; adolescents: b = 0.245, p = 0.496; older adults: b = -0.048, p = 0.913).

5. Discussion

The current study examined age-related differences among children, adolescents, young adults and older adults in initial motor sequence learning and motor memory consolidation. Our results revealed that: (1) the dynamics of initial motor sequence learning, as demonstrated by performance improvements during training, were comparable (i.e., not statistically different) across age groups; (2) children exhibited less sequence-specific learning during the initial training session relative to adolescents and young adults; (3) micro-online and -offline performance changes tended to be the smallest and largest, respectively, in children; (4) children exhibited greater changes in performance from the end of initial training to both the 5-hour and 24-hour retests, suggesting a developmental advantage in the macro-offline consolidation of a newly acquired movement sequence; (5) there was a significant positive relationship between the magnitudes of micro- and macro-offline performance changes.

Initial performance improvements are comparable across age groups, but children exhibit less sequence-specific learning

On the one hand, our results showed comparable performance improvements across training among age groups, which was consistent with a subset of the previous literature (Du et al., 2017; Jongbloed-Pereboom et al., 2019; Meulemans et al., 1998; Salehi et al., 2016; Wilhelm et al., 2013; Bottary et al., 2016; Fitzroy et al., 2021; Fogel et al., 2017; Fogel et al., 2014; Gudberg et al., 2015; Spencer et al., 2007; Vien et al., 2016). This finding thus agrees with the lifespan invariance model that has been discussed in previous literature (Tóth-Fáber et al., 2023). On the other hand, our

results indicated that children exhibited less sequence-specific learning, demonstrating that their performance improvements across sequential training blocks are partially due to general motor improvements (i.e., improvements on the motor task that are *independent* of sequence learning). This finding – which resembles the prototypical developmental trajectory where young adults perform the best and children are progressing towards this optimal performance level - is consistent with a subset of previous literature in which children exhibited smaller sequence-specific motor learning (Lukács & Kemény, 2015; Thomas et al., 2004; Thomas & Nelson, 2001). The pattern of results may explain some of the heterogeneity that is present in the literature with respect to the development of motor sequence learning. That is, previous research that assessed performance improvements across blocks of practice may report comparable learning between children and young adults (e.g., Dorfberger et al., 2007; Wilhelm et al., 2013), whereas studies that afford the extraction of sequence-specific learning may reveal differences between age groups (e.g., Lukács & Kemény, 2015; Thomas & Nelson, 2001). Presumably, the greater general learning that is evident in children is due to this group simply learning how to perform the task itself (i.e., spatially mapping the stimuli on the screen to the appropriate fingers). Future research that aims to isolate and examine sequence learning *per se* could consider incorporating an extended task familiarization phase consisting of additional random runs (i.e., not a sequence to be learned). This would allow children to exhaust their general learning of the task itself prior to sequence acquisition. Nevertheless - and as a point of emphasis - even though sequence-specific learning was smaller in children, they still exhibited significant learning of the motor sequence. That is, their learning magnitude was still significantly greater than zero (see Table S6) and thus a memory trace of the acquired sequence was presumably formed. Interestingly, whereas children showed a

smaller learning magnitude, the adolescents were not different from young adults. This suggests that sequence-specific learning reaches adult-like levels by the teenage years.

Micro-offline consolidation during interspersed rest breaks tended to be larger in children

In line with previous literature (Du et al., 2017) and our hypothesis, children exhibited greater micro-offline performance gains in comparison to the young adults. However, it is important to note that the group main effect within the omnibus group (4 levels) x block ANOVA was a non-significant trend and thus our age effects on the micro-offline gains were weaker in comparison to Du et al. (2017). A potential explanation for our weaker findings could be the specific ages included in the child groups. Specifically, Du et al. (2017) found a micro-offline advantage in younger children (i.e., 6-year-olds) as compared to older children (i.e., 10-year-olds) and adults. In the current research, the online nature of our protocol made it difficult to acquire data in such young children (i.e., 6-year-olds). Moreover, as data acquisition in Du et al. (2017) was limited to these discrete age groups in (i.e., data from 7-9-year-old children were not acquired), an estimate of when this childhood advantage in micro-offline processing disappears was not possible. We speculate that the differences between children and young adults in this study would have been larger in magnitude if the sample included a greater number of younger children (i.e., 6 to 7 year-olds). Another potential consideration is the considerably longer rest breaks (i.e., 3 min) between practice blocks that Du et al. (2017) implemented. In comparison to our 15-second rest intervals, this allowed more time for the recently acquired memory trace to be consolidated over these micro-offline epochs. Future studies are needed to further examine the micro-learning processes in children, with systematic examinations into certain methodological choices such as the age of the participants and the length of the rest epochs.

Although this fast consolidation process occurring over micro-offline intervals has received considerable attention over the last 5 years (Bönstrup et al., 2019; Bönstrup et al., 2020; Buch et al., 2021; Gann et al., 2023; Jacobacci et al., 2020), the current study is the first, to the best of our knowledge, to examine micro-learning processes in older adults. Our results demonstrated comparable micro-online and -offline performance gains in young and older adults. Accordingly, whereas older adults have deficits in the macro-offline consolidation processes occurring between two practice sessions (Fogel et al., 2017; Fogel et al., 2014; Gudberg et al., 2015; Spencer et al., 2007; Vien et al., 2016; Wilson et al., 2012), they do not exhibit deficits in the rapid consolidation process that occurs during the rest periods interspersed with blocks of task practice.

Lastly, similar to previous studies in young adults (Bönstrup et al., 2019; Buch et al., 2021; Du et al., 2017; Jacobacci et al., 2020), our results provide evidence for a significant contribution of the micro-offline gains to overall learning in all four age groups (see Table S6.C). That is, performance improvements across blocks of training are largely due to micro-offline – as compared to micro-online – performance gains. One could argue, however, that the magnitude of the micro-offline gains could be partially attributed to the build-up of fatigue or reactive inhibition as a function of task practice within blocks (Gupta & Rickard, 2022, 2023). Specifically, it has been suggested that performance deteriorates across practice within a block due to reactive inhibition and thus micro-offline performance gains are inflated due to this performance variable that is independent of learning and memory processes. However, it is worth noting that this view would conflict with recent data demonstrating that these micro-offline performance gains are linked to hippocampal activity during the interspersed rest periods (Buch et al., 2021; Jacobacci et al., 2020). Additional

research is necessary to definitively conclude whether these micro-offline performance gains are reflective of a memory consolidation process or are simply attributed to reactive inhibition.

Children exhibited a developmental advantage in macro-offline consolidation

Our results revealed larger sequential performance gains across both the 5-hour and 24-hour macro-offline periods in children. While the young adults showed a performance maintenance (i.e., offline gains that were not significantly different from zero; see Appendix 6, Table S7A in Supporting Information) across the 5-hour interval, children and adolescents significantly improved their performance on the sequential task. Interestingly, children also demonstrated higher offline gains across the 24-hour period as compared to adults. While the enhanced 5-hour consolidation in children is in line with the findings of Ashtamker & Karni (2013) that showed an accelerated consolidation in children across a one-hour offline period, the greater 24-hour gains stand in contrast to previous research that demonstrated impaired overnight consolidation in children [(Fischer et al., 2007; Wilhelm et al., 2008); see below for expanded discussion on sleep-facilitated consolidation].

It could be argued that the larger macro-offline processing in children could be explained by performance levels reached at the end of the training session (Kuriyama et al., 2004; Wilhelm, Metzkow-Mészàros, et al., 2012). For example, perhaps children show greater macro-offline gains due to a continuation of initial learning rather than the offline processing of previously acquired information. This potential explanation, however, is not in line with our data. Notably, during the post-training test phase, there was an absence of a block effect in all groups, including in the children. This indicates that all groups reached a performance plateau at the end of the first session

and thus macro-offline gains are likely not the result of continued learning. Along the same lines, one could speculate that the young adults reached a performance ceiling effect, and thus their potential to further increase their performance over macro-offline intervals was saturated (see plot of absolute reaction times in Figure S4 of the Supporting Information). Again, this is not consistent with our data. Notably, there was a significant session effect in sequential offline gains, whereby gains were larger in the 24-hour retest as compared to the 5-hour retest. Within-group comparisons revealed that this session effect was present for all age groups, including young adults. This suggests that a performance ceiling effect was not reached and thus this explanation cannot fully account for our results. Last, one could raise the question whether perhaps the macro-offline performance gains are inflated in children due to non-sequence-specific improvements (i.e., improvements due to motor task familiarization as opposed to sequence learning). However, the children did not show greater macro-offline gains on the random task variant (see Appendix 5, Figure S7 in Supporting Information). Moreover, and to assess this possibility further, we examined the offline changes in the sequence-specific learning magnitude (i.e., difference between the learning magnitude (i.e., sequence vs. random) of the 5hr and 24hr retest sessions and the learning magnitude of the first session; see Appendix 5, Figure S7 in Supporting Information). These results revealed significant main effects of offline period and group, but no offline period x group interaction effect. Post-hoc pairwise comparisons indicated that children exhibit enhanced sequence-specific offline gains – across both offline periods - in comparison to young and older adults. This finding is consistent with the assessment of the sequential macro-offline gains presented in the main text (Figure 5). Altogether, these data suggest that the offline changes in children likely involved the strengthening of their sequential memory and that this strengthening was greater as compared to young and older adults.

Offline performance gains on the 24-hour retest were largest in children, a result that was unexpected based on previous literature (Fischer et al., 2007; Wilhelm et al., 2008). Specifically, children have typically exhibited impaired sleep-facilitated consolidation as observed in young adults. It is worth noting that most of the previous studies comparing sleep and wake conditions in children employed an AM/PM design. In this design, participants acquire the motor sequence at a different time of day based on the condition and then are retested after a delay of 12 hours. For example, the wake (i.e., AM-PM) group initially learns the sequence in the morning and then is retested following 12 hours of wakefulness. The sleep (i.e., PM-AM) group completes initial learning in the evening and this is retested after a 12-hour interval that included a night of sleep. Although informative, these designs are sensitive to time-of-day effects. And there is evidence that the time of initial practice can affect performance during acquisition and offline consolidation in young adults (Kvint et al., 2011; Truong et al., 2022). Specifically, Kvint et al. (2011) found a greater sequential knowledge acquisition but similar 12-hour consolidation in an AM-trained as compared to a PM-trained group. Furthermore, Truong et al. (2022) showed an enhanced consolidation when the training and retest were completed at 3 pm (as compared to 10 am). These findings indicate time-of-day effects for the acquisition and consolidation outcomes in young adults. Although previous studies that employed AM/PM designs in children did not find differences in motor skill acquisition between morning and evening groups (Wilhelm et al., 2013), the impact on offline consolidation processes has yet to be systematically and exhaustively examined. Although certainly speculative, it is possible that the impaired overnight consolidation that previous studies have found in children could be – at least partially – attributed to the choice of experimental design. An alternative, albeit related explanation, is that the beneficial effect of

sleep – as reported in the current research - requires additional time to emerge at the behavioral level and thus that these previous studies did not show overnight gains due to their retest immediately after sleep (i.e., 12 hours after initial learning). Consistent with this explanation, Desrochers et al. (2016) found that a post-learning nap facilitated the consolidation of a recently acquired motor sequence in pre-school children, but only after an extended period of time that included a night of sleep. Additional research is necessary to further disentangle these potential explanations.

Potential neural correlates of enhanced offline processing in children

An open question is: What are the neural correlates of the greater micro- and macro-offline performance gains observed in children? Based on (a) recent evidence in young adults demonstrating that the patterns of activity observed in the hippocampus and putamen during motor learning are spontaneously reactivated during subsequent micro- and macro-offline intervals (Buch et al., 2021; King et al., 2022); and, (b) the known role of reactivation processes in memory consolidation and longer-term retention (Deuker et al., 2013; Tambini & Davachi, 2013), it is tempting to speculate that the childhood advantages observed in this research can be attributed to enhanced reactivation of learning-related patterns of brain activity. This possibility is pure speculation at this point but deserves attention in future research.

Older adults exhibit impaired overnight consolidation

On the other end of the lifespan, our results showed similar 5-hour but smaller 24-hour offline gains in the older as compared to the young adults. The comparable 5-hour offline gains are in line with previous studies that showed a similar consolidation between young and older adults across

an offline period of wakefulness (Fogel et al., 2014; Gudberg et al., 2015; Vien et al., 2016). Similarly, the smaller 24-hour offline gains observed in the older adults are in line with several studies that demonstrated impaired overnight consolidation with aging (Fogel et al., 2017; Fogel et al., 2014; Gudberg et al., 2015; Spencer et al., 2007; Vien et al., 2016; Wilson et al., 2012). These studies have largely attributed this deficit to age-related decreases in sleep quality and quantity, as well as alterations in the sleep-related electrophysiological markers of plasticity such as sleep spindles and slow waves (Bottary et al., 2016; Fogel et al., 2017; Fogel et al., 2014; but see Fitzroy et al., 2021; Gudberg et al., 2015; and King et al., 2017 for discussion of alternative explanations). Whereas our older adult participants did report shorter sleep duration as compared to both children and adolescents, no differences in sleep quality were found. However, it is important to note that these measures were self-reported and previous research has shown that older adults tend to overestimate their sleep quality (Vitiello et al., 2004). Nonetheless, our results replicate the often demonstrated finding that aging negatively impacts overnight consolidation of recently acquired motor sequences.

Considerations and future recommendations

There are some limitations and methodological considerations of the current research that warrant further attention. *First*, these experiments were conducted online and thus were not monitored by researchers in real-time. Although we cannot completely discard the possibility that the online nature influenced our results, it is worth nothing that previous studies that compared online and in-person experiments in children (Chuey et al., 2022) and young adults (Bönstrup et al., 2020; Cubillos et al., 2023) found comparable results between these study modalities. For instance, Cubillos et al. (2023) showed similar learning curves for the performance of the finger-tapping

task between a supervised-lab and unsupervised-online young adult group. Additionally, Bönstrup et al. (2020) obtained similar micro-offline learning in young adults through an online crowdsourcing platform. It is also worth noting that our protocol was not implemented in common crowdsourcing platforms (e.g., Mechanical Turk) that typically acquire full datasets within hours of posting an experiment and have come under scrutiny for unreliable data (Webb & Tangney, 2022). Furthermore, although there are drawbacks to employing web-based data acquisition, a significant advantage is the recruitment from a large and broad pool of participants, enabling us to include individuals that otherwise would not be able to complete our traditional in-person studies.

Second, and specific to experiment 2, each session ended with a pseudorandom run. The implementation of this random run is often used in sequence learning studies and has the benefit of assessing sequence specificity of performance improvements (Du et al., 2017; Lukács & Kemény, 2015; Salehi et al., 2016; Savion-Lemieux et al., 2009; Thomas & Nelson, 2001). However, we cannot rule out the possibility that the random runs at the end of each session interfered with the macro-offline processing of the sequential motor memory.

Third, it is important to note that, due to concerns surrounding the acquisition of quality data from young children, our minimum age for this research was 7 years. Moreover, this youngest age was relatively under-sampled in our experiments (n = 3 and 1 7-year-olds included in analyses of Experiments 1 and 2, respectively). Due to difficulties with completing the online motor task, several 7-year-old children had to be excluded from data analyses. Future studies could consider implementing certain measures (e.g., monitoring through videocall) to increase the number of young children that successfully complete the experiments.

Fourth, and as outlined in our pre-registration, the age groups were operationally defined based on age (i.e., children and adolescents were between 7 and 12, and 13 and 17 years, respectively), which does not consider the participant's pubertal status. Our questionnaire battery did ask the parents to indicate whether their child exhibited signs of puberty onset at the time of participation. Note that all participants 13 years and older (i.e., classified as an adolescent based on age) were reported to having started puberty. And only a minimal number of child subjects (6 in each of the experiments) were considered to have initiated puberty. Given the relatively few subjects that would be re-classified based on parental report of puberty onset, we do not anticipate our results to substantially change if pubertal status – as opposed to age - was used to demarcate childhood and adolescence.

6. Conclusion

The current study examined initial motor sequence learning and the time course of motor memory consolidation across the human lifespan. Our results demonstrated comparable dynamics of performance improvements during the initial learning session, yet 7- to 12-year-old children exhibited smaller sequence-specific learning. Interestingly, children demonstrated the largest performance gains over micro- and macro-offline intervals. This indicates that children exhibit a developmental advantage in the offline processing of recently practiced movement sequences. The neural underpinnings of this childhood advantage are not yet known and thus future research is warranted to characterize them.

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